ABSTRACT

AUDITORY LOCALIZATION IN PRIMATES:
THE ROLE OF STIMULUS BANDWIDTH

By

Charles Hawkins Brown

A fundamental characteristic of an acoustic event is its location with regard to the observer. The acoustic locus dictates the direction for visual orientation. The ability to accurately determine the location of a sound may play a fundamental role in predator avoidance, in mate location, and in other biologically significant activities. The objective of this research was to psychophysically measure the ability of a nonhuman primate to detect changes in the azimuth, or horizontal coordinate, of high frequency sounds.

Two species of Old World Monkeys, Macaca mulatta and M. nemestrina, were trained by operant conditioning techniques to report the change in location of a sound in space. When the monkey made contact with the response disk an acoustical stimulus was pulsed repetitively from the standard location (zero degrees azimuth). After the presentation of a variable number of pulses the stimulus changed position in azimuth from the standard to one of several comparison locations. If the monkey reported this change in acoustical location by releasing the response disk within two sec, it received a food reinforcer. Thresholds for the minimum discriminable change in locus of a sound in space were

determined psychophysically by the method of constant stimuli. Threshold, or the 50% detectability locus, was determined by two methods, linear interpolation and probit analysis. Testing was conducted under free- field conditions in an anechoic chamber. The monkeys were tested with pure tones and with bands of noise 250, 500, 1000, 2000, 4000, 8000 Hz wide, geometrically centered at 8000, 11200, 16000 Hz; and with a pure tone and noise bands 250, 500, 8000 Hz wide centered at 13454 Hz. The minimum detectable change in location was a function of the bandwidth of the stimulus and ranged from 3° to greater than 20°. Narrow bandwidth stimuli were harder to localize than wide bandwidth stimuli, and threshold for the detection of a change in azimuth was found to be inversely related to the logarithm of stimulus bandwidth. In eight out of nine cases the correlation coefficient of the regression of threshold on the logarithm of stimulus bandwidth exceeded .90. This indicates that stimulus bandwidth accounts for much of the variability in threshold. The slope of the regression of threshold on the logarithm of stimulus bandwidth was approximately -6, -11, and -4 for stimuli centered at 8000, 11200, and 16000 Hz respectively. The results indicate that the stimuli most difficult to localize were pure tones and narrow bandwidth stimuli centered at 11200 or 13454 Hz. These data demonstrate that the macaque's ability to localize sounds in space is dependent upon the acoustical composition of the signal; as the bandwidth of the signal was increased, threshold for the detection of a change in acoustic space decreased.

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By

Charles Hawkins Brown

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Introduction

Biological Transducers and the Consideration of the Acoustic Event

A complete account of the mechanisms by which an organism determines the spatial origin of a sound must begin with an appreciation of the characteristics of acoustical phenomena to which the ear is responsive. An acoustical event generates vibrations in a medium; this disturbance has two components -- displacement and pressure. These components differ in their characteristics of propagation in specific media. In water it is likely that the displacement component of sound is relevant for localization by aquatic vertebrates; however, terrestrial vertebrates are not sensitive to this component (van Bergeijk, 1967). Although Pumphrey (1940) has noted that many insects have acoustic receptors which are sensitive to the displacement component of sound, all terrestrial vertebrates respond solely to the pressure component. The greatest sensitivity to the pressure component of sound is realized by the class mammalia (Manley, 1973; Shaw, 1974; Henson, 1974).

The component of sound to which a species responds has implications for its ability to locate the origin of an acoustic event. Displacement is a vector quantity. A receptor sensitive to this vector would be ideal for determining the location of a sound because it would respond to changes in the angle of incidence of the acoustical wave front. Acoustical pressure, on the other hand, is a scalar quantity, and the

ear of terrestrial vertebrates is insensitive to those changes in the wave front. Consequently, terrestrial vertebrates cannot determine the spatial location of a sound through peripheral mechanism; rather, they must possess central mechanisms which either monaurally or binaurally resolve the origin of an acoustic event. The classical research has focused on the putative binaural mechanisms of auditory localization.

Binaural Differences

Binaural differences are the result of two factors -- 1) the difference in distance (Δd) the sound must travel to each of the observer's ears, and 2) asymmetries in the transmission of the frequency and amplitude of the acoustical signal. The first factor results in differences in the time of arrival and in the phase of the signal at each ear. The velocity of sound in air is 343 meters per sec; consequently, for each additional cm the sound must travel to reach the far ear, it will arrive 29 μsec later than it will to the near ear. The second factor results in binaural intensity differences. Interaural intensity differences can be explained with reference to the characteristics of acoustical waves, including reflection, refraction, and diffraction with bodies of a different density or acoustical impedance. Acoustical reflection is dependent on both the wavelength of the sound and on the size of the reflector. Binaural intensity differences are realized with high frequency sounds when the corresponding wavelength is short with respect to the diameter of the observer's head. The longer wavelengths of lower frequency sounds act as if they "bend around" the observer's head producing minimal binaural

intensity differences. In this context it sould be apparent that species with small heads require higher frequency sounds for binaural intensity differences to be realized.

Geometrical Considerations of Binaural Phenomena

Lord Rayleigh (1876; 1945) was the first to propose that the head be treated as an acoustically opaque spherical object with ears diametrically opposed. This geometrical simplification is still considered reasonably precise for audio frequencies below 1000 Hz. However, for frequencies greater than 1000 Hz this visualization becomes unsatisfactory because characteristics of the external ear and ear canal may cause prominent departures from the predictions which follow from this model (Shaw, 1974).

In this tradition the classical description of binaural differences was proposed by Woodworth (1938). This description assumes that the observer's head is immobile and unable to scan the sound field. However, the duration of most acoustical transients is so brief that scanning is impossible, and consequently head immobility is not physiologically unreasonable. Figure 1 is a construction of the horizontal plane of an observer for a distant sound source. At distances from the sound source greater than one meter the wave front may be approximated by the surface of a plane. Binaural distance differences occur for all sound locations other than those which lie in the median plane. As may be seen in Figure 1, for a sound source to the right of the observer at azimuth α, the extra distance that the sound must travel to reach the left ear is given by the sum of the linear distance $r(\sin \alpha)$ and the curvilinear distance $r(\alpha)$. That is, the distance

difference for the two ears is given by the expression

$$\Delta d = r(\alpha + \sin \alpha)$$

where; Δd is the distance difference in centimeters, r is the radius of the observer's head in centimeters, and angle α is in radians.

The difference in distance to the two ears is acoustically realized as a binaural difference in the temporal and/or phase domain. Temporal differences (Δt) are calculated by dividing the distance difference by the velocity of sound. If the velocity of sound in air is 343 meters per sec, then the relationship between Δt and azimuth is given by the expression

$$\Delta t = \frac{r(\alpha + \sin \alpha)}{3.43 \times 10^{-2}}$$

where; Δt is the temporal difference in sec, r is the radius of the observer's head in centimeters, and the angle α is in radians.

In this context two implications merit emphasis. First, for any given azimuth α , Δt varies directly with r. As a result, observers with large heads will experience a greater binaural temporal difference than will observers with small heads. Consequently if the neural ability to resolve binaural temporal differences is approximately equal across mammalian species, then those organisms with large heads will be able to discriminate finer changes in azimuth than will organisms with small heads. If this is true then one may expect to find that small mammals have exploited alternative mechanisms for localization. Second, binaural temporal differences do not define a specific locus in three dimensional space. Rather it is the case that binaural temporal differences are a function of the binaural distance difference

Figure 1

The Binaural Distance Difference for a Distant Sound Source Located at Azimuth α . The construction illustrates the geometry of the formula $\Delta d = r(\alpha + \sin \alpha)$. Adopted from Woodworth (1938).

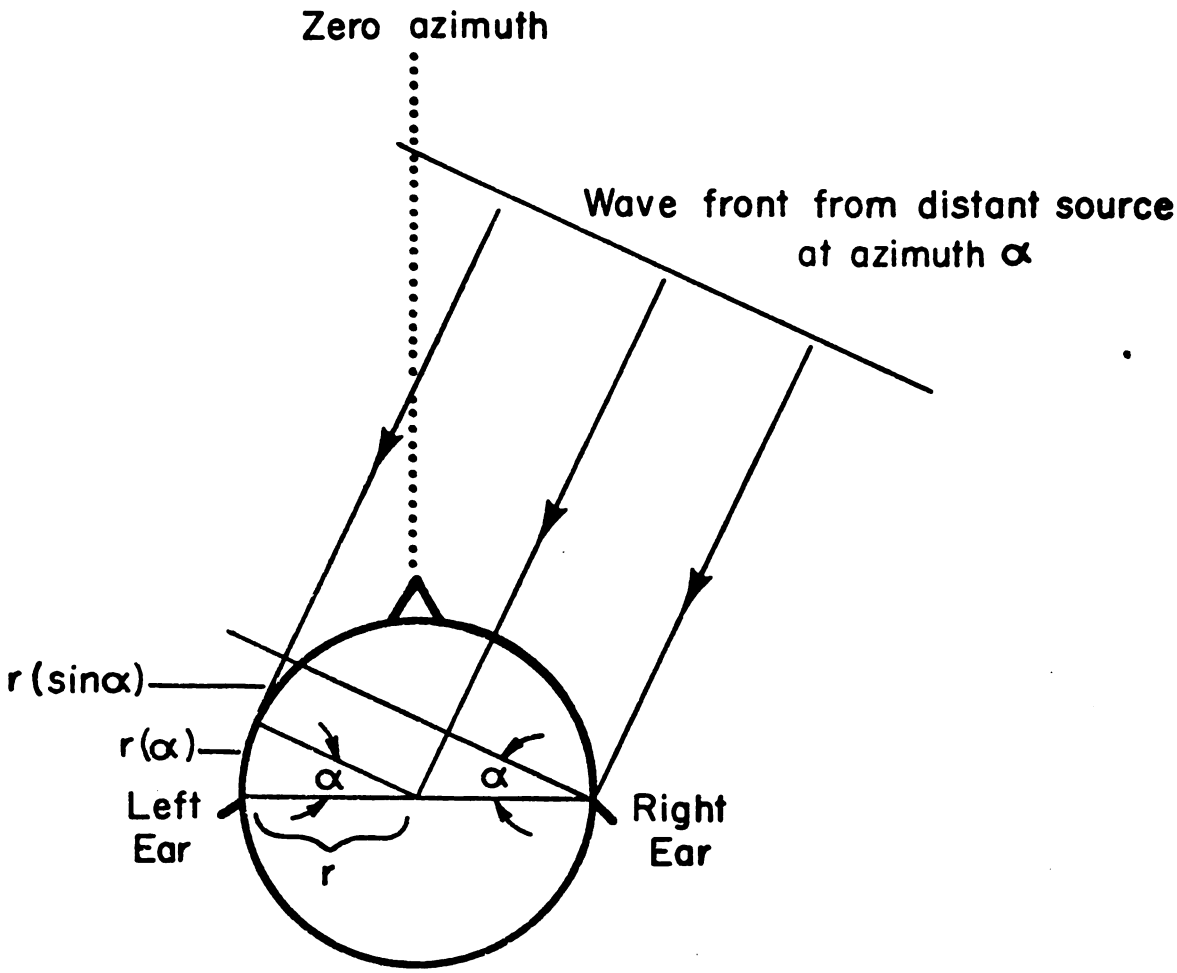

Zero azimuth
Wave front from distant source
at azimuth α
r (sinα)
r(α)
α
α
Left
Ear
Right
Ear
r

Figure 1

and the same distance difference may be described by a circle of identity which is normal to and centered on the interaural axis.

Locational Ambiguity

Binaural differences in the time of arrival may alternatively be expressed as binaural differences in phase. The maximum binaural temporal difference occurs when the acoustic source is at either the 90° or 270° azimuth. Assuming r = 8.75 cm, the usual value assigned to man, then maximum $\Delta t = 656$ μsec. That is, at 90° the sound arrives at the far ear 656 μsec after it arrives at the near ear. This time lag in arrival at the far ear would result in phase differences between ears of approximately 90°, 180°, and 360° for pure tones of 380 Hz, 760 Hz, and 1520 Hz respectively. Note that the phase difference information for a given azimuth can be determined only if the frequency of the sound is also known; the binaural time difference is constant for all frequencies at a given azimuth, but the binaural phase difference is frequency dependent.

The frequency range over which binaural phase differences may be utilized for sound localization is restricted. More than one location may produce the same difference in binaural phase when the period of the impinging sinusoid is equal to or less than twice the maximum binaural temporal difference. In the idealized case for man, such locational ambiguities will occur for frequencies with periods less than or equal to 1312 μsec. For example, a 760 Hz stimulus located at the 90° azimuth (i.e. 90° to the right) will produce a binaural phase difference of 180°; this same difference will be produced by the stimulus at the 270° azimuth (i.e. 90° to the left). Thus

binaural phase information alone will not discriminate between these two locations. Similarly, for all frequencies greater than 760 Hz, the binaural phase difference for a source at any given azimuth will be perfectly matched by at least one other azimuth. This ambiguity in location suggests that phase information can be utilized for sound localization only with low frequency tones. It should be emphasized, however, that the stimulus frequency beyond which acoustical locations are ambiguous is higher for species with smaller heads. For instance, a small rodent with a maximum Δt of 100 μsec will be confronted with ambiguous locations only for frequencies above 5000 Hz. For many of the smaller mammals the geometrically defined frequency limit for unambiguous localization may not, in fact, be fully realized. A lower limit may be determined physiologically by the refractory period of auditory neurons and by the limitations of the auditory system to code and preserve the binaural phase disparity.

The Duplicity Theory of the Localization of Azimuth

The vertebrate ear is confronted by two separate binaural disparities -- interaural differences in phase, or time, and interaural differences in intensity. The change in azimuth of a sound source always results in a change in the former and often results in changes in both dimensions. The relative contribution of either dimension with respect to the determination of azimuth becomes an empirical matter. Psychophysical observations relevant to this question have largely been confined to man; as a result the summary which follows may not generalize to all members of the mammalian community.

Stevens and Newman (1934) were the first, with modern techniques,

to empirically explore the ability of human observers to localize pure tones. They positioned their observers on a platform located on the roof of Harvard University's Biological Laboratory. The stimuli were presented from a speaker attached to a 12 foot boom which rotated around the observer in the horizontal plane. The subjects were required to judge the location of a tone presented in the right hemisphere. Their data were collapsed across azimuths and across observers, yielding a mean error of localization of about 11^{o} for frequencies below 1000 Hz and above 7000 Hz. The mean error of localization increased to about 20^{o} at 3000 Hz. Stevens and Newman interpreted these data as support for a duplicity theory of auditory localization. That is, they argued that both binaural phase differences and binaural intensity differences were utilized by the observers in locating the sound source, the former for low frequencies and the latter for high frequencies. The degradation in spatial acuity at 3000 Hz was regarded to mark the physiological boundary between these two mechanisms. Performance suffered at the boundary because the binaural differences generated at this frequency in either domain were marginal.

The Stevens and Newman study remained the definitive work on auditory localization for twenty years until Mills (1958) reexamined the problem. Mills, one of Stevens's students, conducted his study in an anechoic chamber and required his observers to report the just detectable displacement in location of a sound source for changes in azimuth across the first quadrant locations from straight ahead to 90^{o} to the right. The procedural and acoustical refinements introduced by Mills generated a view of auditory localization strikingly different on three counts. First, localization was specified

in terms of the minimum audible angle -- that is, in terms of the angle at which the observer reliably reported that the comparison tone was right or left of the standard tone for the azimuth in question. The observer's response indicated his ability to resolve acoustic differences produced by a change in azimuth, rather than his ability to identify the spatial location on the stimulus. Second, different azimuths produced different minimum angles. The ability to resolve locations in space is, therefore, azimuth as well as frequency dependent. Third, man's ability to resolve changes in acoustic location is more variable than Stevens and Newman's (1934) work had suggested. Mills reported that at the zero azimuth man can resolve a change in location of 1° or less for low frequency sounds while at a 60° azimuth the minimal audible angle for some frequencies is indeterminably large. More recently Harris (1972) has presented data in which pure tone localization did not deteriorate with changes in azimuth. The reasons for these discrepant results are not clear. However, Harris employed transducers which were separated by approximately 10° in elevation as well as by their displacement in azimuth. The difference in elevation may have generated intensity differences which by themselves were not detectable but which interacted with horizontal displacements to facilitate detection.

Mills invoked the duplicity hypothesis to account for his data, considering binaural phase differences instrumental in low frequency localization and binaural intensity differences instrumental in high frequency localization. To test the adequacy of this explanation, he conducted a study employing dichotically presented stimuli (Mills, 1960). He required his subjects to report the just detectable differences in

binaural phase and intensity for pure tones across the frequency spectrum. His research strategy assumed that phase should be considered the relevant cue in localization for those frequencies where the threshold function for dichotic phase difference was found to coincide with the threshold function for the localization of real sources. Conversely, at those frequencies where threshold functions for dichotic intensity difference and the localization of real sources agreed, binaural intensity difference should be considered the relevant localization cue. The results indicated that for frequencies below 1500 Hz binaural phase differences best fit the data, while for frequencies between 1500 and 6000 Hz, intensity differences agreed well with the localization of real sources. However, neither dimension accounted for the localization of real source stimuli for frequencies greater than 6000 Hz. While Mills's curve fitting approach was not wholly assumption free, his study remains the firmest test of duplicity theory.

Additional support for the duplicity hypothesis of the localization of azimuth in mammals has come recently from studies on the localization of pure tones in cat (Casseday and Neff, 1973) and in sea lion (Moore and Au, 1975). In both cases, experimental results could be explained by the operation of two localization mechanisms -- one for low frequencies and the other for high frequencies. As a result, duplicity theory is generally accepted as characterizing the mechanisms of auditory localization in mammals.

Auditory Localization in an Evolutionary Perspective

Masterton has argued that mammalian hearing reveals the operation of selection for accurate localization mechanisms (Masterton, Heffner, and Ravizza, 1969; Masterton and Diamond, 1973; Masterton, 1974). This evolutionary perspective is founded upon the proposition that selection has operated to favor the individual endowed with the ability to acoustically orient to biologically significant sounds. According to this position the early detection of the locus of other animals through acoustic mechanisms would contribute to an individual's reproductive advantage by alerting and preparing him to fight, flee, mate, etc., as appropriate.

Masterton contends that selection for a superior spatial sense has resulted in an expanded auditory sensitivity range in mammals. The primary evidence for his position is the correlation between a species's interaural distance, or max Δt, and its high frequency cutoff (Masterton, 1974). As seen in Figure 2, mammals with smaller heads are able to hear higher frequency sounds. The correlation supports the selection hypothesis within the context of the duplicity theory of auditory localization. As noted above, species with small heads suffer two disadvantages -- 1) the range for binaural temporal differences is restricted, and 2) they experience binaural intensity differences only for high frequency sounds. Therefore, if an organism with a small head is to take advantage of binaural differences to locate sounds, it must possess an expanded sensitivity to the higher frequencies where binaural differences are produced. Masterton's correlation show that this expectation is indeed realized.

Figure 2

Inverse Relationship Between the Availability of Large Binaural Time Differences and the Availability of Large Binaural Spectrum Differences in 15 Varieties of Mammals. Each number represents the maximum time difference and the upper limit of hearing at 70 dB SPL for one species: 1) opossum, 2) hedgehog, 5) slow loris, 6) potto, 10) macaque, 11) chimpanzee, 12) man, 13) bat (Myotis), 14) bat (Eptesicus), 15) rabbit, 16) wild house mouse, 17) cotton rat, 18) guinea pig, 26) bottle-nosed dolphin. Mammals known to echo locate are circled. Data from several published and unpublished sources, Masterton (1974). Reproduced by permission of author.

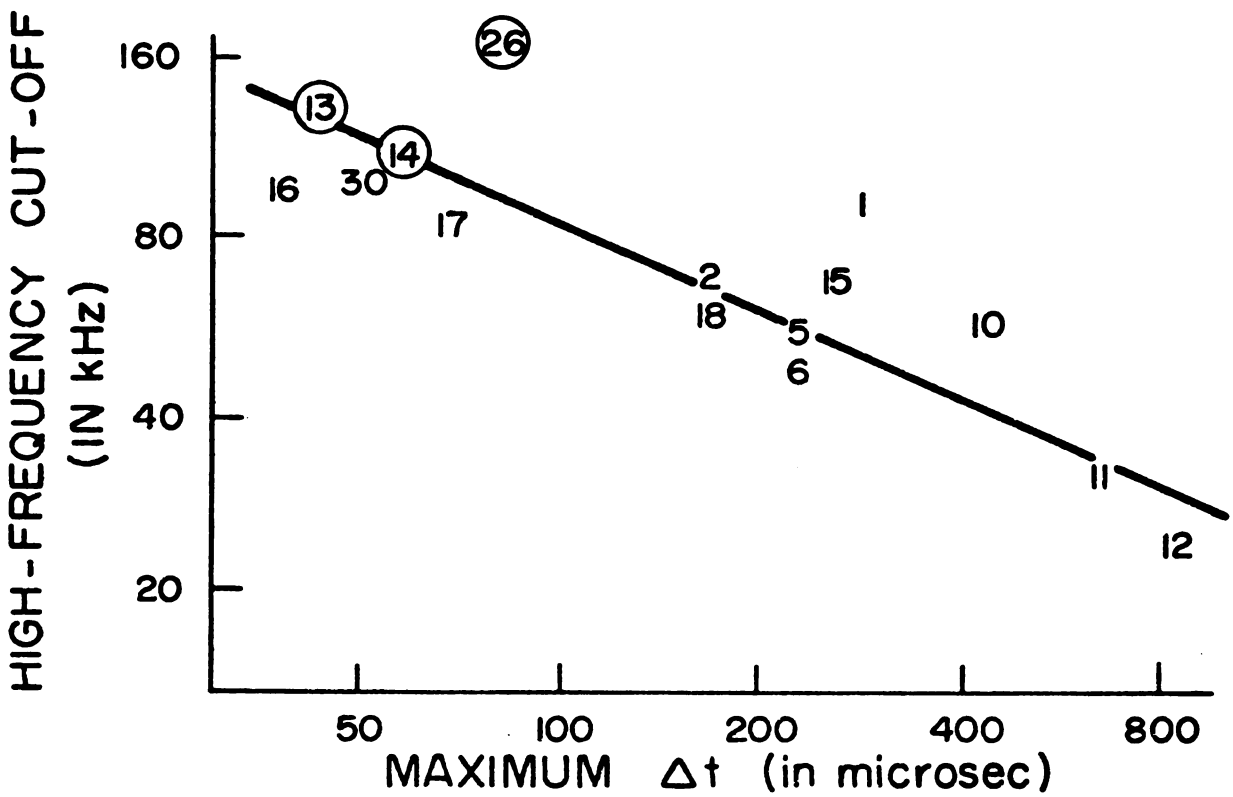

HIGH-FREQUENCY CUT-OFF (IN kHz)
160
80
40
20
50
100
200
400
800
MAXIMUM Δt (in microsec)
26
13
14
16
30
17
2
18
1
15
5
6
10
11
12

Figure 2

The Localization of Complex Sounds

As has been reported here the classical investigation of auditory localization employed pure tones for stimuli. Pure tones have the advantage that one may characterize localization acuity as a function of frequency. However, some problems arise regarding the localization of pure tones. At high frequencies the binaural intensity difference of tonal stimuli is not necessarily monotonically related to position in space. Thus it is possible to have two or more loci with the same binaural intensity difference (Harris, 1972; Harrison and Downey, 1970; Sivian and White, 1933). In addition, the intensity dimension may appear to misbehave to the extent that a stimulus to one side of the observer may actually be more intense at the far ear and consequently appear to originate from the far side. This phenomenon is illustrated in Figure 3. This figure represents intensity measurements obtained from an artificial head by Harris (1972). Those points in the polar coordinates at which the observed binaural intensity difference lie within the radius of the circle denote loci where the sound intensity for the ear near the source was less than the intensity recorded for the ear farther from the source. In short, the tonal stimulus may appear to behave capriciously, and this behavior may be an expression of slight architectural differences between different individuals' heads, external ears, etc.

Two issues merit clarification. First, while a single frequency with reference to several points in space may appear to misbehave, adjacent frequencies in the audio spectra are unlikely to do so; this is because the wavelengths of different frequencies would require different spatial coordinates to reproduce a similar set of standing

Figure 3

Sound Shadows Thrown at Representative Frequencies by a Loudspeaker Rotating Around the Artificial Head Without Pinna and With Either Large or Small Pinna. At loci where the observed measurement lies within the radius of the polar coordinates the sound pressure level recorded at the distant ear was greater than the sound pressure level observed at the near ear. Harris (1972). Reproduced by permission of the author.

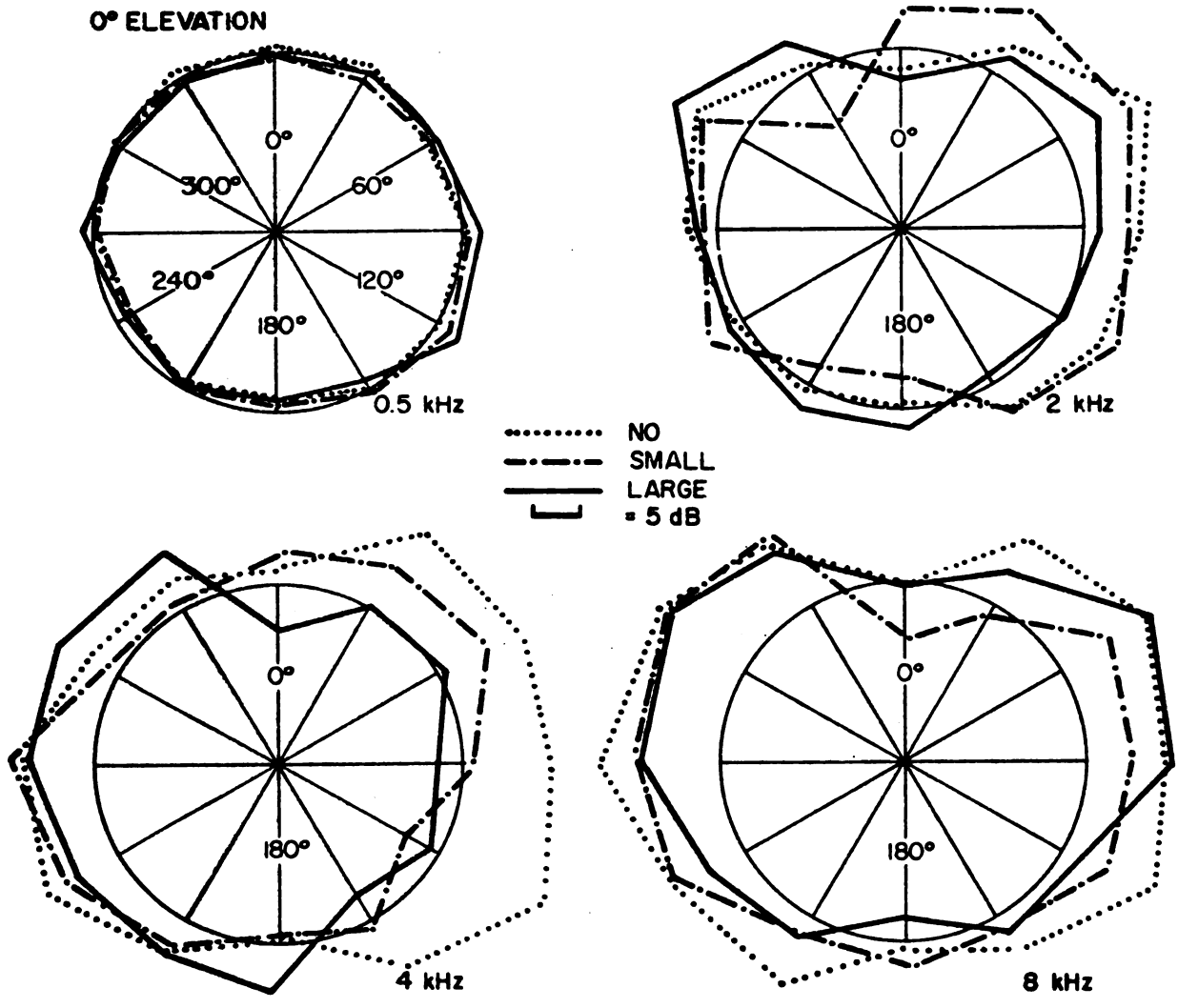

0° ELEVATION
0°
300°
60°
240°
120°
180°
0.5 kHz
0°
180°
2 kHz
NO
SMALL
LARGE
= 5 dB
0°
180°
4 kHz
0°
180°
8 kHz

Figure 3

waves, etc., leading to the intensity inversion. Second, pure tones are not naturally occuring stimuli and the vertebrate auditory system is probably not adapted to localize them. Rather, it is the case that both biologically and non-biologically produced sounds which occur in nature are composed of a family of frequencies of a given spectral extent; and to a first approximation, natural stimuli may be described by their dominant frequency and bandwidth (Rowell and Hinds, 1963; see their description of rhesus vocalizations). This essentially is the level of analysis offered by a sonograph of an acoustic event. The pitch of a sound is dependent on the frequency bandwidth greatest energy (dominant frequency) and its location of the frequency axis. High pitched sounds have a high dominant frequency and vice versa. Sounds also lie on a continuum from very tonal to very noisy signals. Tonality is an expression of bandwidth; signals composed of a narrow range of frequencies are tonal, while broad band signals are noisy. Thus in the context of bioacoustics the emerging question for auditory localization becomes what is the requisite bandwidth of a stimulus at different points on the frequency spectrum for an observer to unambiguously resolve its spatial origin?

The Bioacoustical Context of Auditory Localization

Marler (1955; 1957) has suggested that species specific vocalizations may be differentially locatable according to the frequency content and bandwidth of the call. Marler (1965) has observed that throughout the class mammalia alarm calls are characteristically shrill narrow band barks while screeching, screaming vocalizations are universally emitted under severe distress. A similar parallel

may be observed in the vocal repertoire of many avian species. In this context the proposition arises that if the acoustical characteristics which determine the ability with which a call may be localized are generally held in common by members of the biocommunity (i.e. their auditory systems are basically similar) then species specific vocalizations should possess the acoustical characteristics which make a call more or less localizable as may be appropriate in the social context. For example, one may predict that alarm calls should yield minimal information regarding the location of the vocalizer, while calls emitted to solicit contact with conspecifics may exhibit acoustical characteristics optimal for localizing the caller. Consequently the more generalized case may be described by exploring the ability of organisms to localize bands of noise of various bandwidths at different points within the frequency spectrum.

In this regard limited comparisons are available. Casseday and Neff (1973) reported lower minimum audible angles in cats with broad bands of noise than with pure tones. In monkeys, Heffner (1973) found localization thresholds were lower for clicks than for chords composed of 0.5 and 4 kHz tones. Konishi (1972) found that barn owls would strike at an acoustic prey with greater accuracy for broad bands of noise than for pure tones. Nordlund (1962; 1963) has reproted that humans exhibit a smaller error of estimation of acoustic locus for low pass noise than for pure tones. Additionally several studies of human localization in the median plane, or with monaural observers indicate that the stimulus must contain certain chunks of the auditory spectrum for subjects to exhibit some spatial sense (Angell and Fite, 1901; Batteau, 1967; Belendiuk and Butler, 1975; Butler, 1969; Butler

and Planert, 1975; Hebrank and Wright, 1974a; 1974b; Roffler and Butler, 1968a; Wright, Hebrank, and Wilson, 1974).

Research Objectives

The objective of this research is to psychophysically characterize the abilities of two species of nonhuman primates, Macaca mulatta and M. nemestrina, to detect changes in the azimuth of narrow and wide bandwidth high frequency signals. This objective serves two ancillary issues. One, it helps place the human ability to acoustically localize in a phylogenetic context. Two, it helps characterize the contribution of high frequency sensitivity to auditory localization. With respect to these issues, members of the genus Macaca are appropriate subjects. Their phyletic heritage is sufficiently similar to man's that for descriptive purposes their aural abilities serve as a model of the prehominoid condition. Perhaps more important, however, it is far easier to recognize the selective pressures presently in operation on nonhuman primates than on man. Consequently propositions regarding the ability with which species specific vocalizations may be localized are testable. In addition Masterton, Heffner, and Ravizza (1969) have observed that man's upper limit of hearing on the frequency axis is low with respect to the class mammalia. Thus the expanded sensitivity range possessed by Macaca may provide a more generalized case for describing the contribution of high frequency sensitivity to auditory localization.

Stebbins (1973) has fully described the threshold of hearing function for the macaques; its basic features are shared by all members of the subfamily of Old World monkeys, Cercopithecinae. As may be seen

Figure 4

Threshold of Hearing Function from 60 Hz to 45 kHz for Cercopithicinae Based on Data Obtained from Four Genera. Stebbins (1973). Reproduced by permission of the author.

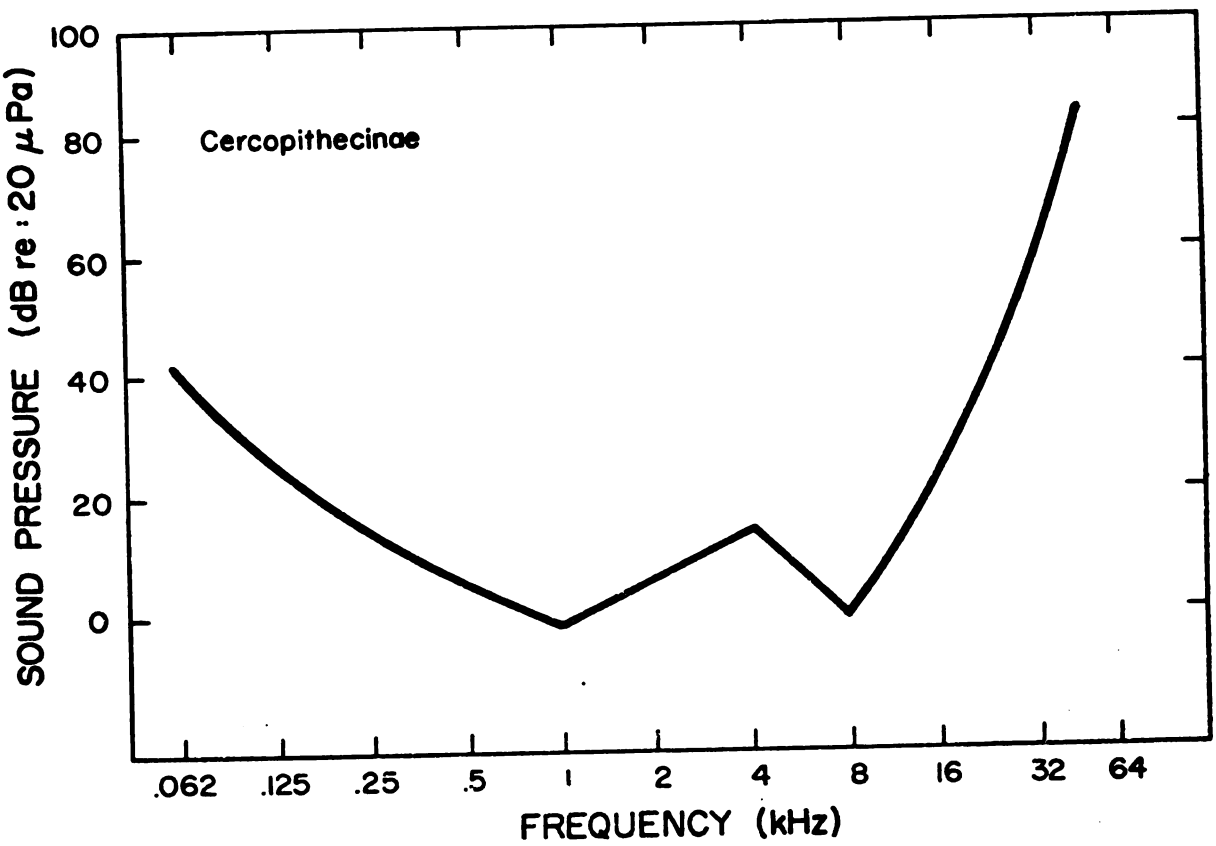

Cercopithecinae
SOUND PRESSURE (dB re: 20 μPa)
100
80
60
40
20
0
.062
.125
.25
.5
1
2
4
8
16
32
64
FREQUENCY (kHz)

Figure 4

in Figure 4, hearing in the macaques ranges from 60 Hz to an upper limit of 45000 Hz. The upper limb of the audiogram shows a peak in sensitivity at 8000 Hz followed by a rapidly ascending threshold of hearing function. The research presented here is directed at characterizing the ability of the macaque to localize changes in azimuth or the horizontal plane for sound in the region of its greatest sensitivity to high frequency stimuli -- 5000 Hz to 20000 Hz. This two octave span contains relatively little energy from the macaque's repertoire of vocalization, thus it participates little in communication in this genus (Rowell and Hind, 1962; Grimm, 1967). The highest octave of the macaque's hearing is not explored here. The macaque is 40 to 80 dB less sensitive to sounds in this region; and in addition these high frequency stimuli are more readily attenuated by the environment. Consequently many sounds in the upper end of the audio spectrum may have insufficient energy to participate in localization.

Experiment I
The Detection of Changes in Azimuth as a Function of Stimulus Bandwidth

Method

Subjects

Three monkeys of the genus Macaca served as subjects. Two species in this genus were represented, M. mulatta (rhesus) and M. nemestrina (pigtail). Miko, a mature adult female pig-tailed macaque was maintained at an experimental weight of 4.2 to 5.0 kg throughout the course of the study. Sidney, a juvenile male pig-tailed macaque, weighed from 3.4 to 4.1 kg. Oscar, a juvenile male rhesus, weighed from 3.0 to 4.3 kg during the course of experimentation. All subjects were wild caught and had been acclimated to laboratory conditions for at least 9 months prior to the commencement of testing.

At the initiation of training Miko was experimentally naive, while Sidney and Oscar had previously served as subjects in an audiometric procedure designed to behaviorally measure the threshold of hearing for nonhuman observers (Stebbins, 1975). The threshold of hearing function (audiogram) for these two observers was well within the normal range as reported for the subfamily of Old World monkeys Cercopithecinae (Stebbins, 1973).

The subjects were maintained under food-restricted conditions. The bulk of their diet was provided by 190 mg whole banana flavored pellets (Noyes) which were earned in 1-2 hour daily experimental sessions. The remainder of their caloric ration was comprised of

Purina monkey chow and fresh fruit; the latter of which was usually available three times weekly.

Subjects were individually housed in stainless steel primate cages located in a large 500 sq ft colony room. Water was continuously available in the home cage. The colony was maintained on a 12/12 light/dark cycle.

Apparatus

Subjects were seated in a primate chair which had been designed to reduce acoustic reflections. The chair was positioned on a pedestal in a 9 by 12 foot anechoic room. As may be seen in the close-up of the subject in Figure 5, the subject's head was held in a fixed position in the sound field by a muzzle restraint. The muzzle restraint and chair pedestal were employed to reduce the variability in the position of the observer in the acoustical environment within and between sessions. The error in positioning subjects between sessions was estimated not to have exceeded 4 or 5 degrees with respect to the zero azimuth.

In Figure 6 it may be seen that the primate chair was located 2.75 m from an arc upon which the acoustical transducers were mounted. The speakers were mounted such that their axis was parallel to the floor of the chamber and directed toward the center of the observer's head. The subject's head and centers of the speakers were located .92 m above the floor of the chamber.

The acoustic stimuli presented were pure tones and bands of noise 250, 500, 1000, 2000, 4000, 8000 Hz wide geometrically centered at three frequencies -- 8000, 11200, 16000 Hz. The auditory stimuli

Figure 5

Subject in Primate Chair Positioned in the Anechoic Chamber. Note the position of the response disk and the feeder cup. The subject's left hand is on the response disk; the feeder cup is to the right of the response disk.

FIGURE 5

Figure 6

The Location of the Observer With Respect to the Speaker Array Mounted on the Arc.

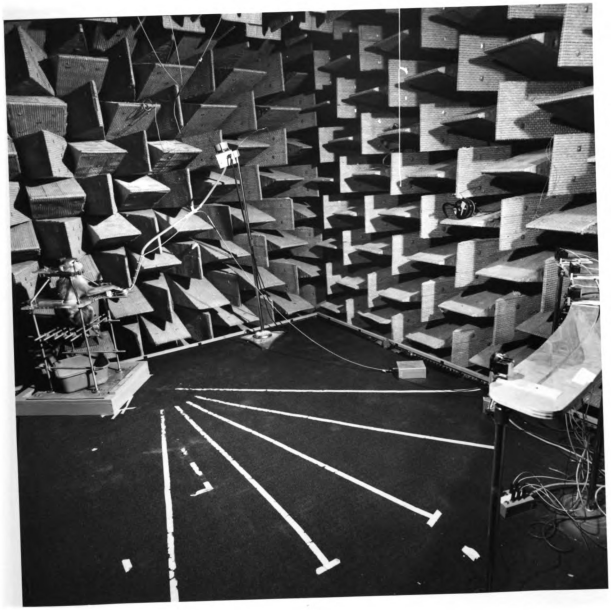


FIGURE 6

were presented (turned on and off) by enabling a random crossing tone switch with a rise and fall time of 25 msec. The stimuli were presented to the subject through a matched array of 5 loudspeakers. Two different models of transducers were used. Stimuli centered at 8000 Hz were presented through University sphericon T202 loudspeakers; while stimuli centered at 11200 and 16000 Hz were presented through 60 mm McIntosh tweeters provided through the courtesy of Roger Russell, McIntosh Laboratories.

Pure tones were generated by an audio oscillator and were amplified, gated, and attenuated according to the circuit depicted in the block diagram in Figure 7. Bands of noise were generated by an analog audio multiplier described by Palen and Gourevitch (1970). The noise generation system produced a double sideband suppressed carrier noise. The bandwidth of the noise was twice the bandpass of a filtered noise signal which was amplified (MC 1433 operational amplifier) and sent to one leg of the multiplier (Analog Devices 428 J). The noise band was arithmetically centered at a carrier frequency which was provided and amplified (MC 1433 operational amplifier) at the other end of the multiplier by an audio oscillator (Hewlett Packard 200 CDR). Thus the bandwidth and the center frequency of the audio stimuli were an expression of the upper cutoff value of a filtered (Allison Laboratories AL 2ABR) noise source (General Radio 1381) which extended from near DC; and the carrier frequency of the oscillator respectively. The audio signal generated by the multiplier was subsequently filtered (Krohn Hite 310 ABR acitve bandpass filter) and amplified. Table 1 presents the filter and oscillator parameters for the stimulus employed. Figure 8 presents the equipment employed for the generation

Figure 7

The Audio Equipment Used for the Generation of Pure Tones

a.	frequency counter	Hewlett Packard 523 DR
b.	audio oscillator	Hewlett Packard 200 CDR
c.	programmable attenuator	custom
d.	tone switch	custom
e.	attenuator	Daven T 690 CR
f.	audio amplifier	McIntosh 240
g.	speaker selector switch	custom
h.	attenuator	Daven PT 324-M
i.	speaker	University spheriçon T 202; McIntosh tweeter

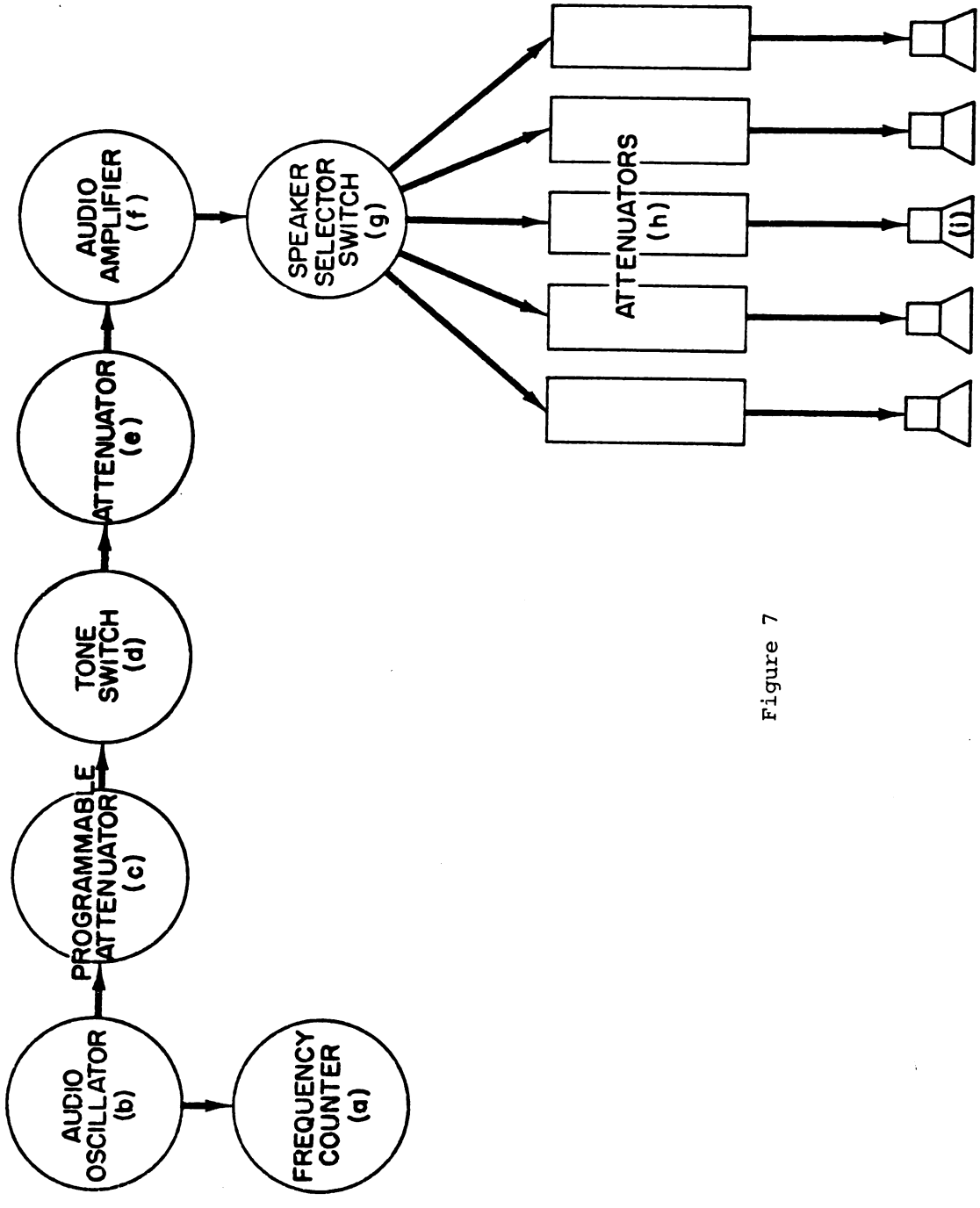

FREQUENCY COUNTER (a)
AUDIO OSCILLATOR (b)
PROGRAMMABLE ATTENUATOR (c)
TONE SWITCH (d)
ATTENUATOR (e)
AUDIO AMPLIFIER (f)
SPEAKER SELECTOR SWITCH (g)
ATTENUATORS (h)
(i)

Figure 7

TABLE 1

Summary of Filter and Oscillator Parameters for the Noise Band Stimuli

Center frequency (Hz)	Bandwidth (Hz)	Low Cutoff (Hz)	High Cutoff (Hz)	Carrier (Hz)	AL 2ABR Upper Cutoff Filter Setting	Krohn-Hite Bandpass Filter Setting[a]
8000	250	7876	8126	8000	1.7 x 75	5-13
	500	7754	8254	8004	1.7 x 150	5-13
	1000	7516	8516	8016	1.7 x 300	5-13
	2000	7062	9062	8062	1.7 x 600	7-9
	4000	6246	10246	8246	1.7 x 1200	6.2-10.2
	8000	4944	12944	8944	1.7 x 2400	5-13
11200	250	11076	11326	11201	1.7 x 75	8-16
	500	10953	11453	11203	1.7 x 150	8-16
	1000	10711	11711	11211	1.7 x 300	8-16
	2000	10245	12245	11245	1.7 x 600	10-12
	4000	9377	13377	11377	1.7 x 1200	9.4-13.4
	8000	7893	15893	11893	1.7 x 2400	8-16
16000	250	15876	16126	16001	1.7 x 75	12.5-20.5
	500	15752	16252	16002	1.7 x 150	12.5-20.5

TABLE 1 (cont'd.)

1000	15508	16508	16008	1.7 x 300	12.5-20.5
2000	15031	17031	16031	1.7 x 600	15-17
4000	14125	18125	16125	1.7 x 1200	14-18
8000	12493	20493	16493	1.7 x 2400	12.5-20.5

[a] Category measured in kHz.

of noise bands. The audio multiplier method of producing noise bands has the advantage of yielding slopes much steeper than those exhibited by filters displaying conventional Butterworth characteristics. The narrowest bandwidths, 250 and 500 Hz, were nearly rectangular with slopes exceeding 80 dB per octave. Appendix A contains acoustical measurements of the stimuli employed. The experimental contingencies, the delivery of stimuli, and the subject's responses were automatically controlled and recorded by solid state logic modules (Digi Bits) located in an adjoining room.

Procedure

One way to study auditory localization is by the employment of the detection paradigm. In this procedure the observer is instructed to report when he has detected a change in acoustic locus. It should be emphasized that the detection paradigm as used here denotes that category of experimentation which was identified by Brindly (1970) as Class A. That is, it was assumed that if the sensations evoked at two stimulus locations are indistinguishable then those locations in space may not be discriminable different. Conversely, when the observer reports that two spatial locations are detectably different, this circumstance is likely an expression of differences in the sensations evoked by the different location. This simple assumption linking the psychological and the physical domains is the logical substrate upon which this research is based.

Figure 8

The Audio Equipment Used for the Generation of Noise Bands

a.	frequency counter	Hewlett Packard 523 DR
b.	audio oscillator	Hewlett Packard 200 CDR
c.	noise generator	General Radio 1381
d.	filter	Allison Laboratories AL 2ABR
e.	audio multiplier	Analog Devices 428 J
f.	audio amplifier	Hewlett Packard 450 AR
g.	filter	Krohn-Hite 310 ABR
h.	programmable attenuator	custom
i.	tone switch	custom
j.	attenuator	Daven T 690 CR
k.	audio amplifier	McIntosh 240
l.	speaker selector switch	custom
m.	attenuator	Daven PT 324-M
n.	speaker	University sphericon T 202; McIntosh tweeter

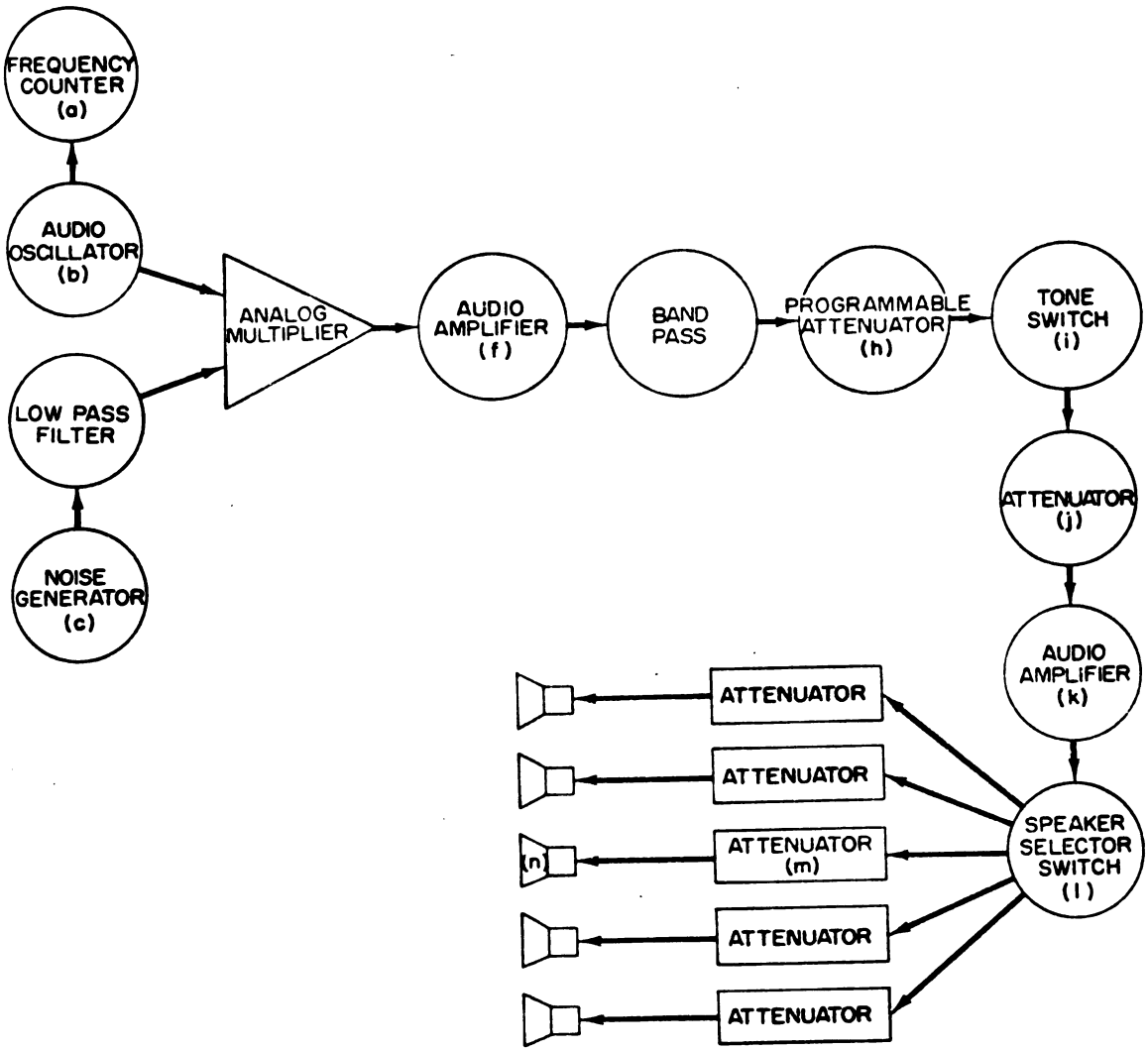

FREQUENCY COUNTER (a)
AUDIO OSCILLATOR (b)
LOW PASS FILTER
NOISE GENERATOR (c)
ANALOG MULTIPLIER
AUDIO AMPLIFIER (f)
BAND PASS
PROGRAMMABLE ATTENUATOR (h)
TONE SWITCH (i)
ATTENUATOR (j)
AUDIO AMPLIFIER (k)
SPEAKER SELECTOR SWITCH (l)
ATTENUATOR
ATTENUATOR
ATTENUATOR (m)
(n)
ATTENUATOR
ATTENUATOR

Figure 8

Pretraining

With nonverbal observers the burden rests with the experimenter to invent a language through which one may communicate the response requirements to the subject. The goal of the training procedure was to instruct the monkey to maintain contact with the response disk when the sound was repetitively presented at zero azimuth from the referent speaker and to release the response disk when the sound was presented at a different location from one of the four comparison speakers. The method by which this was accomplished was as follows:

The subject's ad libitum weight was estimated by averaging the body weight maintained under nonrestricted feeding. Subjects were subsequently food deprived until their body weight dropped to 90% of the free-feeding level. They were seated in a primate chair and trained to extract and eat banana flavored pellets delivered to the food cup. After several daily sessions the monkey habituated to the primate chair and would readily take food when it was presented into the food cup. At this point the subjects were ready for the initiation of training.

The subject was seated in the primate chair, and the chair was positioned in the anechoic chamber. The pellet dispenser was attached to the feeder cup. The subject was then shaped by the method of successive approximations (Whaley and Malott, 1971) to manually make contact with the response disk. Typically by the end of one session the monkey would make contact with the response disk, a banana pellet would be delivered and the monkey would consume the reinforcer.

The response requirements for the delivery of the reinforcer were altered in the following session. Contact with the response disk

produced a noise burst which pulsed repetitively from the standard speaker located at zero degrees azimuth. When the subject released the response disk, reinforcement was delivered. A small light mounted adjacent to the standard speaker was continuously lit during this stage. Under these conditions the latency for releasing the response disk gradually grew shorter and typically by the end of this session the subject was releasing the disk by the first or second pulse of noise.

In the next session a time-out was introduced into the procedure. The time-out was initiated every time the subject released the response disk. The duration of the time-out was gradually lengthened from a minimum value of 200 msec to 6 sec over the course of several sessions. During the time-out the trial light was unlit. If the subject made contact with the response disk during the time-out, the time-out was reset and timing was not reinitiated until the subject broke contact with the response disk. Following several sessions of training the subject would pause until the trial light was presented, make contact with the response disk and release synchronously with the presentation of the noise burst.

In the next stage of training the subject made contact with the response disk and then was required to wait for successively longer durations until the auditory stimulus was presented. Releasing the disk would then result in the delivery of reinforcement. After several sessions of training the subject would maintain contact with the response disk until the acoustic stimulus was presented. At this stage of training the subject was required to maintain contact with the response disk for an average duration of 8 sec (range 250 msec to

16 sec) at which point the stimulus was presented from a speaker located to the right of the observer.

In the last stage of training the monkey was subjected to the identical schedule and reinforcement contingencies as were presented in the previous stage except that during the period in which the subject had to maintain contact with the response disk (prior to the presentation of the auditory stimulus from the subject's right) a very low intensity auditory stimulus was repetitively pulsed from the zero azimuth. Thus the subject had to discriminate between acoustic stimuli which differed along two dimensions, intensity and location. The intensity difference between the pretrial stimulus (S-) and the trial stimulus (the stimulus during which releasing the response disk produced reinforcement, (S+)) was initially 40 dB. Over the course of 5 to 10 sessions, this intensity difference was gradually reduced (faded out) by increasing the intensity of S-.

Psychophysical Testing Procedure

A diagram of the testing procedure in state notation is presented in Figure 9 (Snapper, Knapp, and Kushner, 1970). The testing procedure differed from the last stage of pretraining along two dimensions. One difference was the position on the arc of the comparison speakers. During pretraining the comparison speakers were clustered at one end of the arc about 30° from the standard transducer. However, when the method of constant stimuli is employed it is desirable to adjust the steps within the physical stimulus continuum to bracket the subject's threshold. In this case threshold was

defined as the change in spatial location which was detectably different from zero azimuth on 50% of the trials. The 50% detectability locus is an empirical entity which varies for different acoustical parameters. Thus the speakers were positioned and repositioned until a satisfactory arrangement was determined. Table 2 presents the spatial configurations employed for the acoustical parameters explored in this research. The second difference between pretraining and the last stage of testing was the incorporation of catch trials. Perhaps the most significant contribution of signal detection theory to psychophysics is the measurement of the subject's probability of reporting the presence of the stimulus when it was not presented. With reference to classical psychophysical procedures it is desirable to monitor the subject's flase alarm, or random release rate so that any changes in the observer's response bias do not distort the estimation of the observer's threshold (sensitivity). In the data reported here sessions are excluded from analysis when the observer's false alarm rate exceeded 20%. Only infrequently were data excluded by this criterion; and the majority of the unacceptable sessions occurred either when Miko, the only female monkey, was in estrus, or when the acoustical parameters were recently changed.

With the incorporation of the modification described above the maintained testing procedure was as follows: The trial light was presented and the subject was free to initiate the trial by manually making contact with the response disk. Disk contact, the subject's observing response, had the consequence of producing the auditory stimulus which was reiteratively presented from the standard transducer located zero degrees azimuth.

Figure 9

State Diagram of the Testing Procedure.

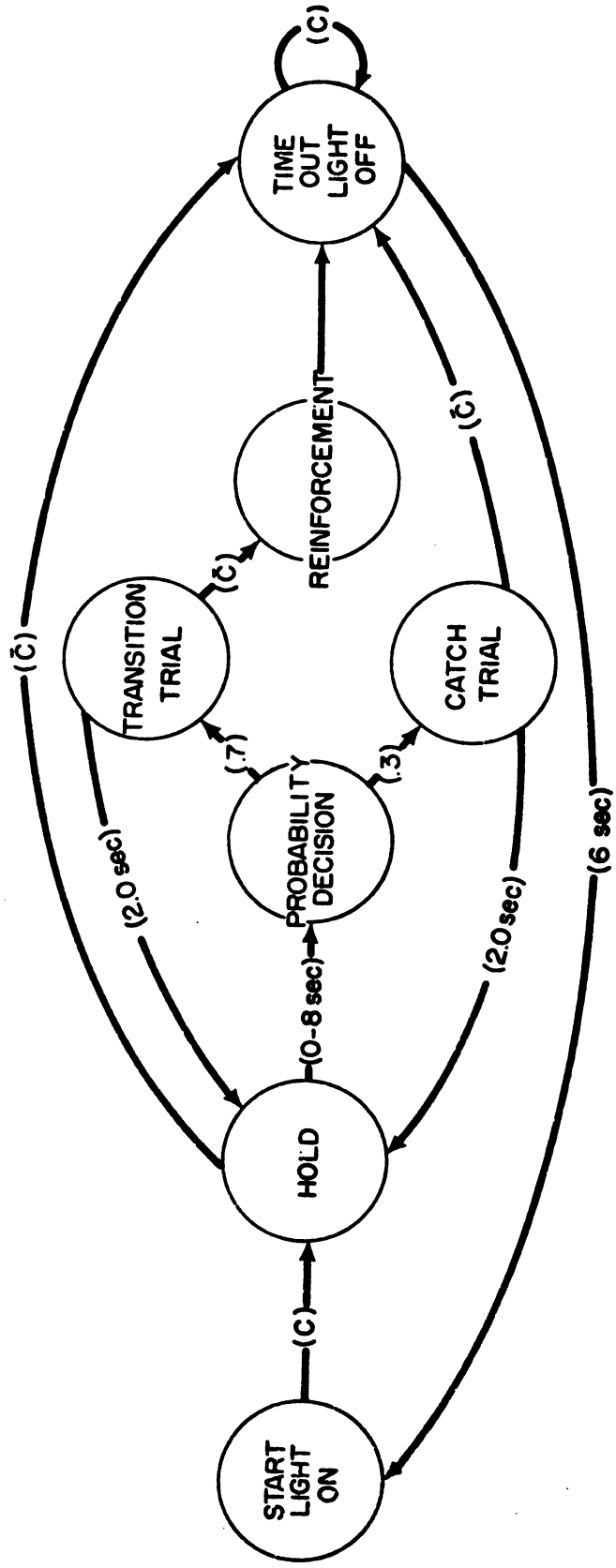

START LIGHT ON
(C)
HOLD
(0-8 sec)
PROBABILITY DECISION
(.7)
TRANSITION TRIAL
(.3)
CATCH TRIAL
(C)
REINFORCEMENT
(C)
TIME OUT LIGHT OFF
(C)
(2.0 sec)
(2.0 sec)
(6 sec)

Figure 9

TABLE 2

Speaker Locations With Respect to the Zero Azimuth

Configuration	Speaker A	B	C	D	E
1	0.0	2.9	12.0	17.2	28.6
2	0.0	2.9	8.6	17.2	28.6
3	0.0	2.9	8.6	17.2	L[a]
4	0.0	1.3	7.8	15.5	29.5

Subject	Stimulus Bandwidth (kHz) .001	.25	.50	1	2	4	8	Center Frequency
Sidney	1	1	1	1	1	3	3	8000 Hz
Miko	2	2	2	2	2	3	3	
Oscar	2	2	2	2	2	3	3	
Sidney	4	4	4	4	4	4	4	11200 Hz
Miko	4	4	4	4	4	4	4	
Oscar	4	4	4	4	4	4	4	
Sidney	4	4	4	4	4	4	4	16000 Hz
Miko	4	4	4	4	4	4	4	
Oscar	4	4	4	4	4	4	4	

[a] Speaker mounted at zero azimuth below standard speaker. See control for speaker differences in text.

At some random point in time (number of pulses) later the auditory simulus was presented from one of the four comparison speakers from the observer's right - then it was presented from the standard speaker - then once more from the comparison speaker. If the monkey detected this transition in acoustic locus and reported this detection by releasing the response disk (within the 2 sec trial duration) it received a banana pellet in the food cup. A 6 sec time-out followed reinforcement, then the trial light was presented and the monkey could make its observing response - hand on the disk - reinitiating the sequence. The comparison speaker at which the acoustical transition occurred was randomly determined. The failure to report a transition had no consequence and the sequence was recycled. The release of the disk at all times other than in a transition trial did not produce reinforcement and entered the subject into the time-out.

Contact with the response disk led to the presentation of a trial on the average once every 8 sec (range 0-16 sec). The subject was confronted with two different kinds of trials -- transition trials which when reported produced reinforcement and catch trials through which the experimenter monitored the subject's random release rate. Trials were unmarked other than by the presence or absence of an acoustic transition. The probability of a trial being a catch trail was typically .3; however, the proportion of catch trials was elevated on occasions to .4 or .5 when the suject's catch trial rate began to exceed the criterion level of 20%. Experimental sessions were conducted daily and ranged in duration from 60 to 120 minutes. In the data to be reported here each daily session was partitioned into two halves during each of which a different bandwidth

of the same center frequency was presented. The stimulus bandwidths within a session were arbitrarily selected. Usually a narrow and a wide band were employed. In each half of a daily session 200 to 300 trials were presented, and subjects typically received 100 to 200 banana pellets within this period.

Stimulus Parameters

Each acoustical pulse was presented with a duration of 300 msec with a 25 msec rise and fall time. The pulsed stimuli were repeated at a rate of 1.5 per second. The sound pressure level of the auditory stimulus was randomly varied for each pulse. The randomization was in 3 dB steps within a 21 dB range. Thus the subject was required to detect changes in the location of an acoustic event under conditions in which the intensity of the sound varied. The adoption of this requirement served two purposes. One, under natural conditions biologically significant sounds vary in intensity. Thus the testing procedure was consonant with the conditions under which an observer must localize sounds in nature. Two, the randomization of intensity minimized the likelihood of the subject detecting slight intensity differences between speakers. The sound pressure level between speakers was equated within 1 dB and the significance of this slight difference in intensity was reduced by this technique. (See Appendix A).

As presented in Figure 4 the threshold of hearing is a function of frequency. The threshold of hearing for the macaque is about 1 dB, 9 dB, 23 dB re 20 μPa at 8000, 11200, 16000 Hz respectively. The acoustic stimuli were presented at a mean intensity level of 40 dB SL.

Thus at 8000, 11200, 16000 Hz the corresponding sound pressure levels were 41 dB, 49 dB, 63 dB re 20 μPa. As the bandwidth of an acoustic stimulus in increased, the energy level per cycle must be decreased to maintain a constant sound pressure level. With rectangular bands of noise this requires that the energy level per cycle be decreased 3 dB per doubling of the bandwidth.

The Control for Speaker Differences

Psychophysical investigations of auditory localization which employ different transducers at different loci require that the experimenter demonstrate that the observed level of detection was dependent on location in space and independent of any differences which could be expressed by the transducers. In the data presented here the possibility of this artifact was dismissed in the following manner: For all acoustical parameters at least one comparison speaker was positioned in a location at which its associated probability of detection was below threshold. Consequently a high level of detection at other comparison locations was not likely due to differences between speakers. At the stimulus bandwidths of 4000 Hz and 8000 Hz, centered at 8000 Hz a location in azimuth for a comparison speaker was mounted at zero azimuth directly under the standard speaker. The threshold for changes in the median plane is greater than the threshold for changes in azimuth; thus a low probability of detection associated with the lower speaker served as the same control.

At the 4000 Hz and 8000 Hz stimulus bandwidth centered at 8000 Hz an additional manipulation was executed. The comparison speakers at two loci with markedly different levels of detection were exchanged.

Thus this manipulation served to differentiate if the observed level of detection was dependent on differences between speakers or dependent on differences in location.

Results

The Method of Constant Stimuli

While the method of constant stimuli is a relatively inefficient procedure, it is regarded as the most accurate and one of the most generally applicable psychophysical methods (Guilford, 1954). In the procedure employed here one standard location in space, zero degrees azimuth, was specified and four comparison locations were arbitrarily selected such that they sampled the entire range of the observer's psychometric function. That is, the observed probabilities of detection typically ranged from less than .2 to greater than .9. These conditions were met for those cases in which detection increased monotonically with angle. As was stated previously, the measurements made by Harris (1972), Harrison and Downey (1970), and Sivian and White (1933) demonstrate that with some acoustic stimuli binaural differences may not be monotonically related to spatial location. The shape of the psychometric function then serves as an index of the presence or absence of monotonicity. Thus one of the advantages of the method of constant stimuli is that monotonicity of the psychometric function is directly displayed, while in alternative procedures, such as the method of tracking, it is often only assumed and may or may not be demonstable by inspection of the raw data.

The Theory of Data

The observer was presented via some random order the values, or change in location, which composed the stimulus set. For each stimulus presentation the observer was required to judge if the stimulus location was different from the standard locus, zero degrees azimuth. For each acoustical parameter, the 50% detectability locus was computed from the proportions of the correct detections associated with each location. The values which constituted each proportion were typically collected over 8 or more daily sessions. These data are available in Appendix B.

With data obtained by the method of constant stimuli, the anaysis of choice is probit. A probit is the entity produced by transforming the proportions of correct detections at each comparison location to Z-scores and adding the constant 5 (Finney, 1952). These transformed data are then fit to a normal distribution following the principle of maximum likelihood. In the derivation of the solution, the probabilities of detection are weighted in a similar manner as employed in the Muller-Urban least squares determination. That is, the Z value is more likely to be in error for small or large proportions than for proportions near 0.5. Thus the Z values are weighted so that the solution is not greatly affected by errors in Z (Guilford, 1954). The major advantage of probit analysis is that the 50% detectability locus is computed using all of the psychophysical data. A second feature of probit analysis is that a chi-square estimate is computed for the goodness of fit of the observed data to a gaussian distribution.

The data presented here were subjected to a probit analysis.

Sixty-three psychophysical functions were entered in the analysis. Of these 63 functions, in only 13 cases was the null hypothesis not rejected, indicating that these data did not satisfy a normal distribution. That is, in 75% of the cases $\chi^2 > 7.8$; at $p < .05$, 3 degrees of freedom. Thus any analysis that assumes that the data conform to normality is subject to this objection.

An alternative procedure for the estimation of the 50% detectability locus is linear interpolation. As a procedure its only assumption is that the distribution underlying the data is symmetical. Given any symmetrical distribution, the values near the midpoint of the cumulative representation of the distribution lie on a linear segment of the curve. Linear interpolation has the advantage that it is more conservative in being free of assumptions regarding the nature of the distribution, but it is statistically less powerful by not taking advantage of all the data in the psychometric function.

The data reported here were analyzed by both procedures. The 50% detectability point for each psychophysical function was estimated by probit analysis and by linear interpolation.

Acoustical Stimuli Geometrically Centered at 8000 Hz

Figure 10 presents the psychometric functions for the three monkeys for the 8000 Hz pure tone. The ordinate is percent correct detection, the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point. In all three observers the proportion of the trials detected increases monotonically with azimuth. As may be seen in this figure the location of the comparison speakers bracketed the observer's threshold. The estimations of the 50%

Figure 10

The Probability of Detection as a Function of Azimuth for the 8000 Hz Pure Tone. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

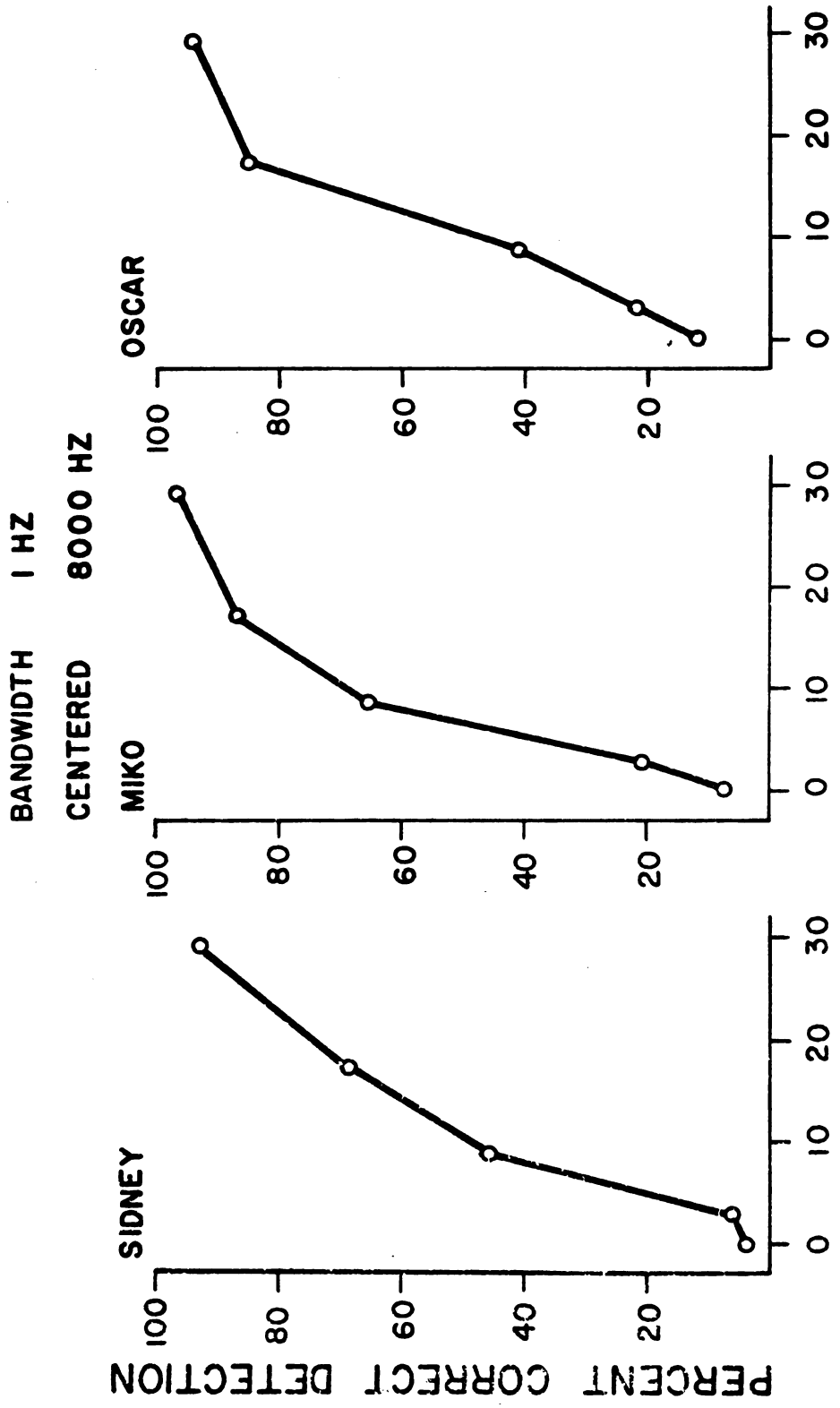

BANDWIDTH 1 HZ
CENTERED 8000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 10

TABLE 3

Threshold Angles for Bandwidths Centered at 8000 Hz

	Bandwidth (Hz)						
	1	250	500	1000	2000	4000	8000
Sidney							
Linear Interpolation	13.0	14.2	12.5	10.0	9.4	7.0	6.1
Probit	13.2	14.0	11.8	11.7	10.2	7.1	6.3
Chi-square[a]	126.6*	112.9*	361.1*	643.1*	311.0*	0.7	1.9
Miko							
Linear Interpolation	6.6	10.9	8.9	7.7	7.0	4.0	3.0
Probit	8.3	11.9	9.8	7.7	7.4	3.8	3.1
Chi-square[a]	135.1*	40.5*	26.8*	38.3*	250.4*	0.8	0.7
Oscar							
Linear Interpolation	10.4	10.5	10.6	8.7	7.2	3.4	2.9
Probit	10.5	11.5	10.3	8.5	7.4	3.2	3.1
Chi-square[a]	48.2*	18.4*	7.4	8.3*	2890.5*	0.5	3864317.5**

[a] Chi-square associated with departure from normality

* $p < .05$, df=3

** $p < .05$, df=2

detectability locus as provided by probit analysis as well as by linear interpolation are presented in Table 3. These three psychophysical functions are very similar, yet the differences between subjects observed at 8000 Hz are greater than those observed for any of the bands of noise centered at 8000 Hz.

The psychophysical functions for the narrowest band of noise, 250 Hz, may be seen in Figure 11. The functions for 500, 1000, 2000, 4000, and 8000 Hz noise bands are presented in Figures 12, 13, 14, 15, and 16 respectively. Careful inspection of these functions reveals two characteristics. First, the functions are highly similar among observers. Second, as the bandwidth is increased, the slope of the function becomes steeper and the locus of threshold decreases. The effect of increasing the bandwidth of the stimulus is well indexed by the change in the proportion of the trials detected at the 9° azimuth. At the 250 Hz bandwidth these proportions were .35, .40, and .42 for Sidney, Miko, and Oscar respectively. At the 8000 Hz bandwidth the corresponding values were .76, .95, and .99. Consequently at 9°, the probability of detection dramatically increased from well below to well above threshold when the bandwidth of the stimulus was increased from 250 to 8000 Hz.

As may be seen in Figures 15 and 16, when the two widest bands of noise were employed, threshold had decreased sufficiently that the detection of the comparison speaker adjacent to the standard (i.e. 3°) was approaching 50%. This may be observed in the psychometric functions for two of the three subjects, Miko and Oscar, at the 4000 and 8000 Hz stimulus bandwidths. At these two bandwidths one comparison speaker was mounted at the zero azimuth location, directly under

Figure 11

The Probability of Detection as a Function of Azimuth for the 250 Hz Stimulus Bandwidth Centered at 8000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

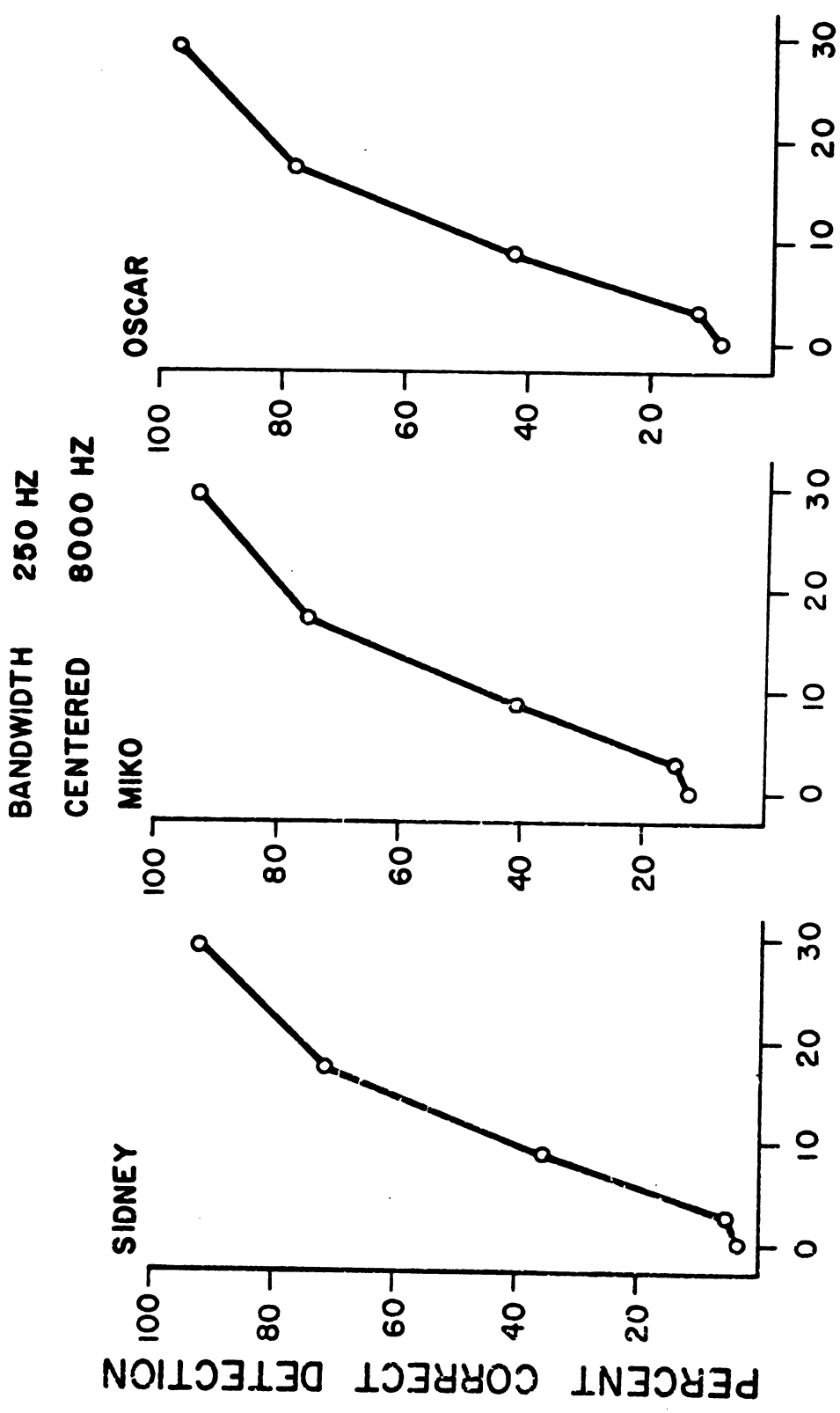

BANDWIDTH 250 HZ
CENTERED 8000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 11

Figure 12

The Probability of Detection as a Function of Azimuth for the 500 Hz Stimulus Bandwidth Centered at 8000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

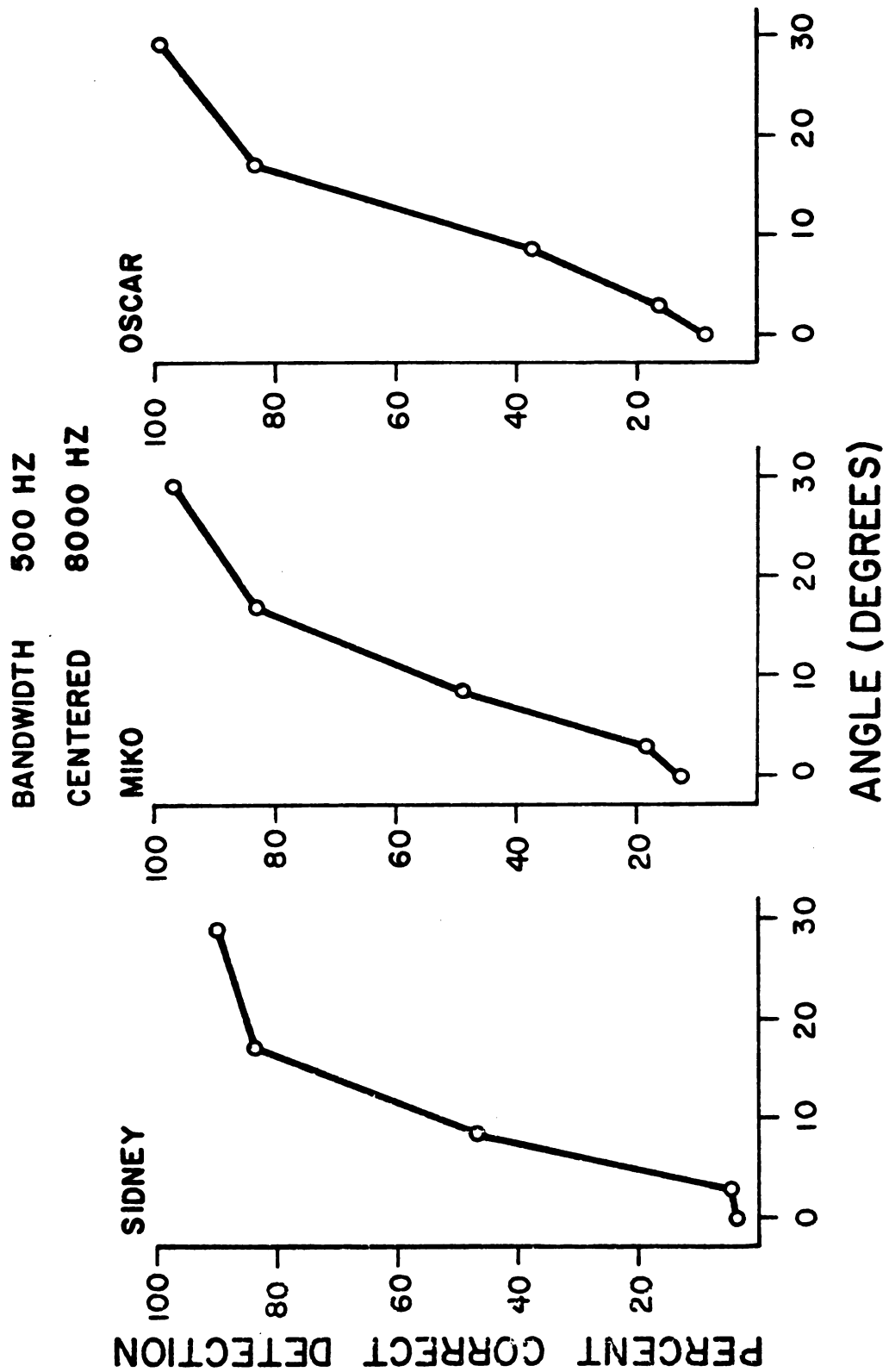

BANDWIDTH 500 HZ
CENTERED 8000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
100
80
60
40
20
0
10
20
30
ANGLE (DEGREES)

FIGURE 12

Figure 13

The Probability of Detection as a Function of Azimuth for the 1000 Hz Stimulus Bandwidth Centered at 8000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth.

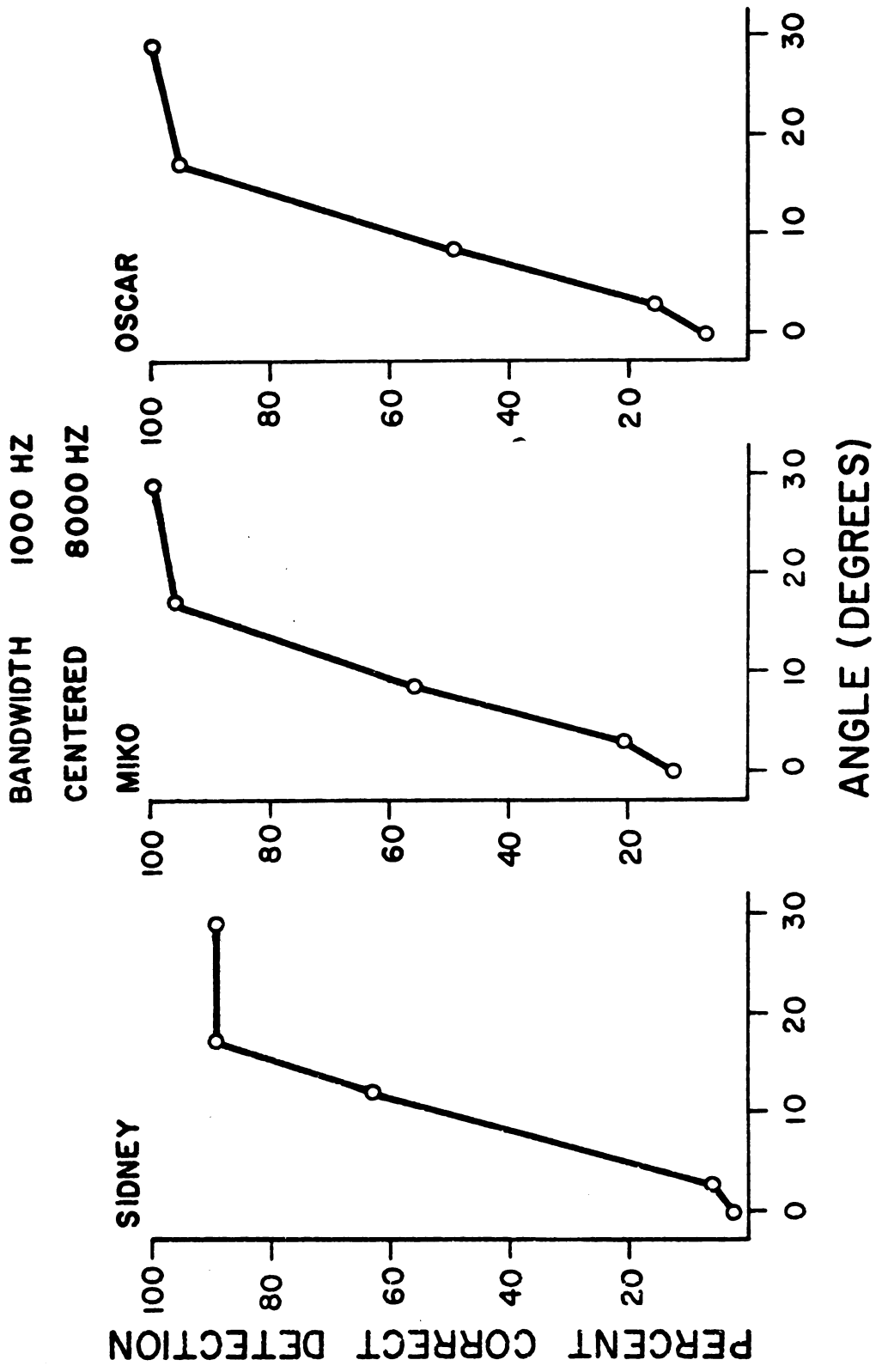

BANDWIDTH 1000 HZ
CENTERED 8000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 13

Figure 14

The Probability of Detection as a Function of Azimuth for the 2000 Hz Stimulus Bandwidth Centered at 8000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth.

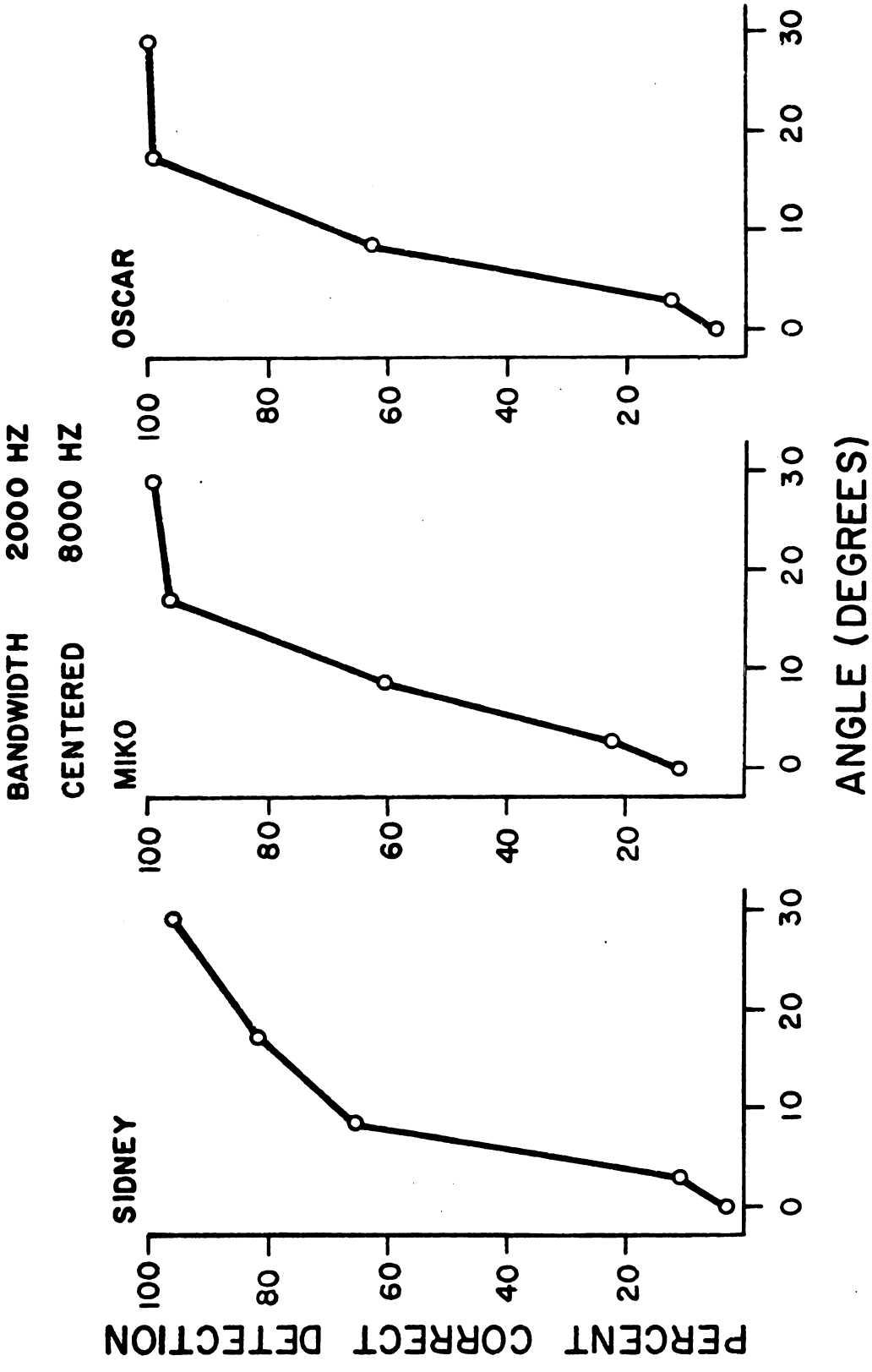

BANDWIDTH 2000 HZ
CENTERED 8000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 14

Figure 15

The Probability of Detection as a Function of Azimuth for the 4000 Hz Stimulus Bandwidth Centered at 8000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth. The probability of detection of the lower speaker is displayed over L. See text for details.

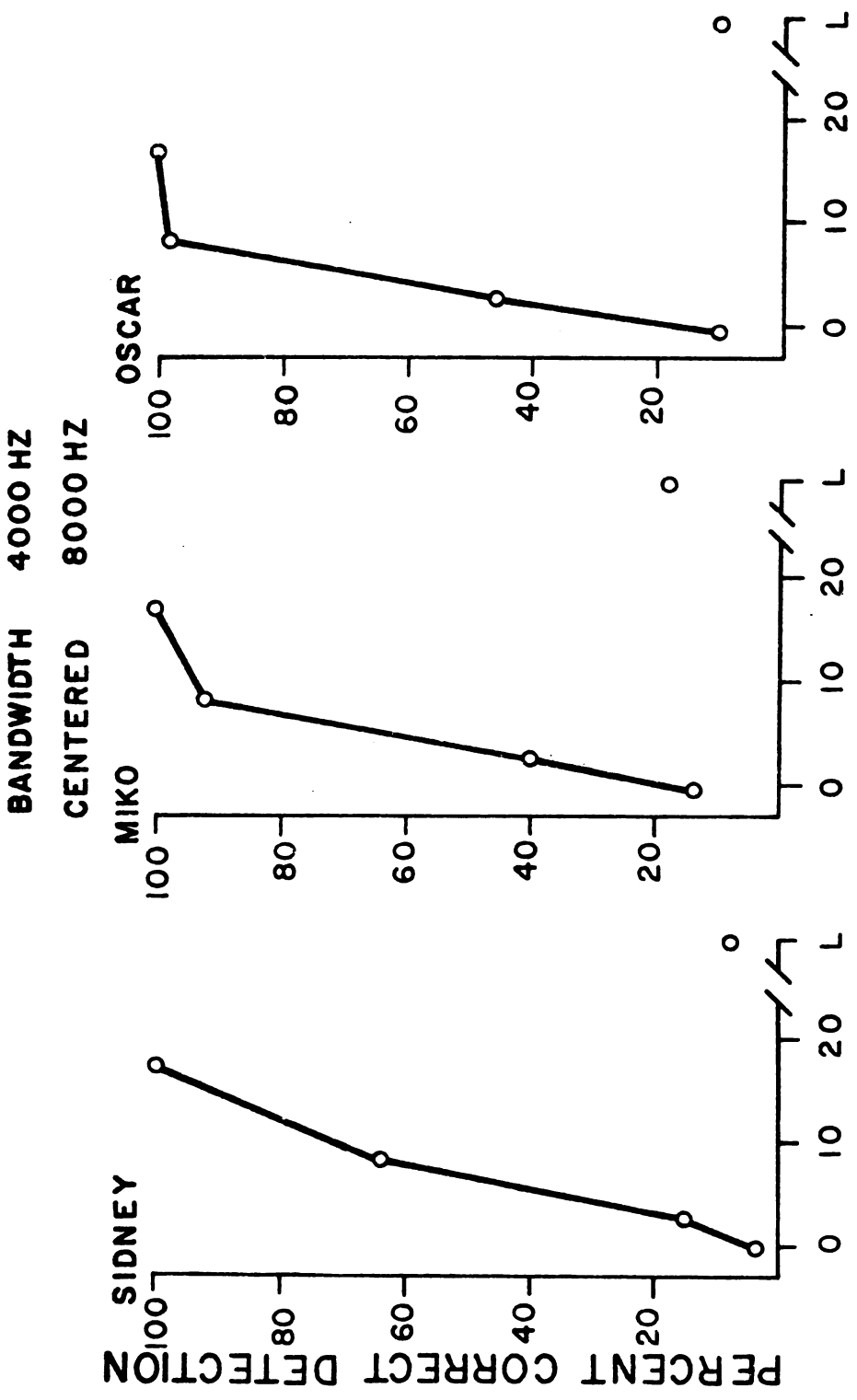

BANDWIDTH 4000 HZ
CENTERED 8000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
100
80
60
40
20
0
0
10
20
L
ANGLE (DEGREES)

FIGURE 15

Figure 16

The Probability of Detection as a Function of Azimuth for the 8000 Hz Stimulus Bandwidth Centered at 8000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth. The probability of detection of the lower speaker is displayed over L. See text for details.

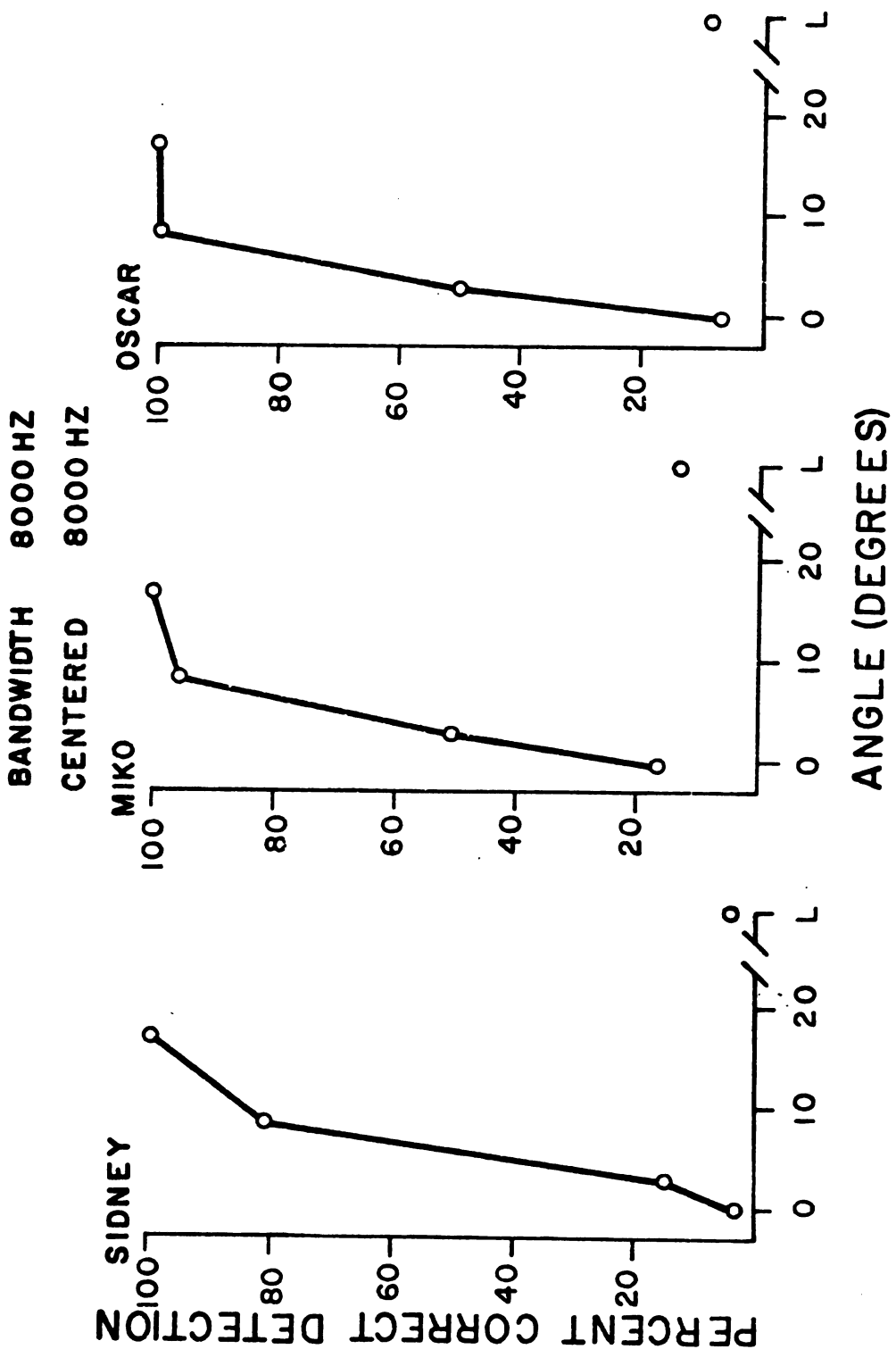

BANDWIDTH 8000 HZ
CENTERED 8000 HZ
PERCENT CORRECT DETECTION
SIDNEY
MIKO
OSCAR
100
80
60
40
20
0
10
20
L
ANGLE (DEGREES)

FIGURE 16

the standard speaker. The probability of detection for the lower speaker is denoted by L on the abscissa for Figures 15 and 16; and as may be seen in these figures the proportion of trials detected at this location approximated the observer's random release rate. Once a speaker location (L) had been determined with a low associated probability of detection, the transducers associated with this point and the 9° azimuth point were arbitrarily exchanged. The consequences of this manipulation are presented in Table 4. As may be seen in this table the proportions of the trials detected were determined by the locations of the transducers and not by which transducers occupied that location.

Figure 17 provides a summary of the psychophysical functions presented in Figures 10-16. The panel A shows the 50% detectability locus according to the linear interpolation; panel B presents the corresponding analysis given by probit analysis. As the width of the stimulus band increases the threshold for detectability decreases. It may also be seen from this figure that the threshold varies more widely between observers for the 8000 Hz pure tone than for any of the noise bands and that the threshold value for the pure tone is not directly predictable from the bandwidth data. As may be seen by the comparison of panel A and B of Figure 17 or from Table 3, differences in the estimation of threshold between procedures are essentially trivial. The inspection of Figure 17 suggests that the log of stimulus bandwidth is linearly related to the threshold for the detection of changes in azimuth. That is, threshold is related to bandwidth according to the expression in Table 5.

TABLE 4

Test for Speaker Differences: Estimated Proportions for Two Bandwidths

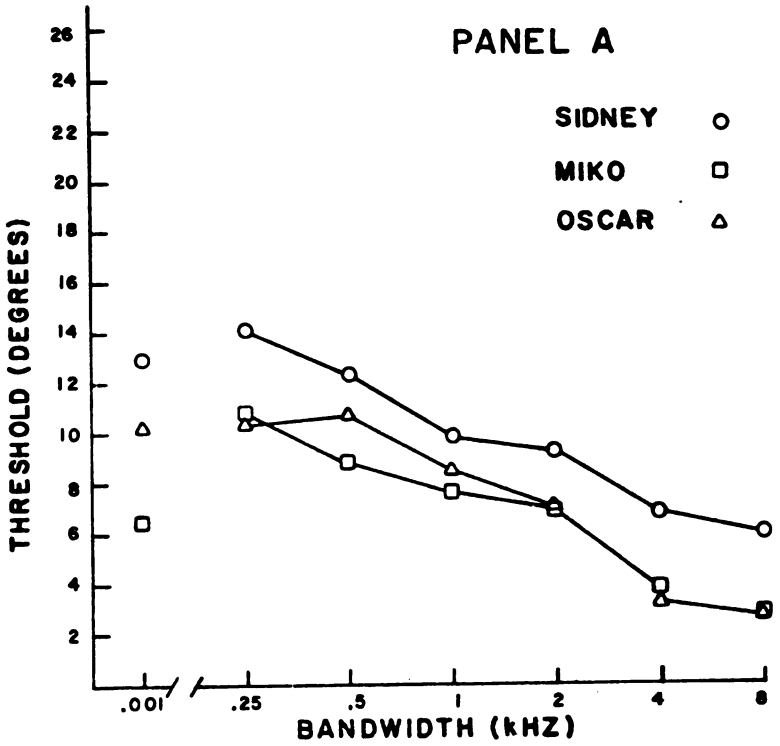
Subject and Bandwidth[a]	Speaker	Speaker Location	
		L	8.6°
Sidney 4000 Hz	A	10/177 or .056	121/193 or .627
	B	25/295 or .085	84/102 or .824
Miko 4000 Hz	A	28/198 or .171	65/81 or .802
	B	17/74 or .229	190/196 or .969
Oscar 4000 Hz	A	31/299 or .104	72/72 or 1.00
	B	3/54 or .056	235/243 or .967
Sidney 8000 Hz	A	5/222 or .023	152/189 or .804
	B	14/264 or .053	93/96 or .969
Miko 8000 Hz	A	14/186 or .075	137/150 or .913
	B	30/155 or .194	195/198 or .985
Oscar 8000 Hz	A	22/308 or .071	64/64 or 1.00
	B	10/58 or .172	216/218 or .991

[a] Bandwidths are centered on 8000 Hz.

Figure 17

Threshold as a Function of Bandwidth for Stimuli Centered at 8000 Hz. Panel A presents the 50% detectability locus as determined by linear interpolation; panel B presents the same locus as determined by probit analysis.

CENTERED 8000 HZ



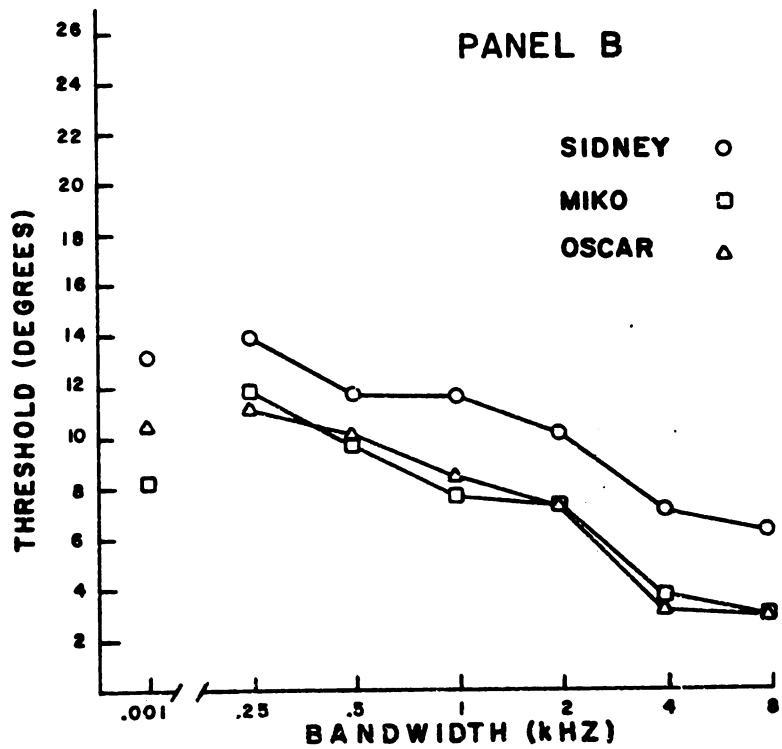


FIGURE 17

TABLE 5

The Regression of Threshold on Bandwidth Centered at 8000 Hz.

Observer	Probit Analysis	Linear Interpolation
Sidney	t=-5.1 log b + 26.4 (r=-.97)	t=-5.5 log b + 27.1 (r=-.99)
Miko	t=-5.9 log b + 25.9 (r=-.98)	t =- 5.2 log b + 23.3 (r=-.99)
Oscar	t=-6.0 log b + 26.1 (r=-.97)	t=-5.9 log b + 25.8 (r=-.96)

Note: t is threshold in degrees, b is bandwidth in Hz, r is the correlation coefficient.

Figure 18

The Probability of Detection as a Function of Azimuth for the 11200 Hz Pure Tone. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth.

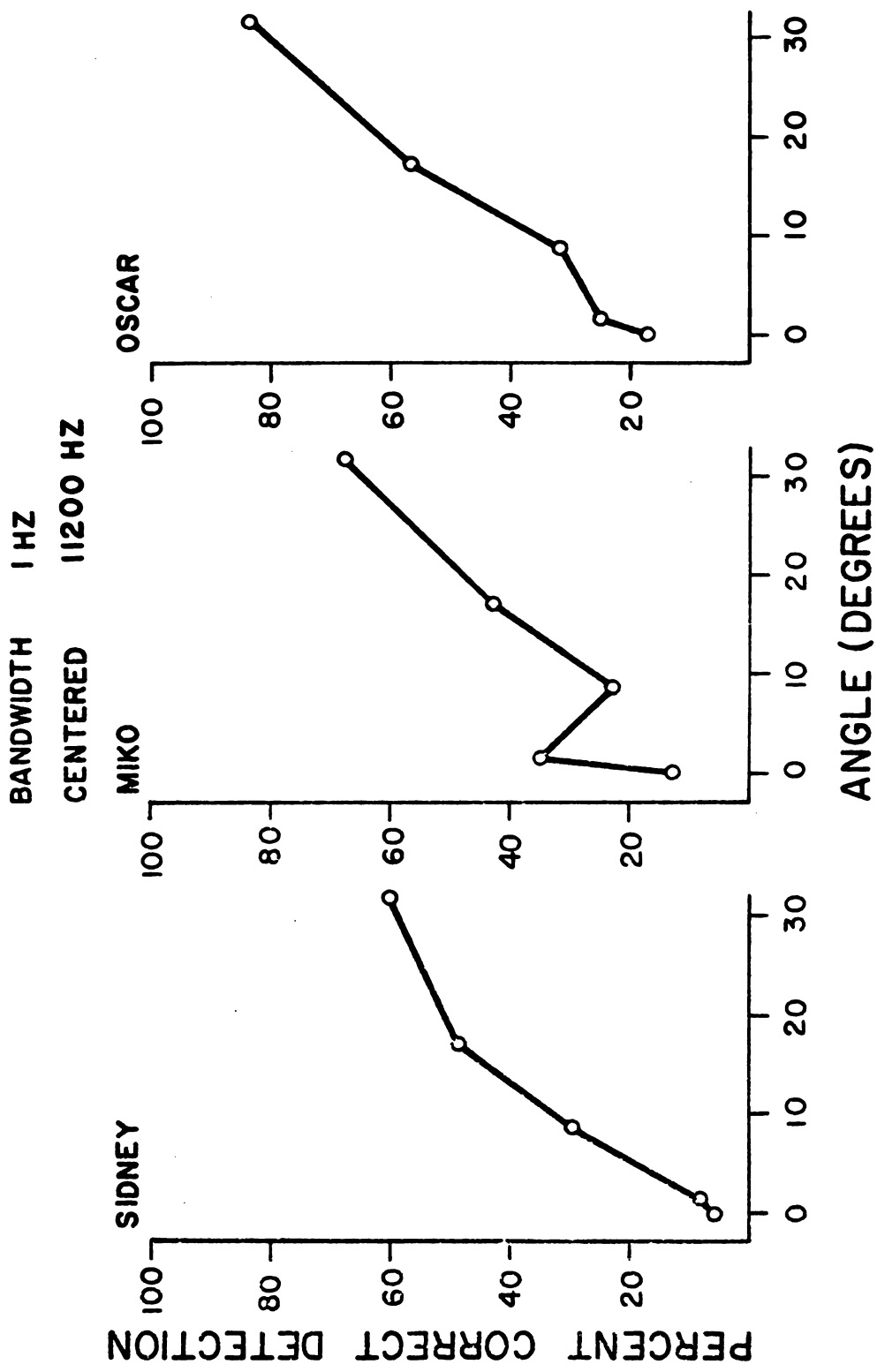

BANDWIDTH 1 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 18

Acoustical Stimuli Geometrically Centered at 11200 Hz

Figure 18 presents the monkeys' three psychophysical functions for the 11200 Hz pure tone. The proportion of trials detected at the largest angle, 30°, was less than .70 for Sidney and Miko and only .83 for Oscar. In all the previous psychometric functions the probability of detection was approaching 100% for this change in azimuth. Figures 19 and 20 present the corresponding functions for the 250 and 500 Hz band stimuli. Again, the figures reveal that the subjects had difficulty discriminating changes in azimuth of these stimuli. The irregularities in the shape of the psychophysical functions are reflected in the differences between the estimations of threshold given by probit analysis and by linear interpolation shown in Table 6. This difference is greatest for Miko at the 500 Hz bandwidth stimulus -- 13.0 by linear interpolation vs. 20.2 by probit analysis. These discrepant results are likely the result of the departure from monotonicity in Miko's psychometric function (Figure 20). Figures 21-24 present the psychophysical functions for stimulus bandwidths of 1000, 2000, 4000, 8000 Hz respectively. These functions are monotonic and relatively steep for each observer.

Figure 25 presents the summary functions relating stimulus bandwidth to threshold. Panel A of the figure presents the estimations of threshold determined by linear interpolation and panel B the thresholds determined by probit analysis. While the two methods of analysis yield different absolute values of threshold, the effect of stimulus bandwidth on localization is clear: threshold varies inversely with the bandwidth of the stimulus. The slope of the function relating

Figure 19

The Probability of Detection as a Function of Azimuth for the 250 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

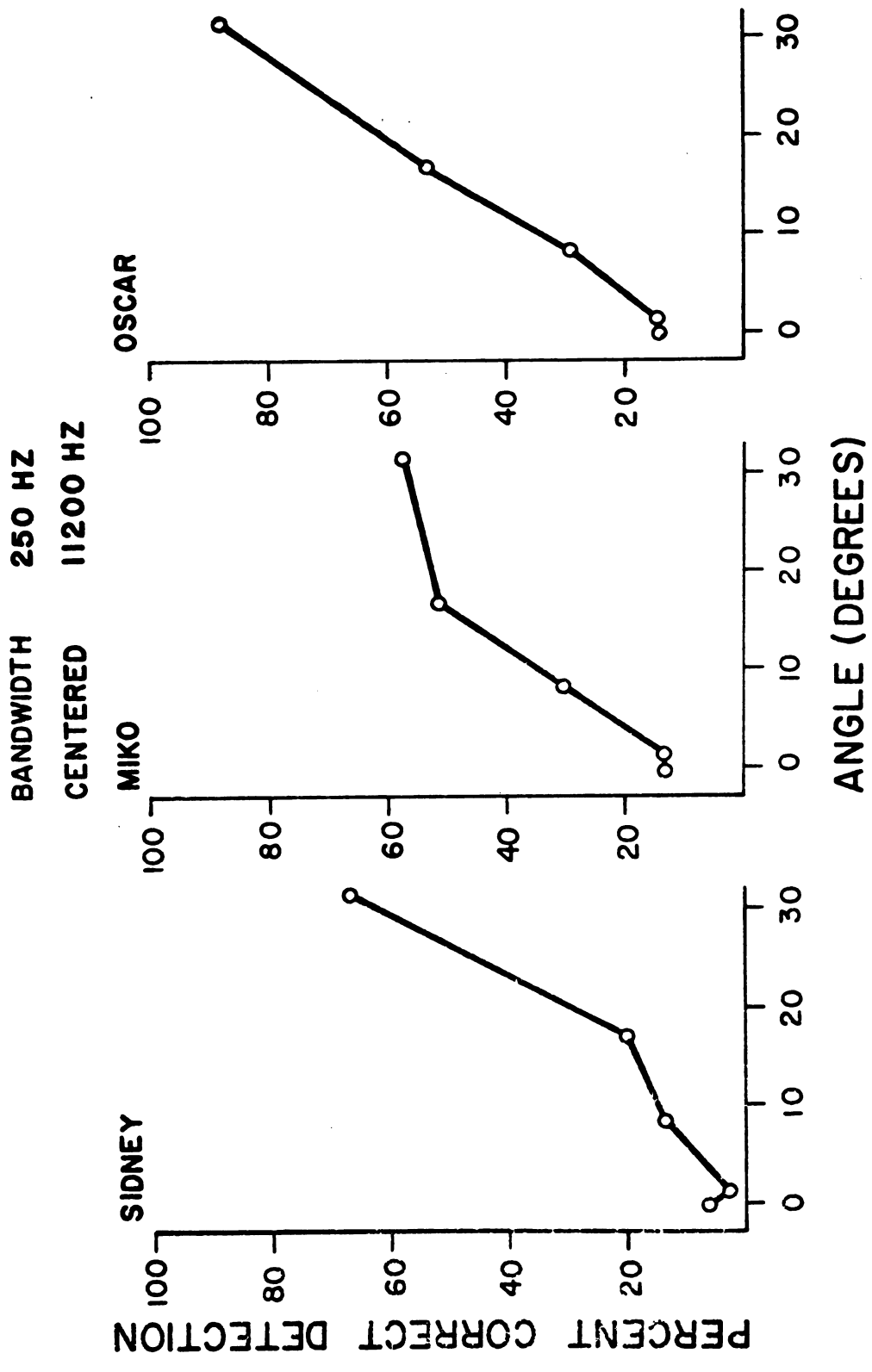

BANDWIDTH 250 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
100
80
60
40
20
0
10
20
30
ANGLE (DEGREES)

FIGURE 19

Figure 20

The Probability of Detection as a Function of Azimuth for the 500 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

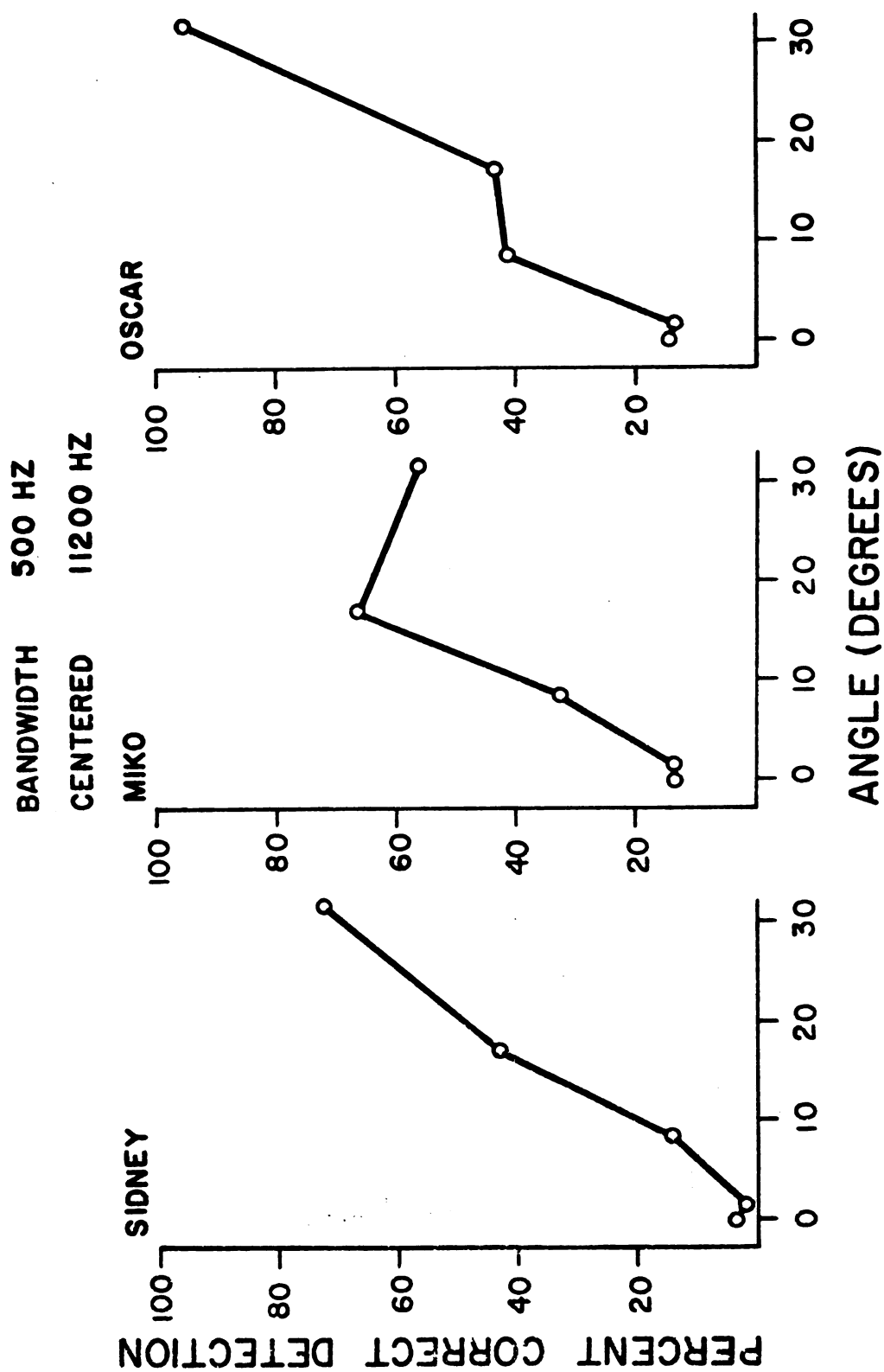

BANDWIDTH 500 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 20

TABLE 6

Threshold Angles for Bandwidths Centered at 11200 Hz

	Bandwidth (Hz)						
	1	250	500	1000	2000	4000	8000
Sidney							
Linear Interpolation	17.3	24.5	18.9	15.0	9.3	7.1	5.4
Probit	20.6	23.9	20.4	17.6	11.4	7.7	6.3
Chi-square[a]	88.7*	28.1*	25.7*	27.5*	123.5*	15.8*	XXXX[b]*
Miko							
Linear Interpolation	19.2	14.9	11.7	9.4	5.8	4.5	3.9
Probit	20.1	20.7	18.4	12.0	6.3	4.3	4.8
Chi-square[a]	67.2*	51.1*	146.3*	121.8*	9803.9*	7.7	1185416.8*
Oscar							
Linear Interpolation	13.5	14.4	17.3	15.7	5.8	4.2	3.7
Probit	13.9	14.2	13.0	.415	8.0	3.7	3.4
Chi-square[a]	3.0	3.2	64.5*	10.6*	155.2*	4.0	83463.6*

[a]Chi-square associated with departure from normality

[b]Value too large to be calculated with Probit program

*$p < .05$, df=3

Figure 21

The Probability of Detection as a Function of Azimuth for the 1000 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

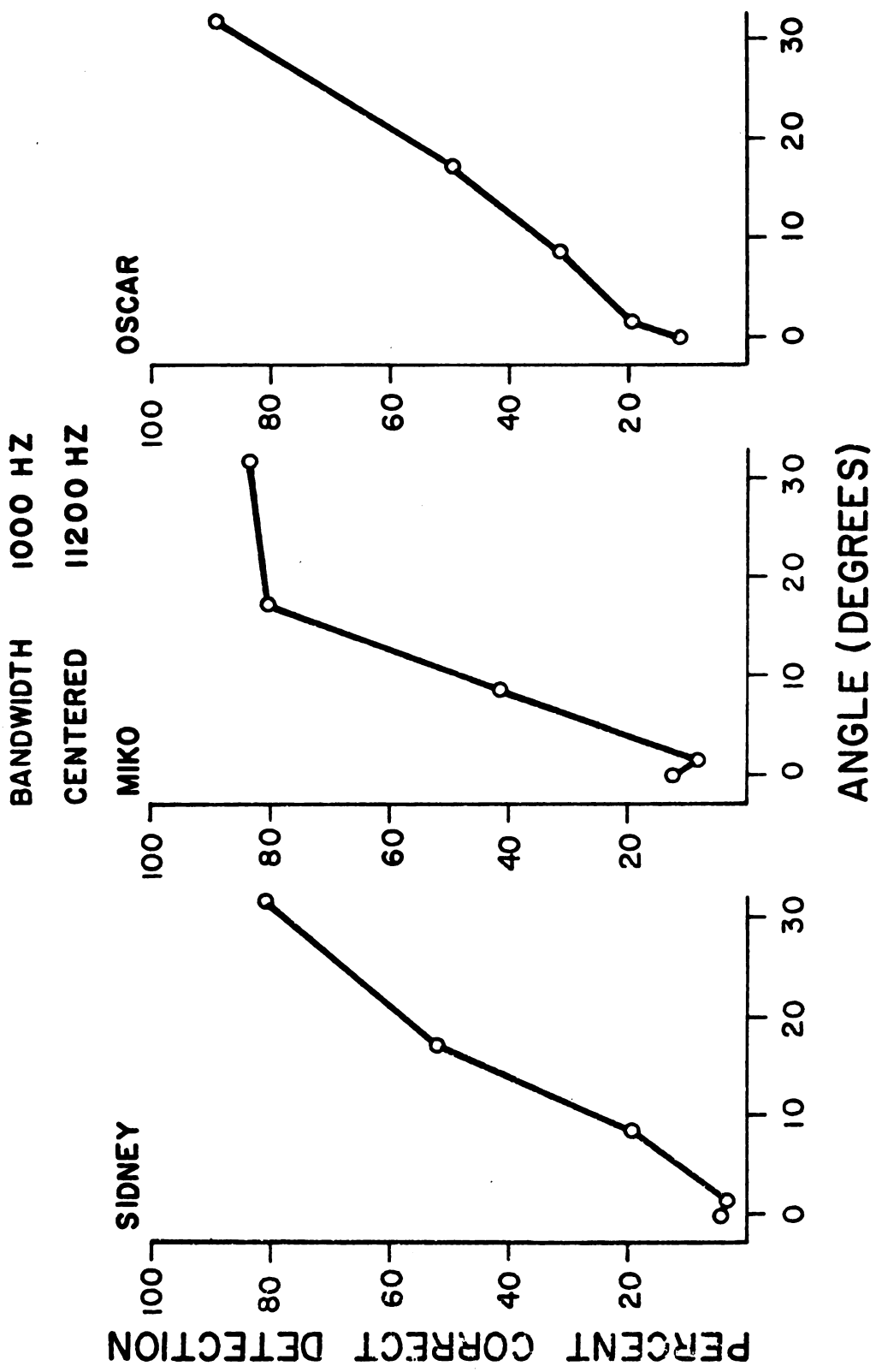

BANDWIDTH 1000 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 21

Figure 22

The Probability of Detection as a Function of Azimuth for the 2000 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

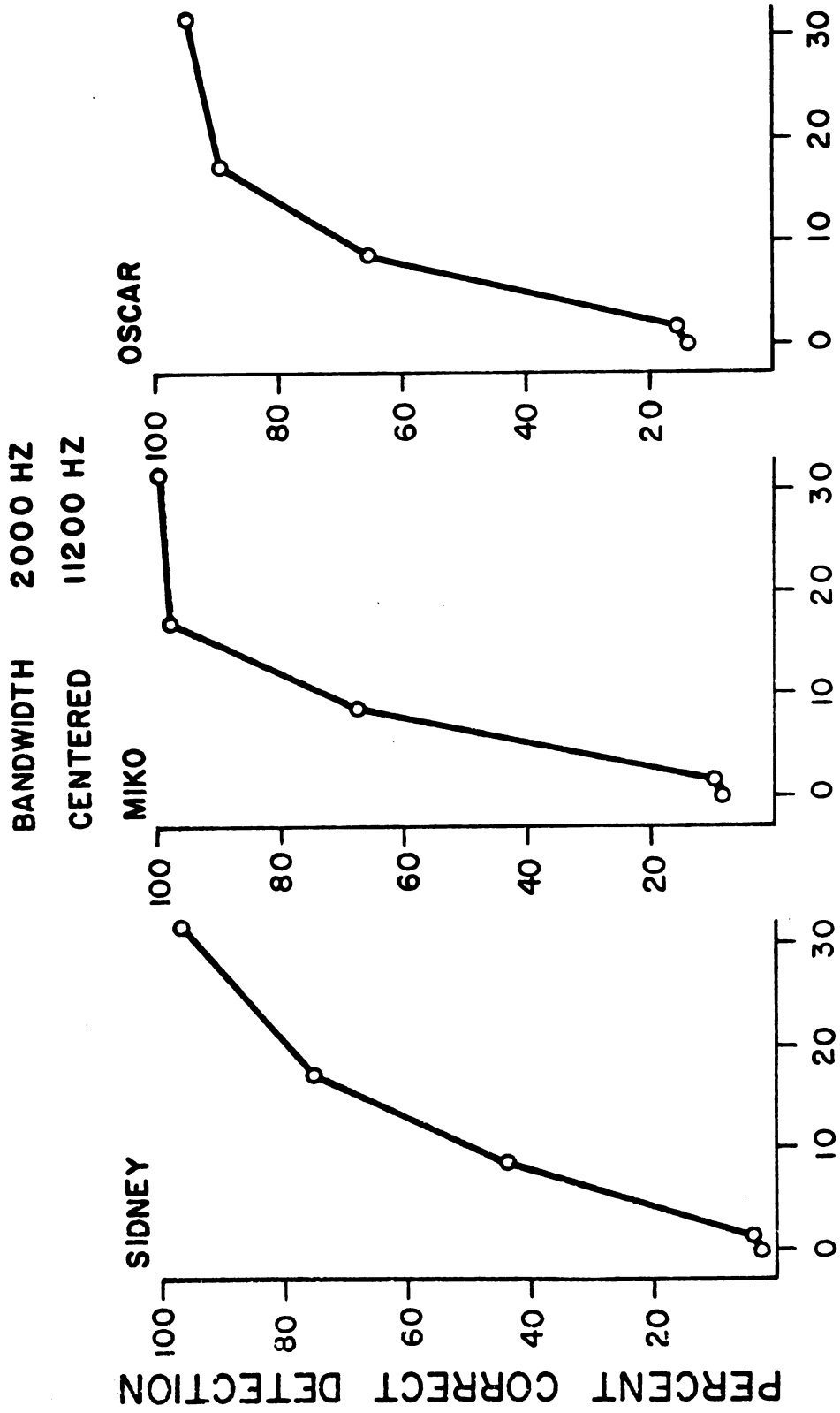

BANDWIDTH 2000 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 22

Figure 23

The Probability of Detection as a Function of Azimuth for the 4000 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

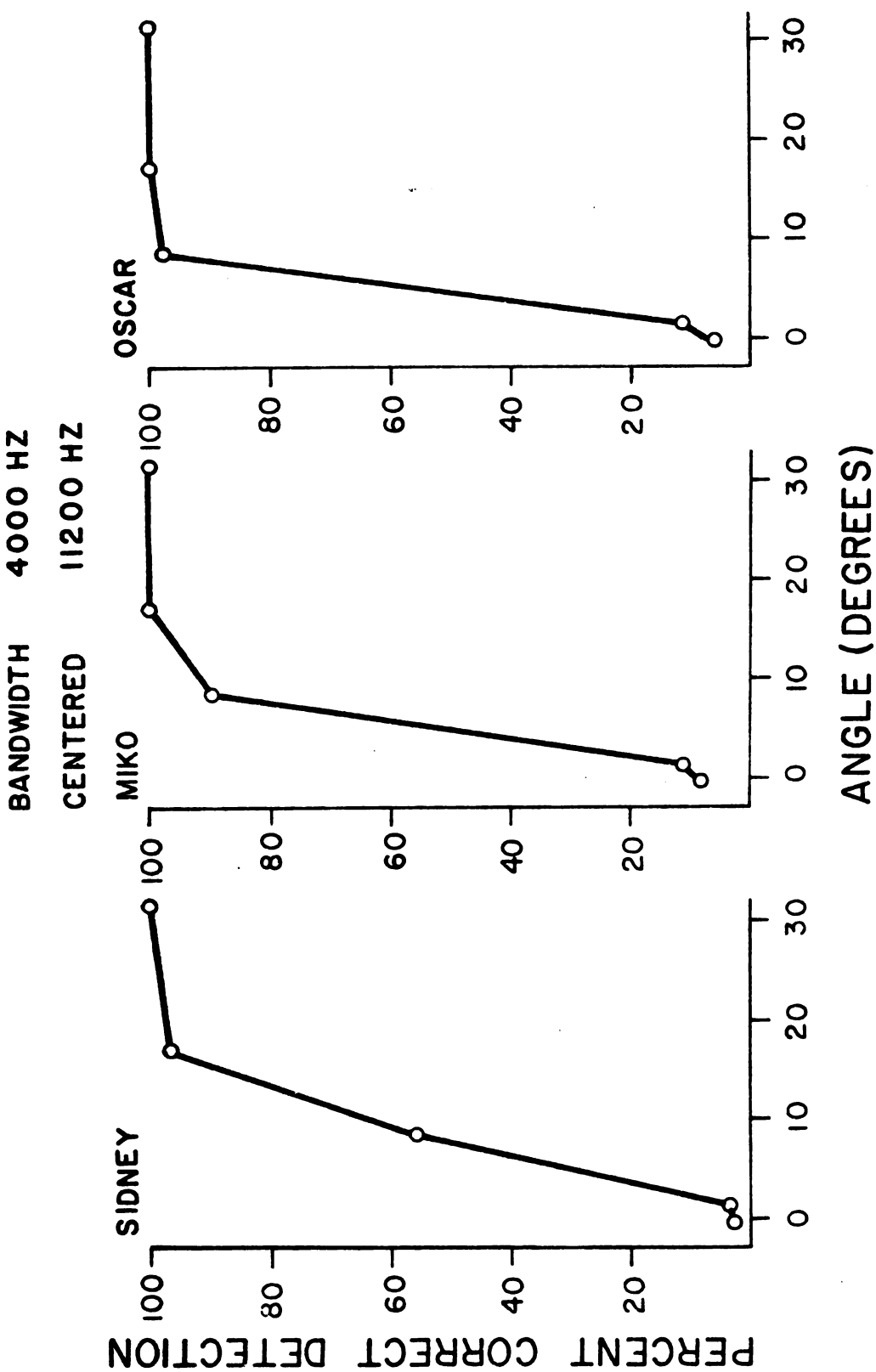

BANDWIDTH 4000 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 23

Figure 24

The Probability of Detection as a Function of Azimuth for the 8000 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

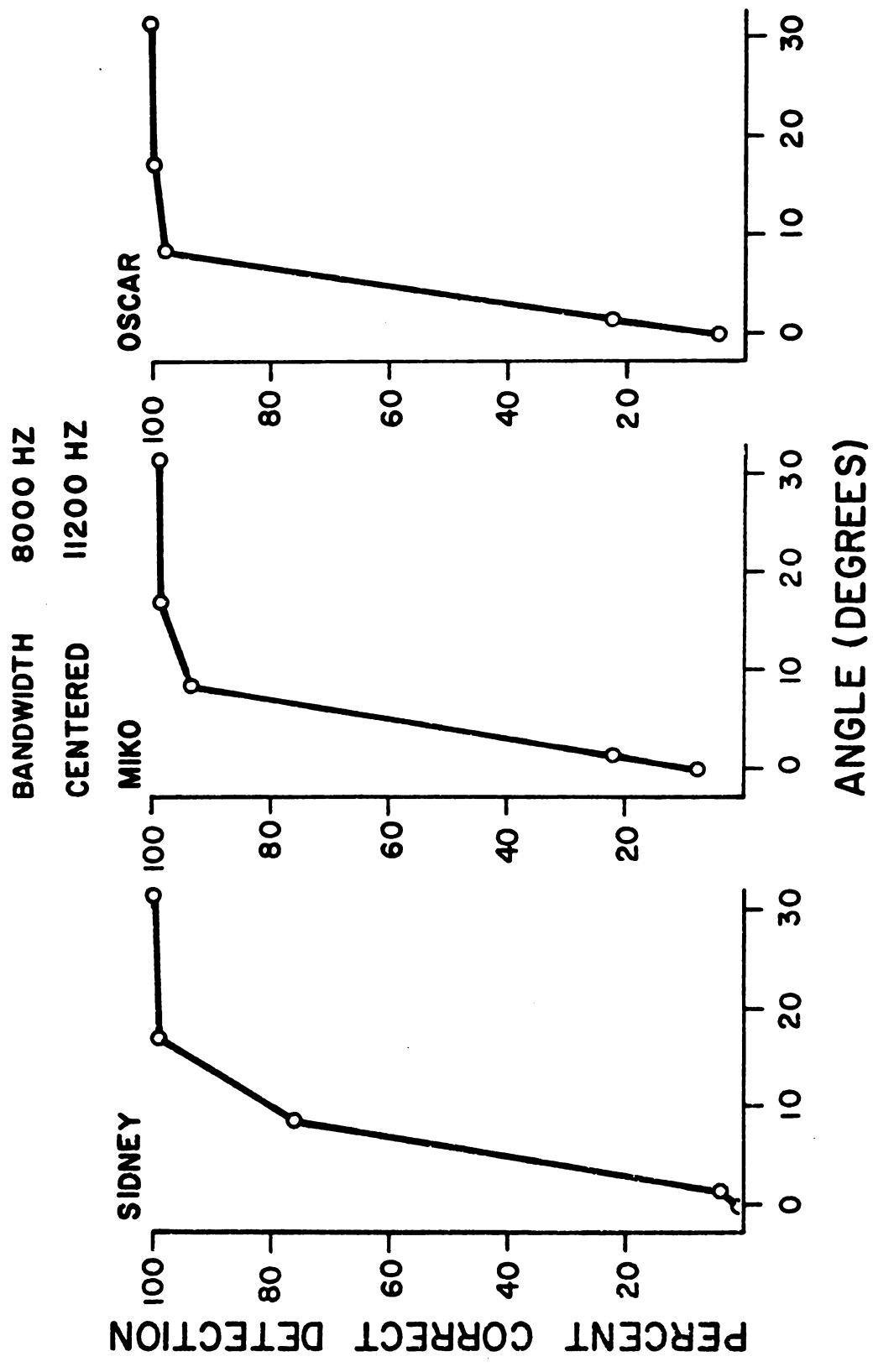
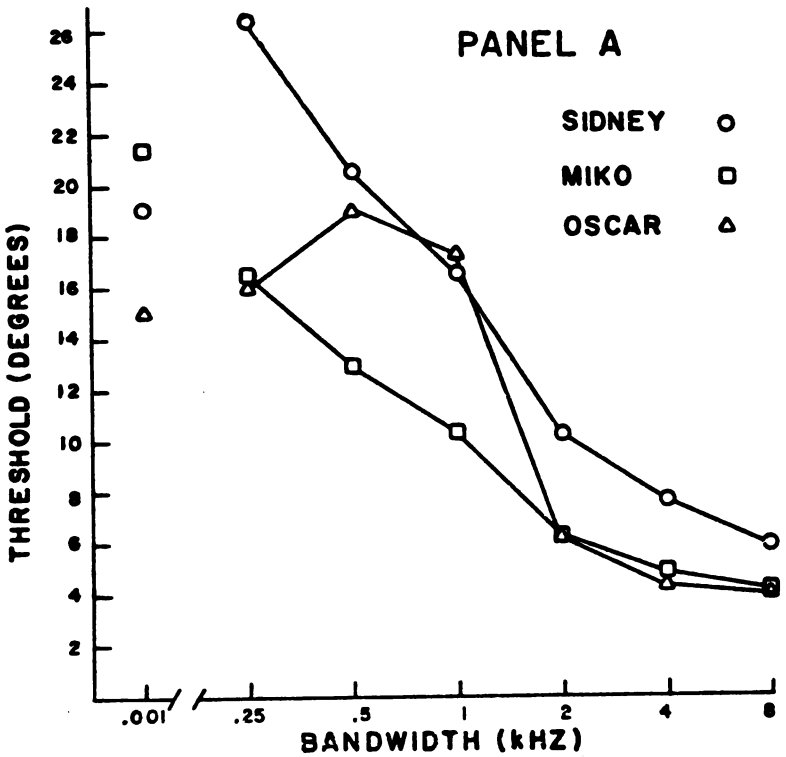

BANDWIDTH 8000 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
0
10
20
30
20
40
60
80
100

FIGURE 24

Figure 25

Threshold as a Function of Bandwidth for Stimuli Centered at 11200 Hz. Panel A presents the 50% detectability locus as determined by linear interpolation; panel B presents the same locus as determined by probit analysis.

CENTERED 11200 HZ



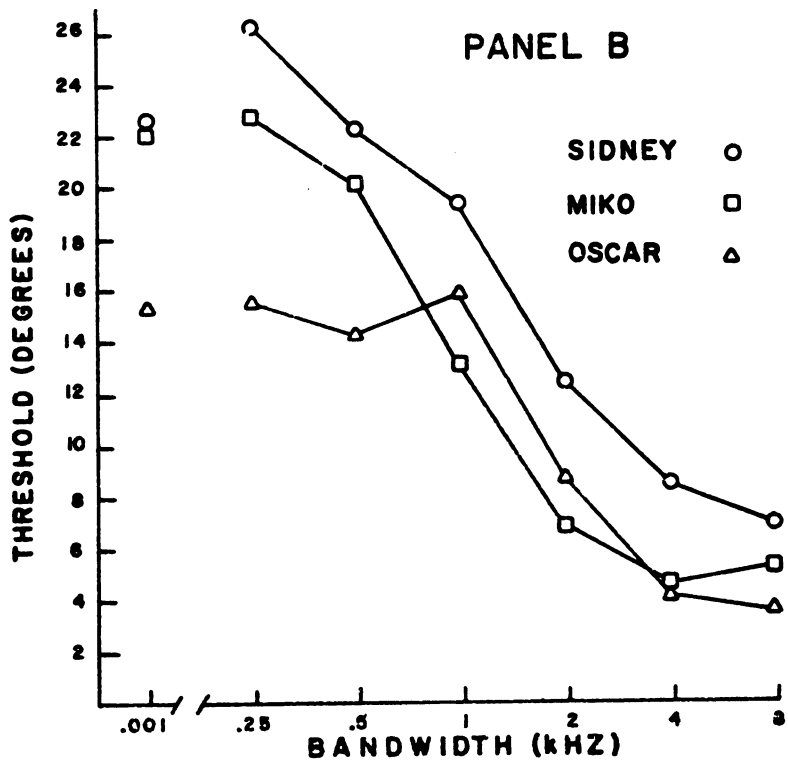


FIGURE 25

TABLE 7

The Regression of Threshold on Bandwidth Centered at 11200 Hz

Observer	Probit Analysis	Linear Interpolation
Sidney	t=-12.6 log b + 54.1 (r=-.99)	t=-13.8 log b + 54.2 (r=-.98)
Miko	t=-12.1 log b + 49.2 (r=-.95)	t=- 7.6 log b + 32.3 (r=-.98)
Oscar	t=- 8.4 log b + 35.9 (r=-.92)	t=- 9.7 log b + 40.9 (r=-.88)

Note: t is threshold in degrees, b is bandwidth in Hz, r is the correlation coefficient.

bandwidth to threshold is steeper for stimuli centered at 11200 Hz than for stimuli centered at 8000 Hz, a half octave lower in frequency. This is empirically expressed in the linear regressions presented in Table 7. It should be clear from Figures 17 and 25 that the major difference between stimuli centered at 8000 and 11200 Hz was the degradation in detectability of the narrow band stimuli at 11200 Hz. That is, the minimum change in azimuth required for the detection of the 8000 Hz bandwidth was about equal for either center frequency, while the minimum change in azimuth required for the detection of the 250 Hz bandwidth was elevated by a factor approaching 2 for the 11200 Hz center frequency with respect to the 8000 Hz center frequency.

Acoustical Stimuli Geometrically Centered at 16000 Hz

Figure 26 presents the psychometric functions for the three observers for the 16000 Hz pure tone. As may be seen in this figure the functions are quite different between observers. The proportion of the trials detected for the maximum change in azimuth, 30°, was .66, .91, and 172 respectively, for Sidney, Miko, and Oscar. The corresponding thresholds were 22.2°,9.6°, and 6.2° given by linear interpolation; 22.7°, 8.8°, and 11.9° given by probit analysis. These were the largest inter-subject differences encountered for any acoustical parameter.

The psychophysical functions for the two narrowest stimulus bandwidths -- 250 and 500 Hz -- are presented in Figures 27 and 28. The functions at these two bandwidths are striking in one characteristic; they are monotonic and more regular in shape than the corresponding functions centered at 11200 Hz, one half octave lower in frequency.

Figure 26

The Probability of Detection as a Function of Azimuth for the 16000 Hz Pure Tone. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

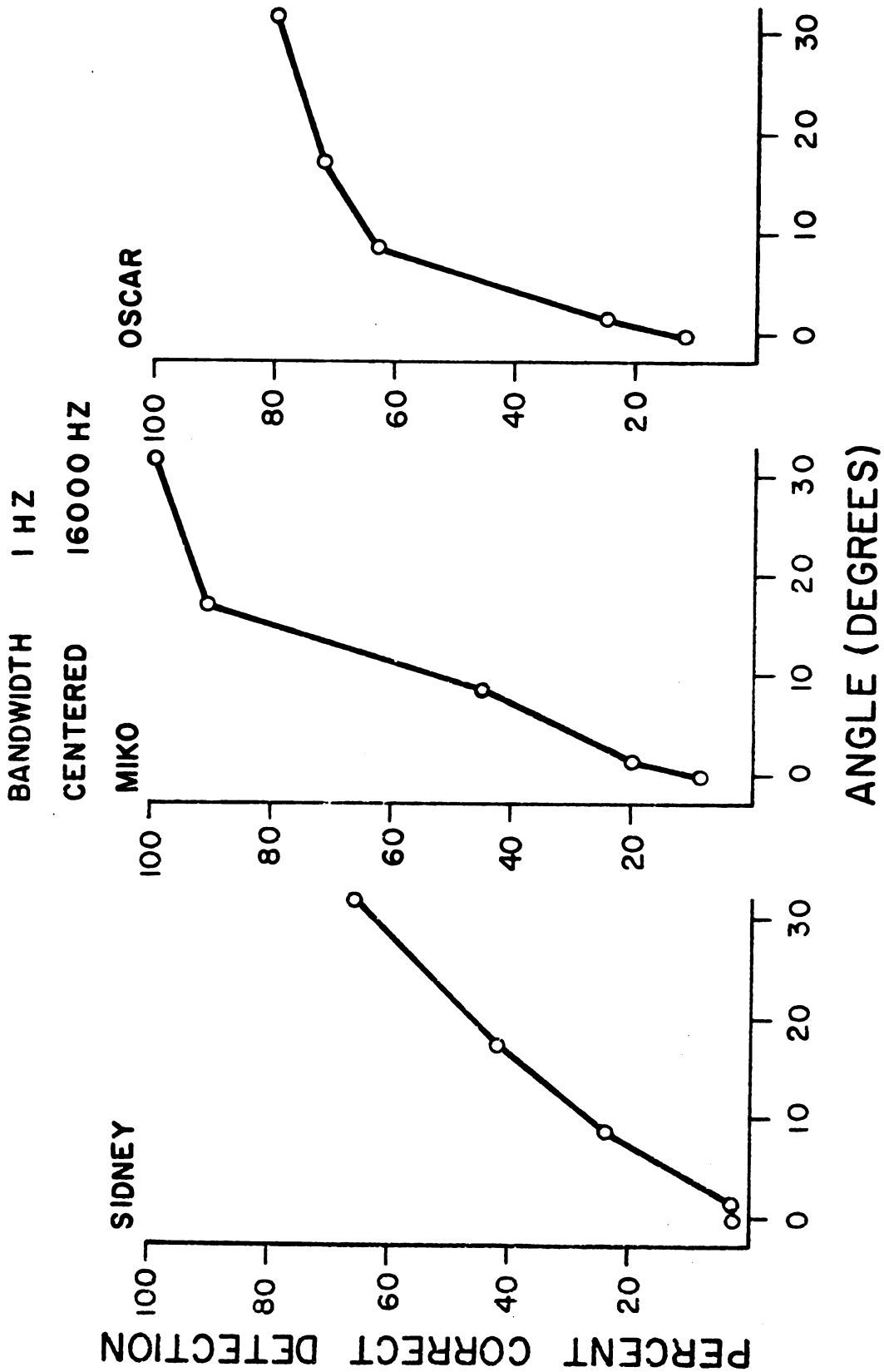

BANDWIDTH 1 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 26

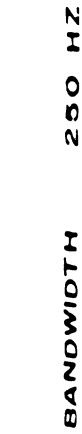


Figure 27

The Probability of Detection as a Function of Azimuth for the 250 Hz Stimulus Bandwidth Centered at 16000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

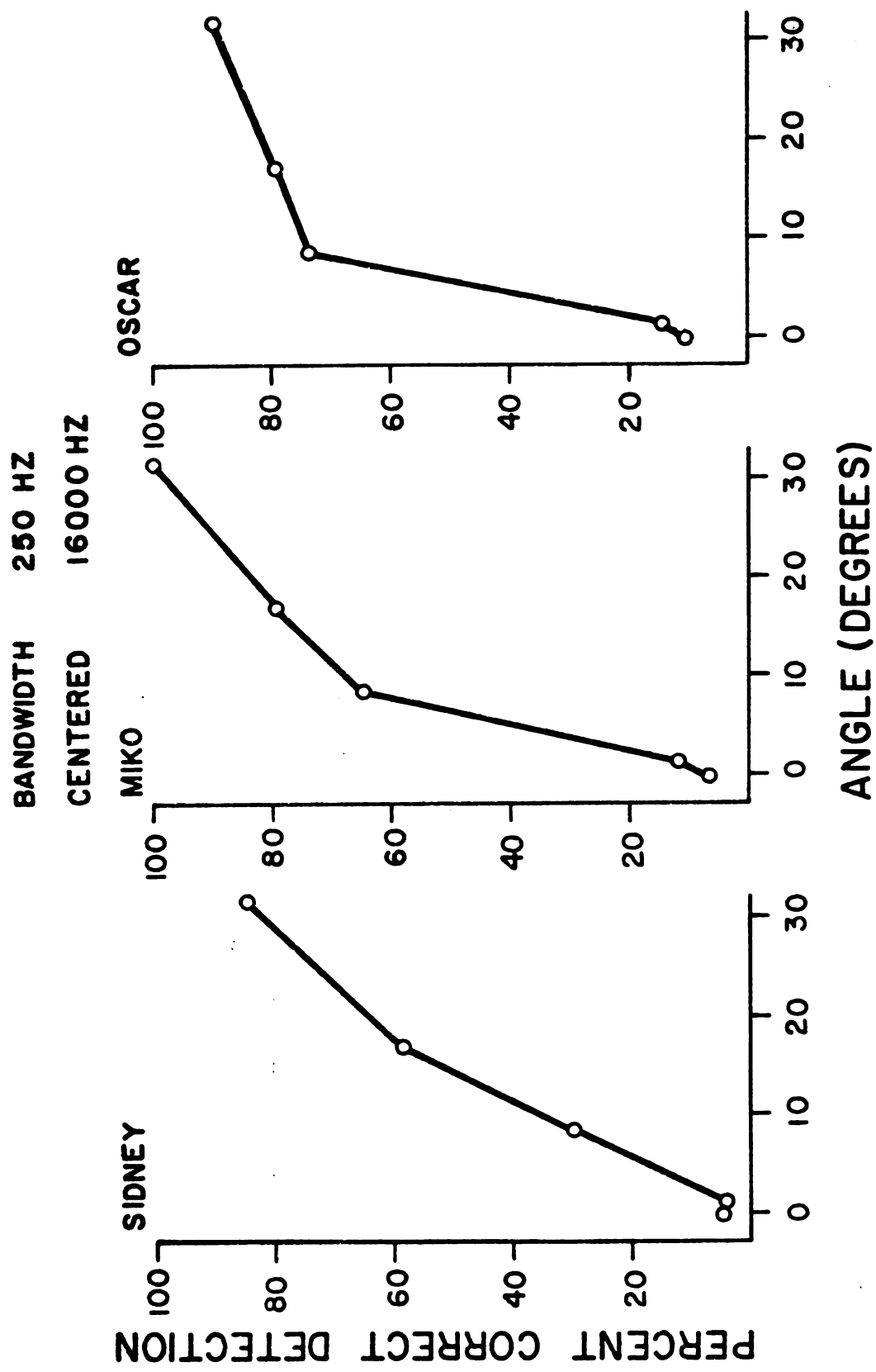

BANDWIDTH 250 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 27

Figure 28

The Probability of Detection as a Function of Azimuth for the 500 Hz Stimulus Bandwidth Centered at 16000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

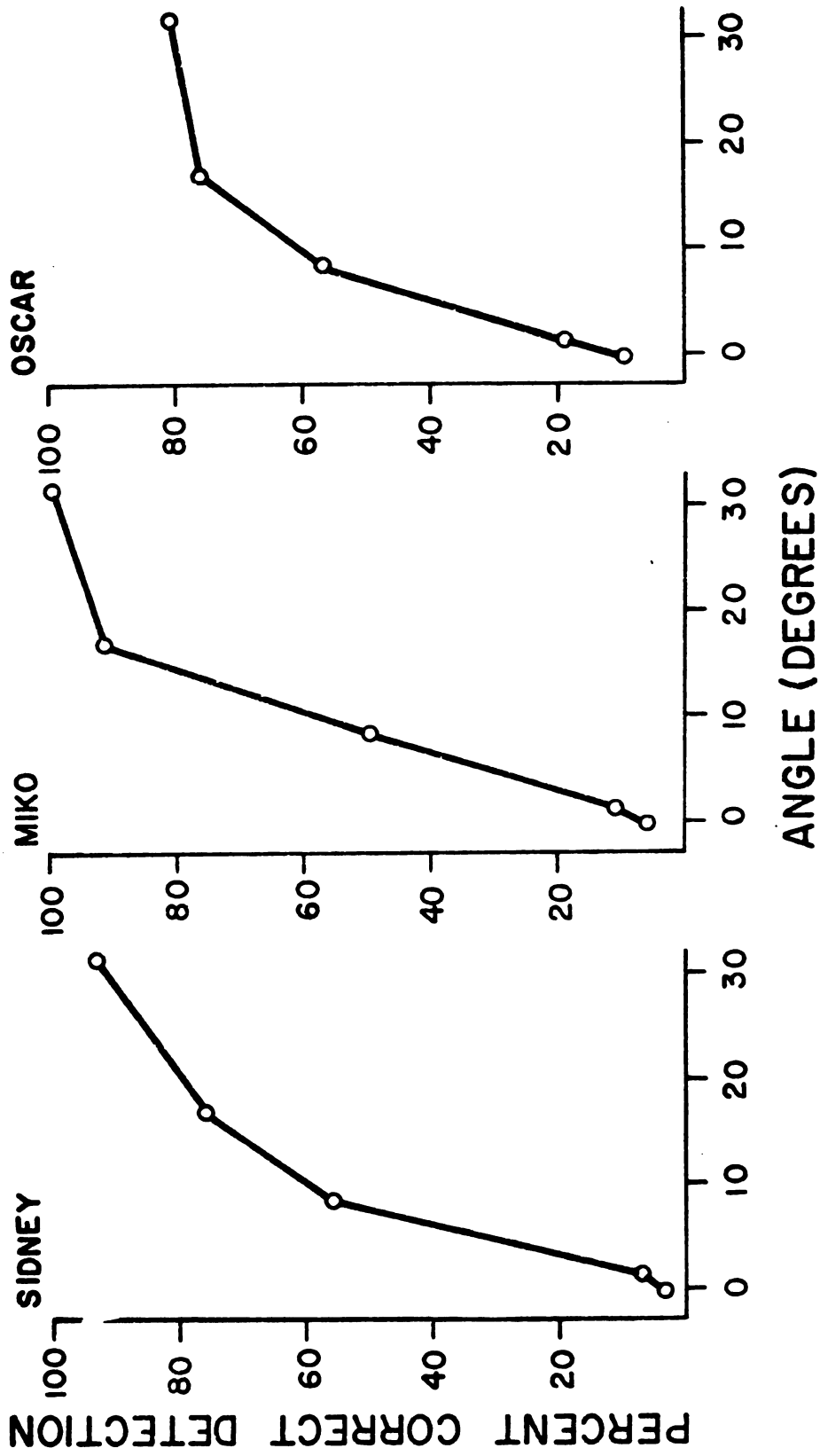

BANDWIDTH 500 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 28

Figure 29

The Probability of Detection as a Function of Azimuth for the 1000 Hz Stimulus Bandwidth Centered at 16000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

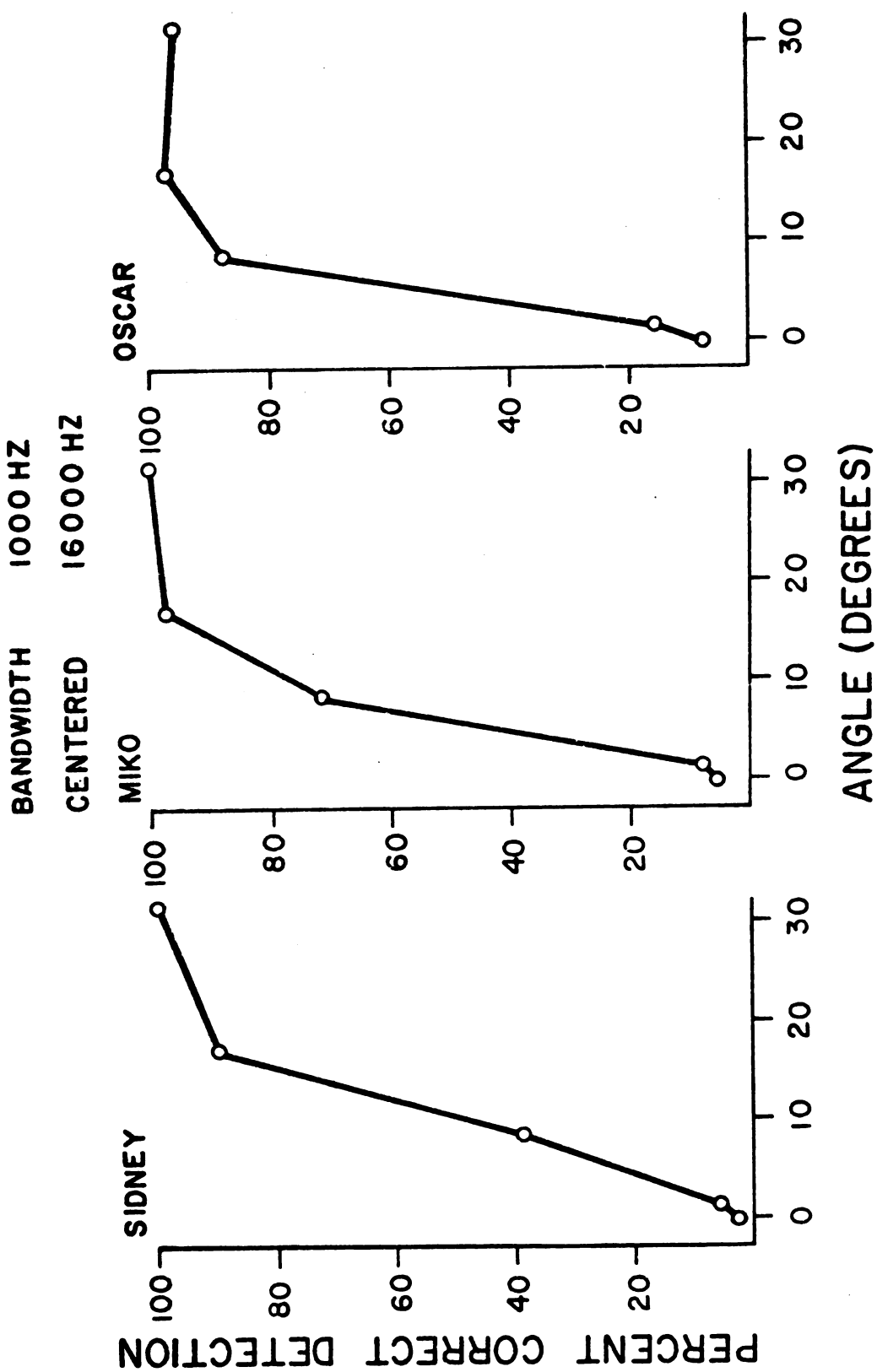

BANDWIDTH 1000 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 29

Figure 30

The Probability of Detection as a Function of Azimuth for the 2000 Hz Stimulus Bandwidth Centered at 16000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

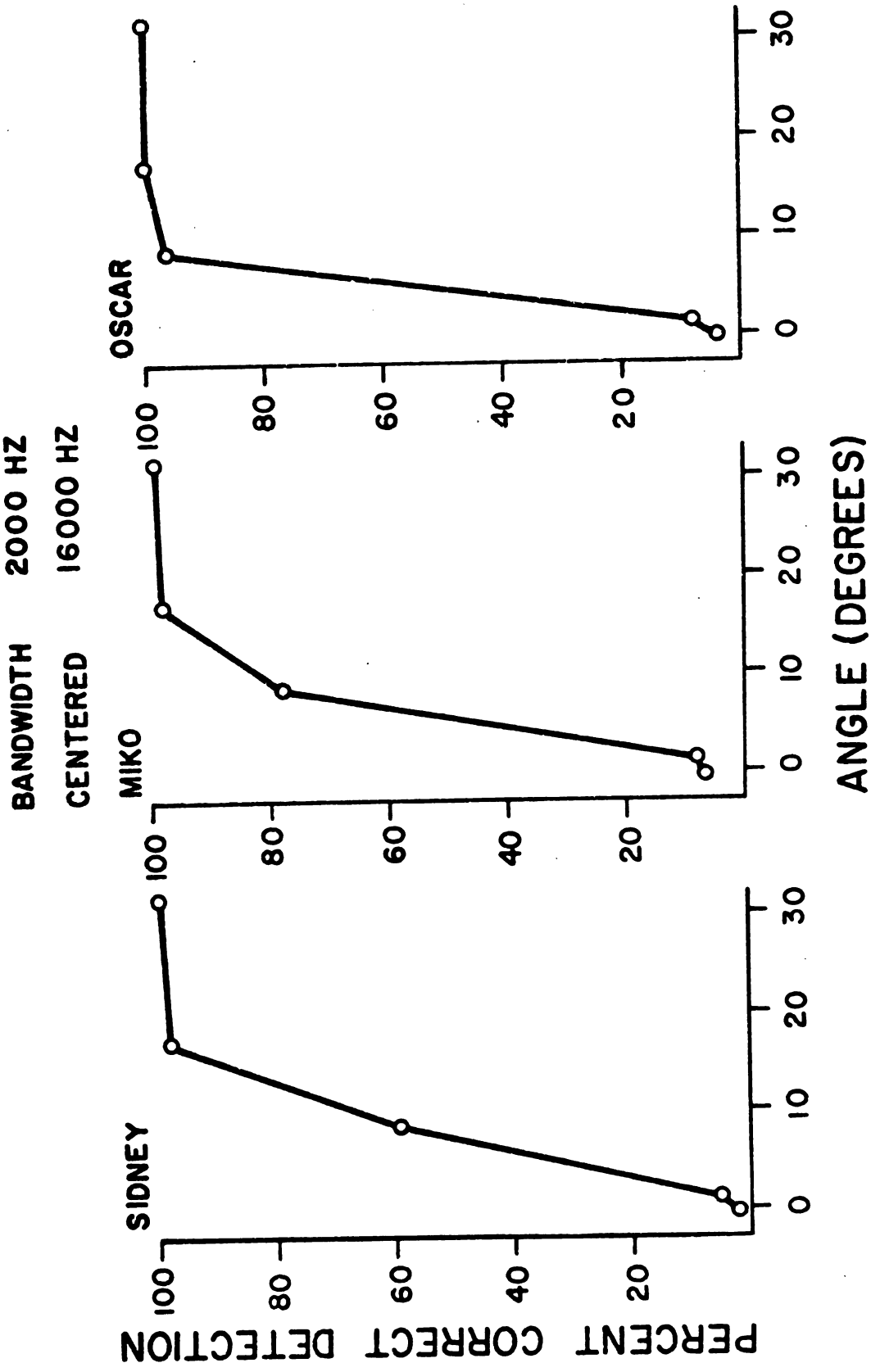

BANDWIDTH 2000 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 30

The results indicate that the detection of change in azimuth of narrow bands of noise was less capricious and easier for all three observers with stimuli centered at 16000 Hz than with stimuli centered at 11200 Hz.

A similar phenomenon may be observed in the psychophysical functions for the 1000 and 2000 Hz bands presented in Figures 29 and 30. For these two bandwidths the proportion of the transition trials on which the change in location was detected ascends monotonically with azimuth; and in all cases threshold is less than or approximately equal to the corresponding value obtained from the function centered at 11200 Hz.

Figures 31 and 32 present the psychophysical functions for the 4000 and 8000 Hz stimulus bandwidths. In all cases for all observers the functions are monotonic and the slopes are steep; however, the 50% detectability locus as derived from these functions is no longer less than the corresponding estimations from the data centered at 11200 Hz. Rather, it appears to be the case that the 50% detectabiltiy locus for wide band stimuli is relatively independent of the center frequency.

Table 8 presents the estimations of threshold as determined by linear interpolation and probit analysis for stimuli centered at 16000 Hz. In Figure 33 these same data are displayed as a function of stimulus bandwidth. As may be seen in Figure 33 the slope of the function relating threshold to bandwidth is less at 16000 Hz than at the two previous center frequencies. This may be empirically seen in Table 9.

Figure 31

The Probability of Detection as a Function of Azimuth for the 4000 Hz Stimulus Bandwidth Centered at 16000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

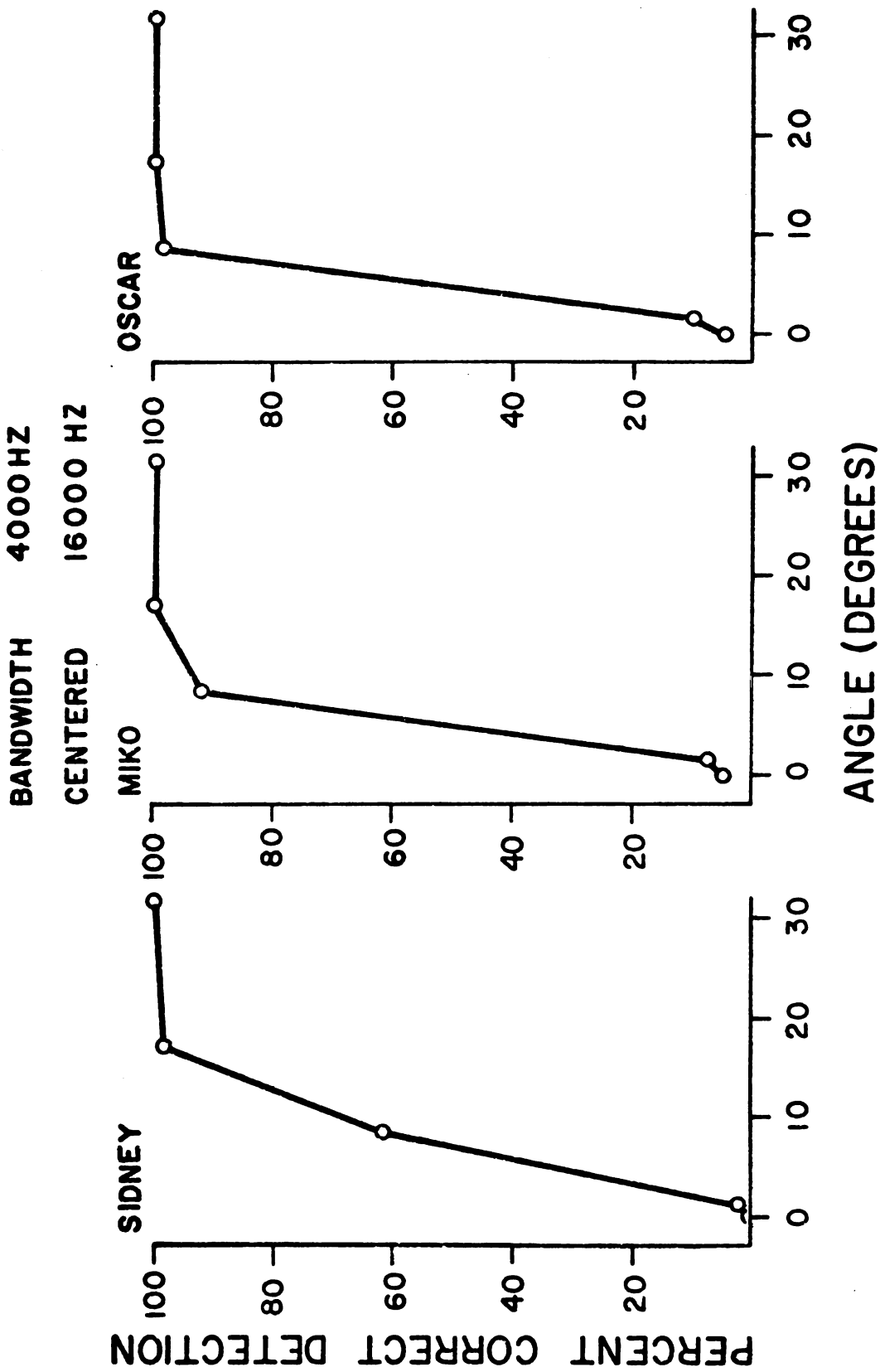

BANDWIDTH 4000 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 31

Figure 32

The Probability of Detection as a Function of Azimuth for the 8000 Hz Stimulus Bandwidth Centered at 16000 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

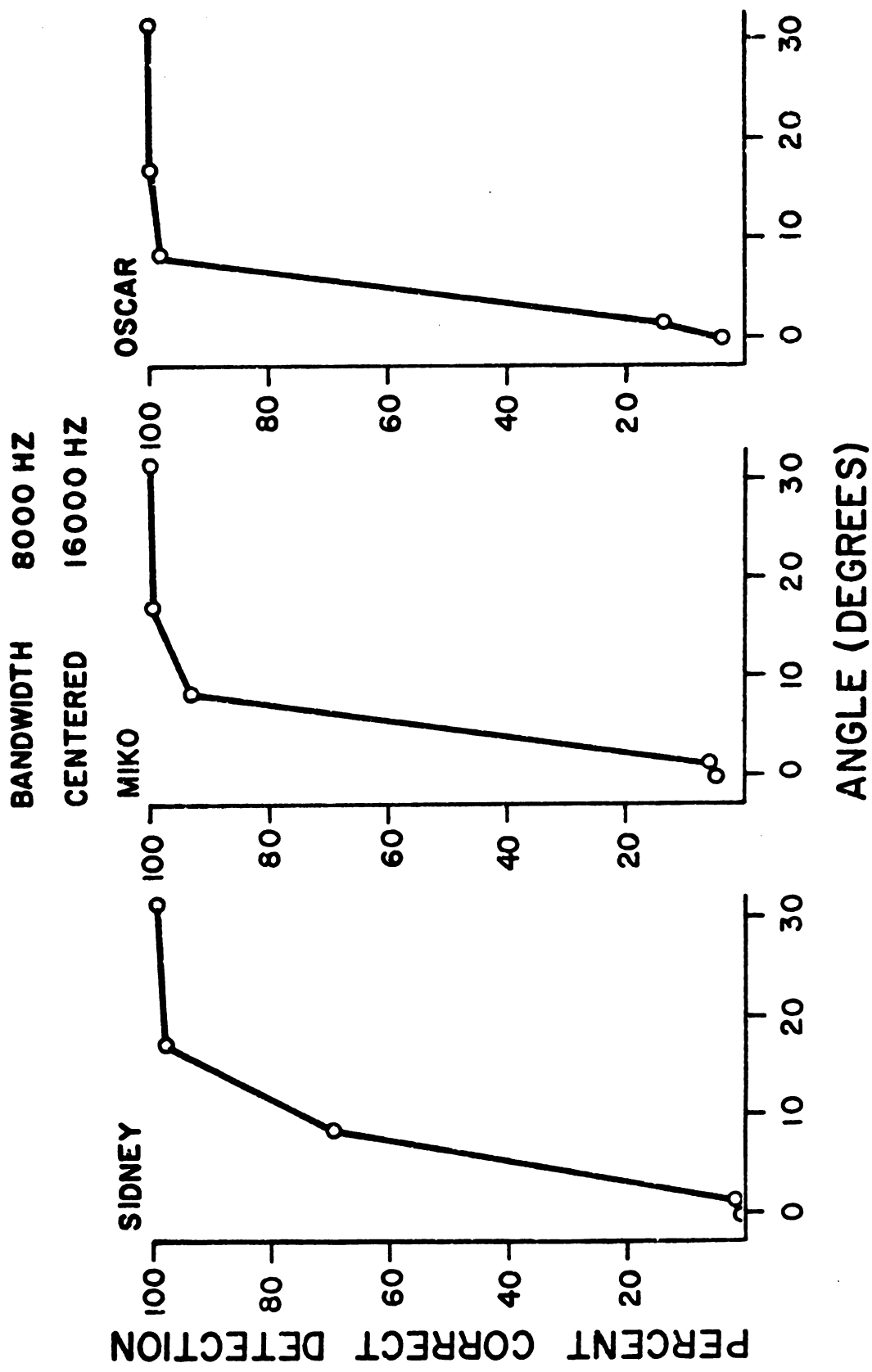

BANDWIDTH 8000 HZ
CENTERED 16000 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 32

TABLE 8

Threshold Angles for Bandwidths Centered at 16000 Hz

	Bandwidth (Hz)						
	1	250	500	1000	2000	4000	8000
Sidney							
Linear Interpolation	20.4	13.2	7.0	9.5	6.7	6.7	5.9
Probit	20.6	15.5	10.9	9.5	7.6	7.4	7.0
Chi-square[a]	72.3*	63.1*	228.7*	181.4*	105773.8*	15.6*	XXXX[b]*
Miko							
Linear Interpolation	8.7	6.0	7.9	5.6	5.2	4.6	4.6
Probit	8.0	7.9	8.2	6.1	6.3	4.5	4.5
Chi-square[a]	30.9*	94.9*	143.1*	18.2*	165585.9*	491.5*	1378.0*
Oscar							
Linear Interpolation	5.6	5.2	6.7	4.4	4.4	4.2	4.1
Probit	10.8	8.7	12.4	5.8	4.1	3.8	3.5
Chi-square[a]	191.9*	281.7*	331.2*	10276.1*	4.3	187849.6*	0.03

[a]Chi-square associated with departure from normality

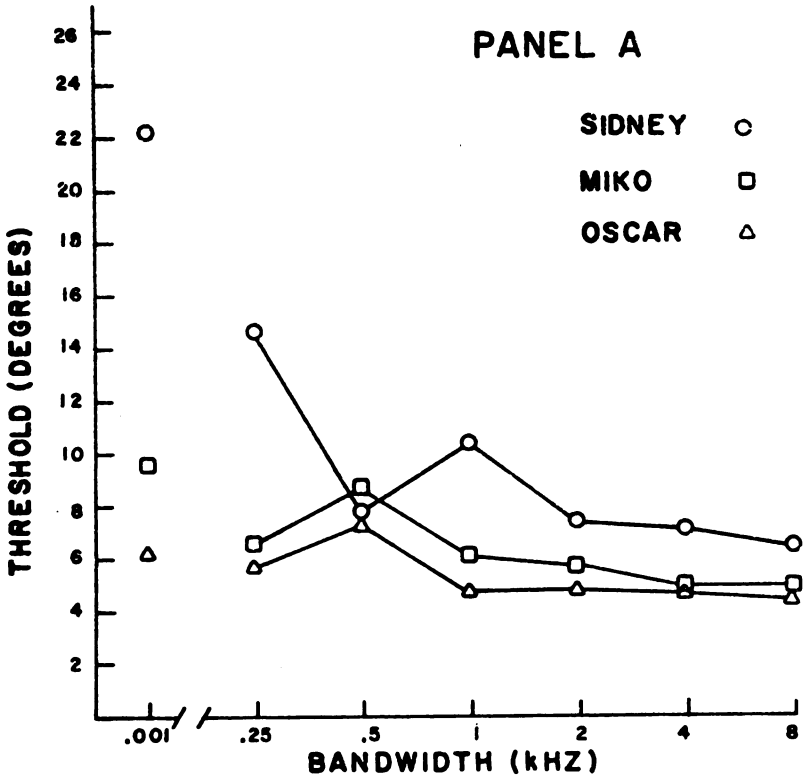
[b]Value too large to be calculated with Probit program

*$p < .05$, df=3

Figure 33

Threshold as a Function of Bandwidth for Stimuli Centered at 16000 Hz. Panel A presents the 50% detectability locus as determined by linear interpolation; panel B presents the same locus as determined by probit analysis.

CENTERED 16000 HZ



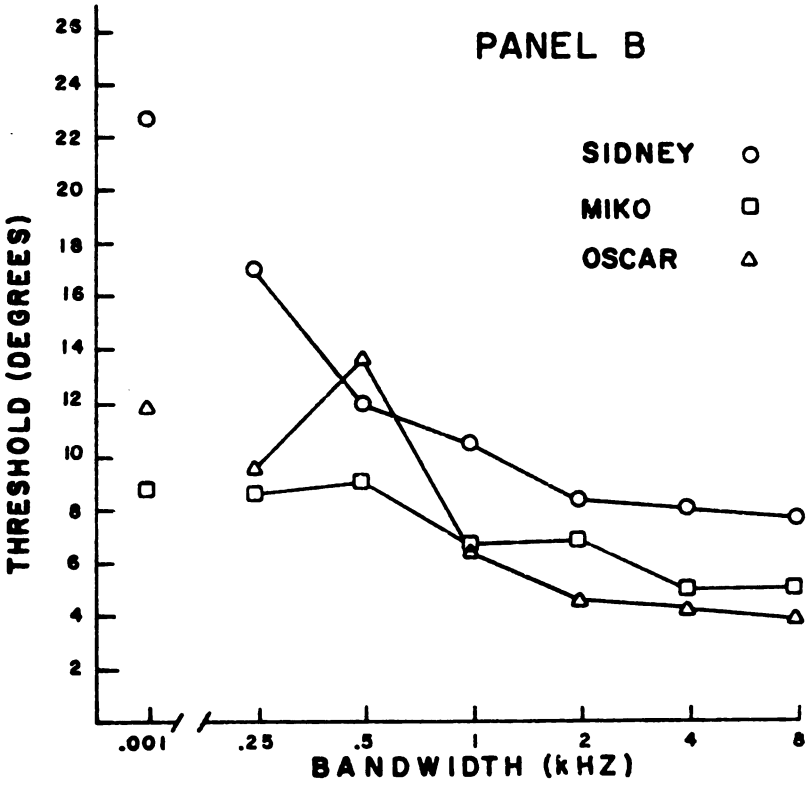


FIGURE 33

TABLE 9

The Regression of Threshold on Bandwidth Centered at 16000 Hz

Observer	Probit Analysis	Linear Interpolation
Sidney	t=-5.2 log b + 26.1 (r=-.91)	t=-3.8 log b + 20.2 (r=-.78)
Miko	t=-2.6 log b + 14.6 (r=-.94)	t=-1.7 log b + 10.8 (r=-.75)
Oscar	t=-5.1 log b + 22.4 (r=-.81)	t=-1.2 log b + 8.7 (r=-.70)

Note: t is threshold in degrees, b is bandwidth in Hz, r is the correlation coefficient.

Experiment II
The Detection of Changes in Azimuth as a Function of Stimulus Bandwidth: Systematic Replication

A very conservative strategy for scientific research advanced by Sidman (1960) is the systematic replication and extension of the corpus of empirical results. In this tradition, Experiment II was designed to (a) replicate the extreme values of the stimulus bandwidths centered at 11200 Hz and (b) obtain psychophysical functions at selected stimulus bandwidths centered at the quarter-octave point between 11200 and 16000 Hz. These values were selected to determine if the differences between the psychophysical functions at 11200 Hz and 16000 Hz were orderly and reliable. Specifically psychophysical functions were obtained for the 250 and 8000 Hz bandwidths centered at 11200 Hz, for a 13454 Hz pure tone, and for bandwidths of 250, 500, and 8000 Hz centered at 13454 Hz.

Method

Subjects, Apparatus, and Procedure

The experimental apparatus, contingencies, and subjects were the same as employed in Experiment I. However, at the center frequency of 11200 Hz the locations of the transducers at the 250 Hz bandwidth stimulus were changed with respect to the same bandwidth in Experiment I. For the replication the speakers were located at 0.0°, 8.7°, 15.5°, 29.5°, 46° azimuth V.S. 0.0°, 1.3°, 7.8°, 29.5°. When these data were

collected Miko was in estrus and as had been the case before, this monkey was a poor observer of narrow band stimuli under this condition. As a consequence, a psychophysical function was also obtained from Miko with the sitmulus bandwidth of 500 Hz.

As in Experiment I the stimuli presented at 11200 Hz had a mean sound pressure level of 49 dB re 20 μPa. At 13454 Hz the speakers were located at 0.0°, 1.3°, 7.8°, 29.5°. For the macaques the threshold of hearing function at 13454 Hz is 16 dB re 20 μPa. The acoustical stimuli presented at 13454 Hz had a mean sound pressure level of 56 dB re 20 μPa, or 40 dB SL.

Results

Acoustical Stimuli Geometrically Centered at 11200 Hz

Figure 34 presents the psychometric functions for the three monkeys with the stimulus bandwidth of 250 Hz and for Miko at 500 Hz. As may be seen in Figure 34 the obtained functions were monotonic for Sidney and Oscar, but not for Miko. Miko's performance was better with the 500 Hz stimulus band than it was with the 250 Hz band; however, it was still non-monotonic.

Figure 35 presents the psychophysical function for the 8000 Hz stimulus bandwidth. As may be seen in the figure the psychometric functions agree well with the comparable data in Experiment I, presented in Figure 24. The number of observations constituting this replication was limited, consequently sampling error should lead to some discrepancies with the data from Experiment I. However, the psychophysical functions are qualitatively comparable with the data presented in Experiment I. Table 10 presents thresholds as provided

Figure 34

The Probability of Detection as a Function of Azimuth for Narrow Band Stimuli Centered at 11200 Hz: A Replication. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

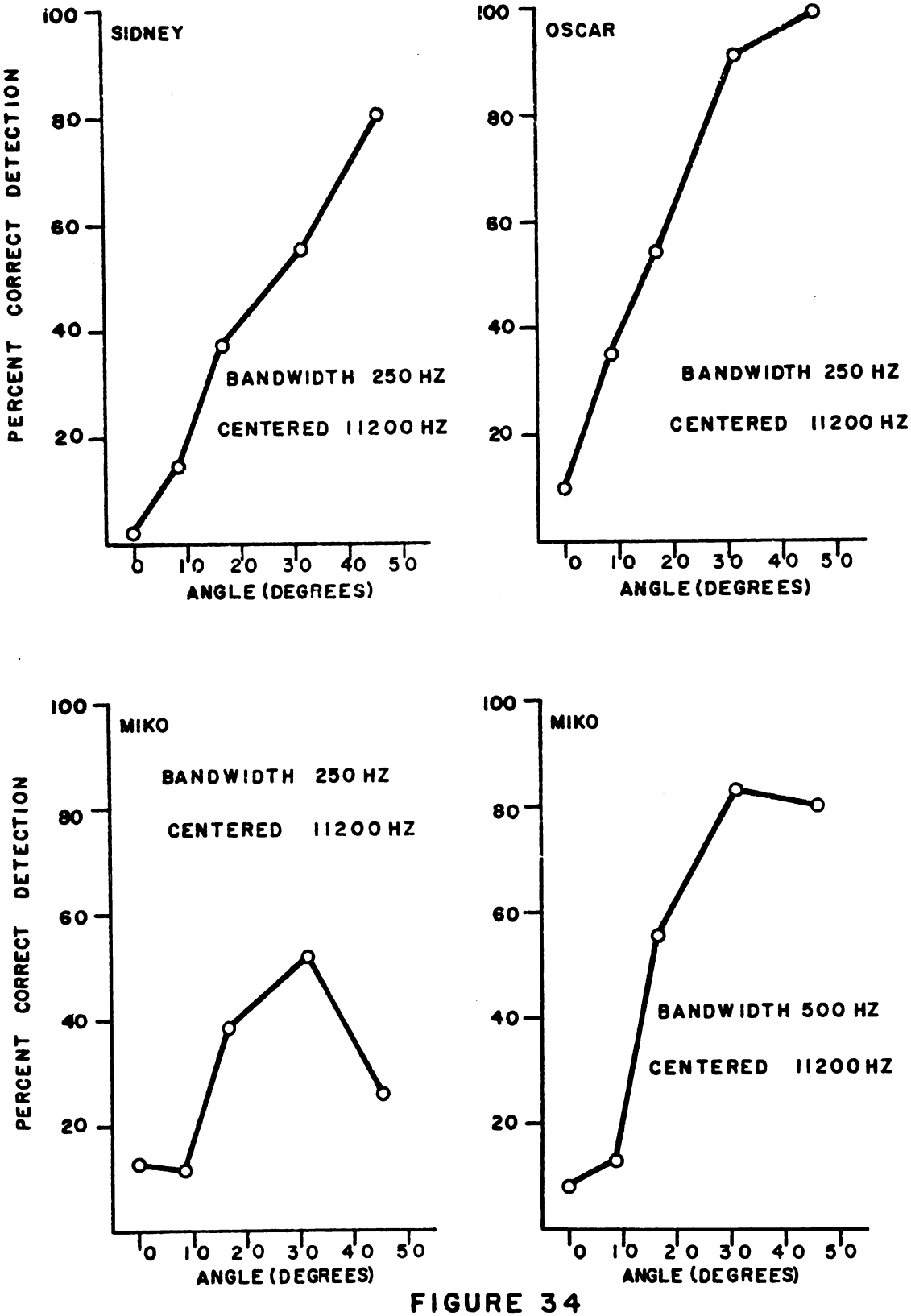

SIDNEY
PERCENT CORRECT DETECTION
100
80
60
40
20
BANDWIDTH 250 HZ
CENTERED 11200 HZ
0 10 20 30 40 50
ANGLE (DEGREES)
OSCAR
BANDWIDTH 250 HZ
CENTERED 11200 HZ
MIKO
BANDWIDTH 250 HZ
CENTERED 11200 HZ
MIKO
BANDWIDTH 500 HZ
CENTERED 11200 HZ

FIGURE 34

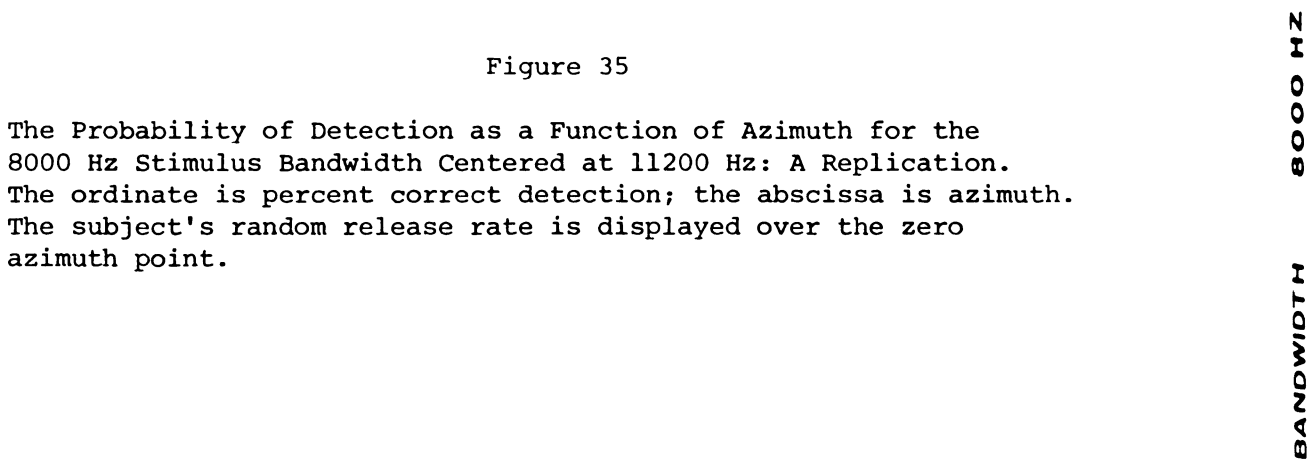


Figure 35

The Probability of Detection as a Function of Azimuth for the 8000 Hz Stimulus Bandwidth Centered at 11200 Hz: A Replication. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

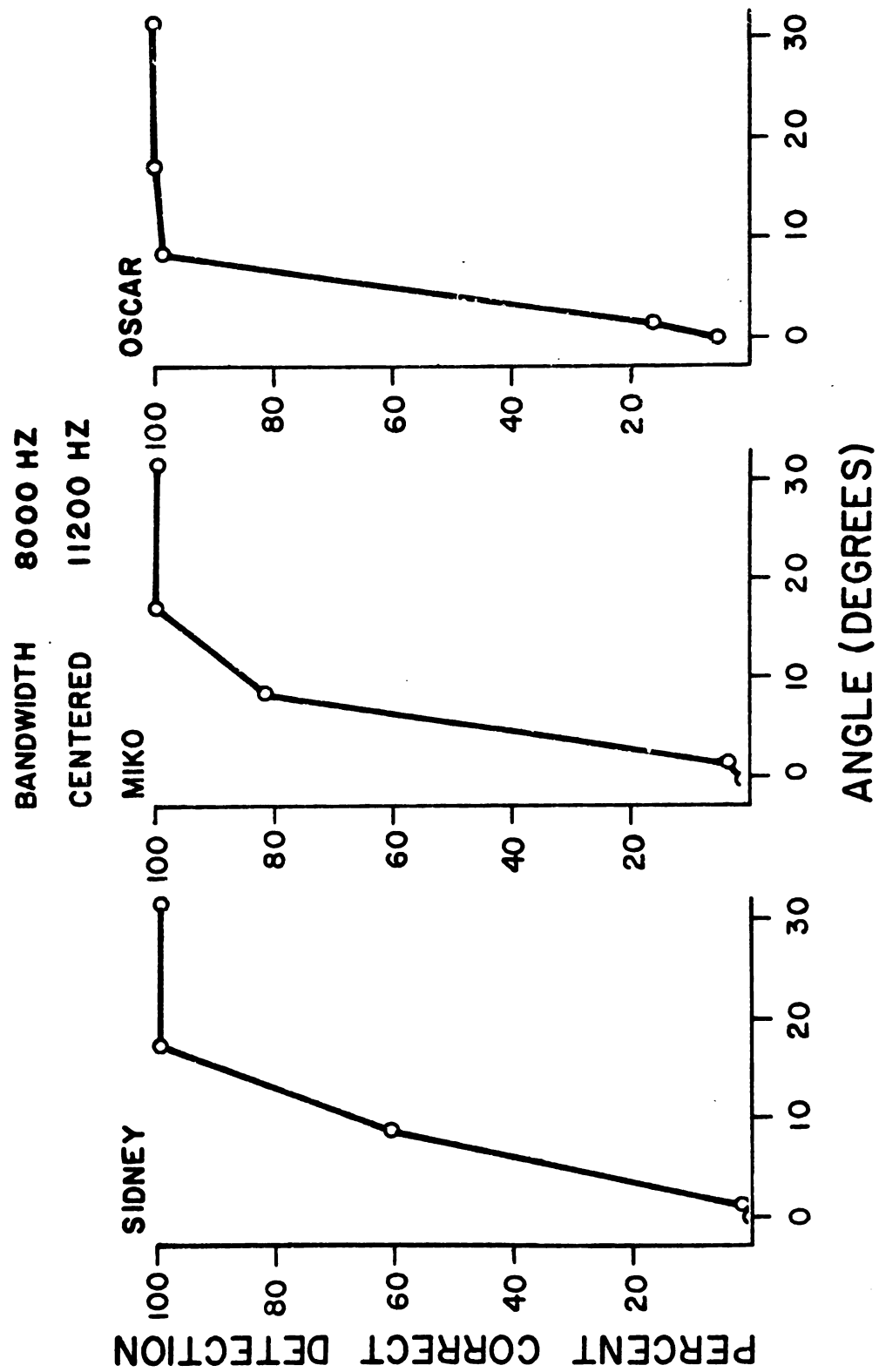

BANDWIDTH 8000 HZ
CENTERED 11200 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 35

TABLE 10

Threshold Angles for Replications at 11200 Hz

	Bandwidth (Hz)		
	250	500	8000
Sidney			
Linear Interpolation	25.4		6.6
Probit	25.2		6.3
Chi-square[a]	30.1*		XXXX[b]*
Miko			
Linear Interpolation	27.3	14.5	5.2
Probit	52.6	20.1	5.6
Chi-square[a]	48.9*	40.6*	0.6
Oscar			
Linear Interpolation	17.2		4.0
Probit	14.5		3.4
Chi-square[a]	39.9*		0.002

[a] Chi-square associated with departure from normality

[b] Chi-square value too large to be calculated with Probit program

*$p < .05$, df=3

by linear interpolation and probit analysis. The comparison of Table 10 with the corresponding values in Table 6 again indicate that changes in azimuth for the narrow bandwidth stimuli centered at 11200 Hz were difficult for the monkeys to discriminate. This phenomenon is thus replicable.

Acoustical Stimuli Geometrically Centered at 13454 Hz

Figure 36 presents the psychophysical functions for the three observers for the 13454 Hz pure tone. As may be seen in this figure the functions for Sidney and Oscar are non-monotonic and the functions are individually distinct for different observers. For Sidney only the 9° azimuth was detected for greater than 50% of the trials. In contrast, Oscar detected at a greater than .5 level all changes in azimuth except for the maximum exchange of 30°. The concept of threshold is inappropriate for these two cases as the locus of 50% detectability occurs twice in each function. In the treatment of the data here, the linear interpolation of threshold was arbitrarily assigned to the smaller of the two 50% detectability loci. For these functions the two estimations of threshold are presented in Table 11. The values for Oscar diverge by 25.8°, while Miko's agreed within 0.3°; and Miko's psychophysical function satisfied a cumulative normal distribution.

Figures 37 and 38 present the corresponding psychophysical functions for stimulus bandwidths of 250 and 500 Hz. As may be seen in these figures the functions for Sidney only approached the 60% level of detection at the greatest angle, 30°. The curves for Miko are reasonably steep monotonic functions, while for both bandwidths

Figure 36

The Probability of Detection as a Function of Azimuth for the 13454 Hz Pure Tone. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

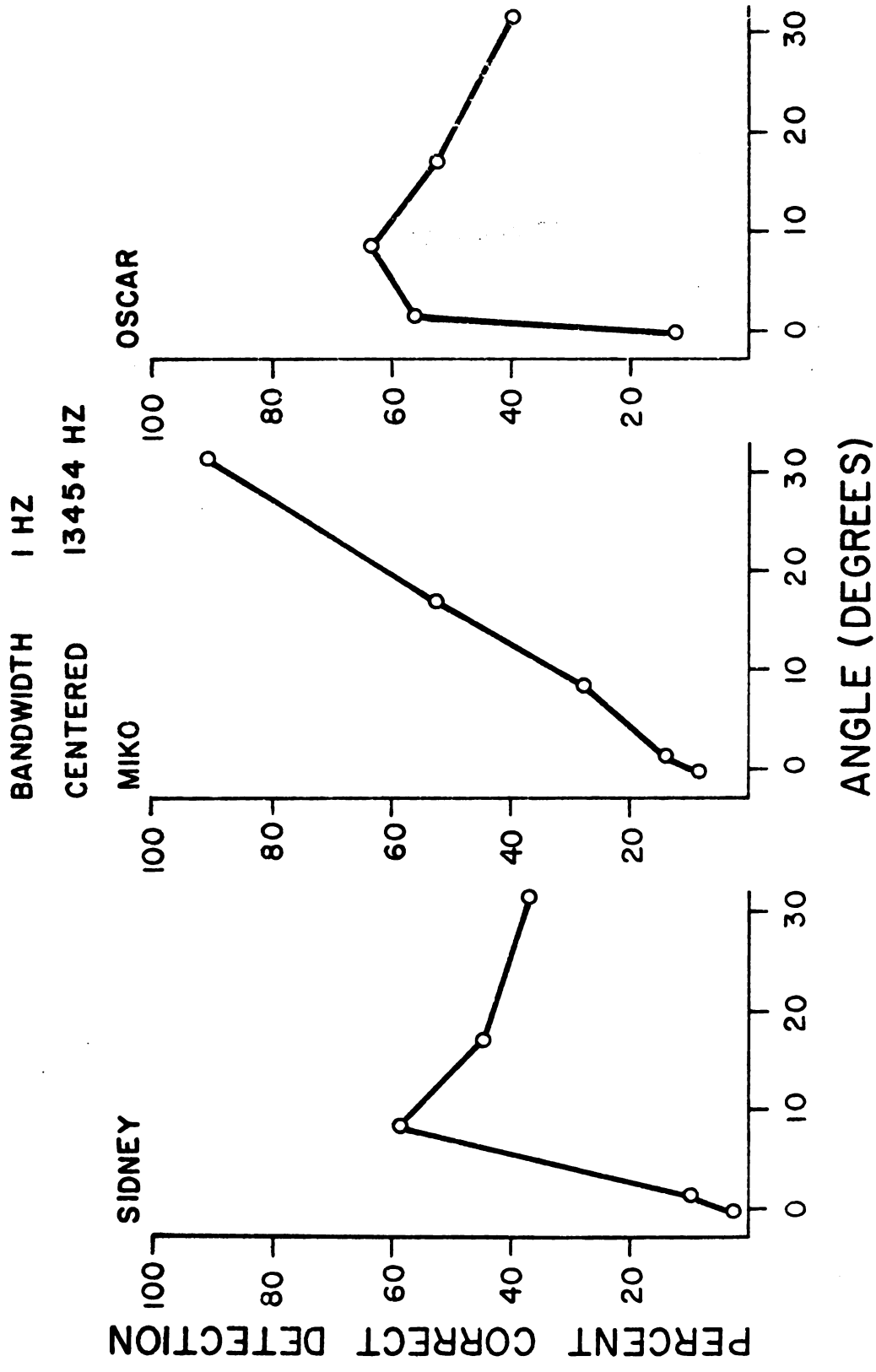

BANDWIDTH 1 HZ
CENTERED 13454 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 36

TABLE 11

Threshold Angles for Bandwidths Centered at 13454 Hz

	Bandwidth (Hz)			
	1	250	500	8000
Sidney				
Linear Interpolation	6.7	24.0	24.8	5.5
Probit	26.5	21.9	23.3	6.3
Chi-square[a]	519.9*	171.5*	86.7*	XXXX[b]*
Miko				
Linear Interpolation	14.7	6.8	7.6	4.2
Probit	14.4	8.8	8.9	4.1
Chi-square[a]	4.3	51.0*	68.1*	701.0*
Oscar				
Linear Interpolation	1.2	4.1	6.6	4.3
Probit	27.0	16.1	20.5	5.3
Chi-square[a]	323.1*	286.5*	180.6*	XXXX[b]*

[a]Chi-square associated with departure from normality

[b]Chi-square value too large to be calculated with Probit program

* $p < .05$, df=3

Figure 37

The Probability of Detection as a Function of Azimuth for the 250 Hz Stimulus Bandwidth Centered at 13454 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

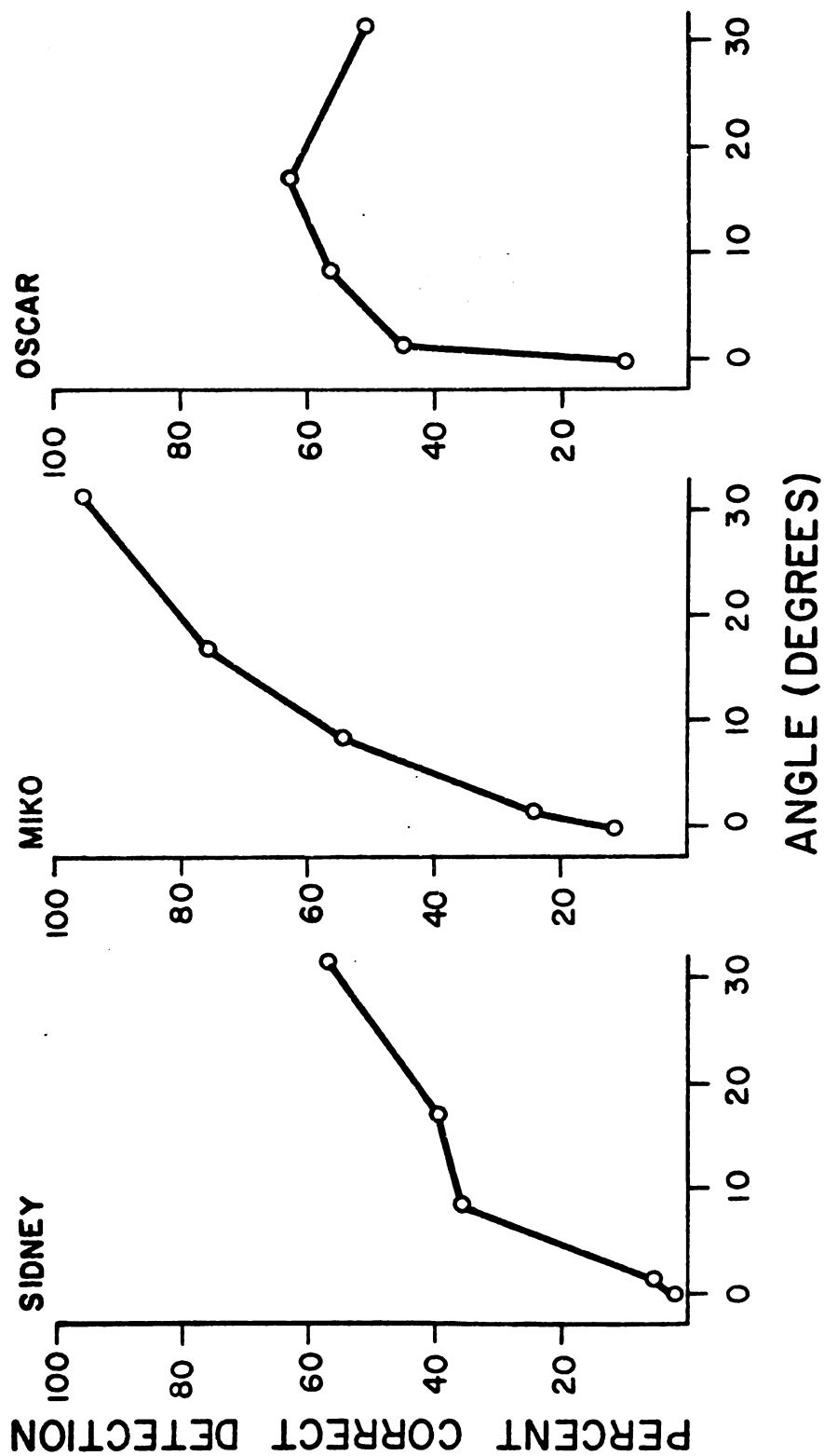

BANDWIDTH 250 HZ
CENTERED 13454 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 37

Figure 38

The Probability of Detection as a Function of Azimuth for the 500 Hz Stimulus Bandwidth Centered at 13454 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

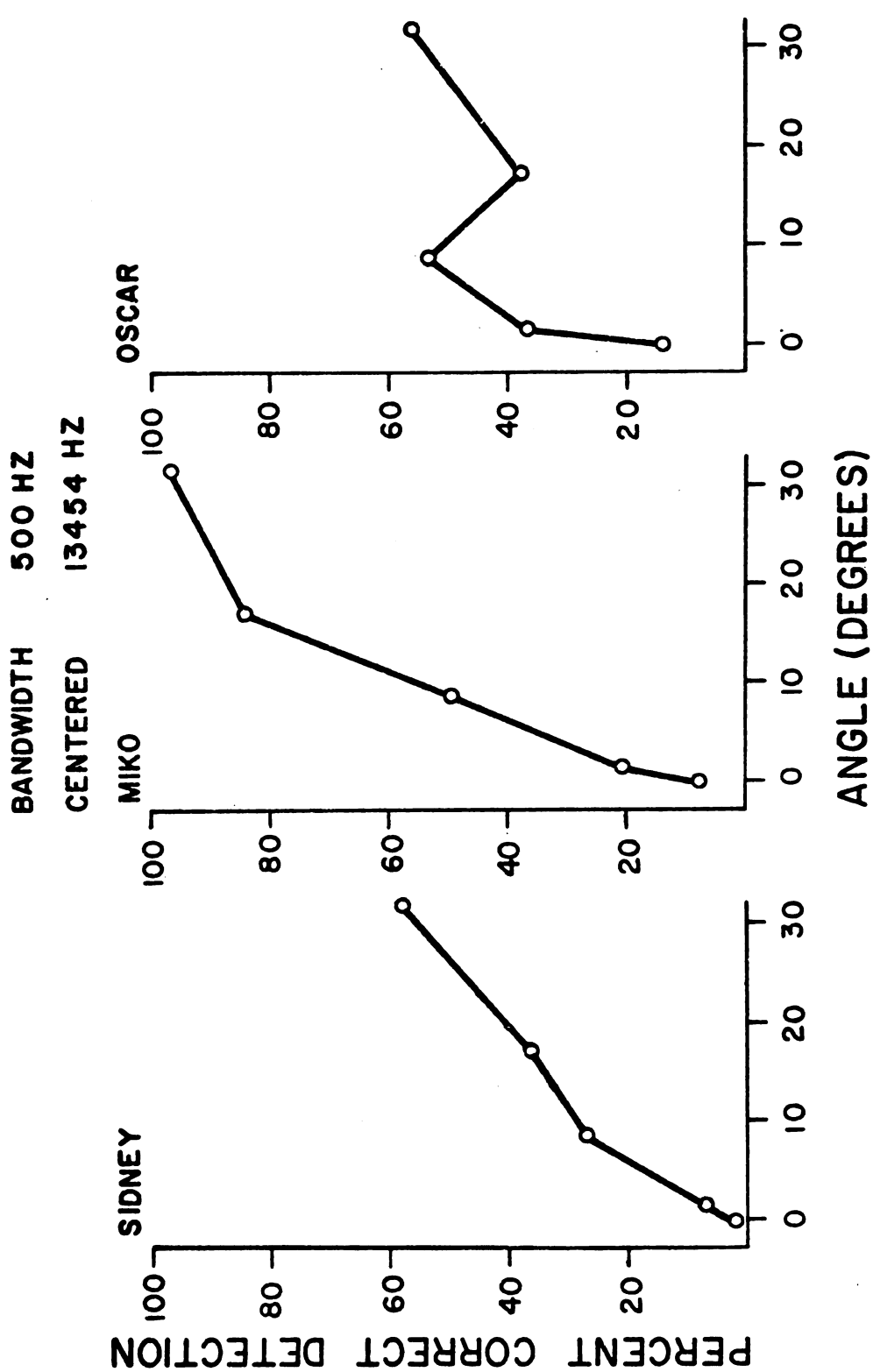

BANDWIDTH 500 HZ
CENTERED 13454 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 38

Figure 39

The Probability of Detection as a Function of Azimuth for the 8000 Hz Stimulus Bandwidth Centered at 13454 Hz. The ordinate is percent correct detection; the abscissa is azimuth. The subject's random release rate is displayed over the zero azimuth point.

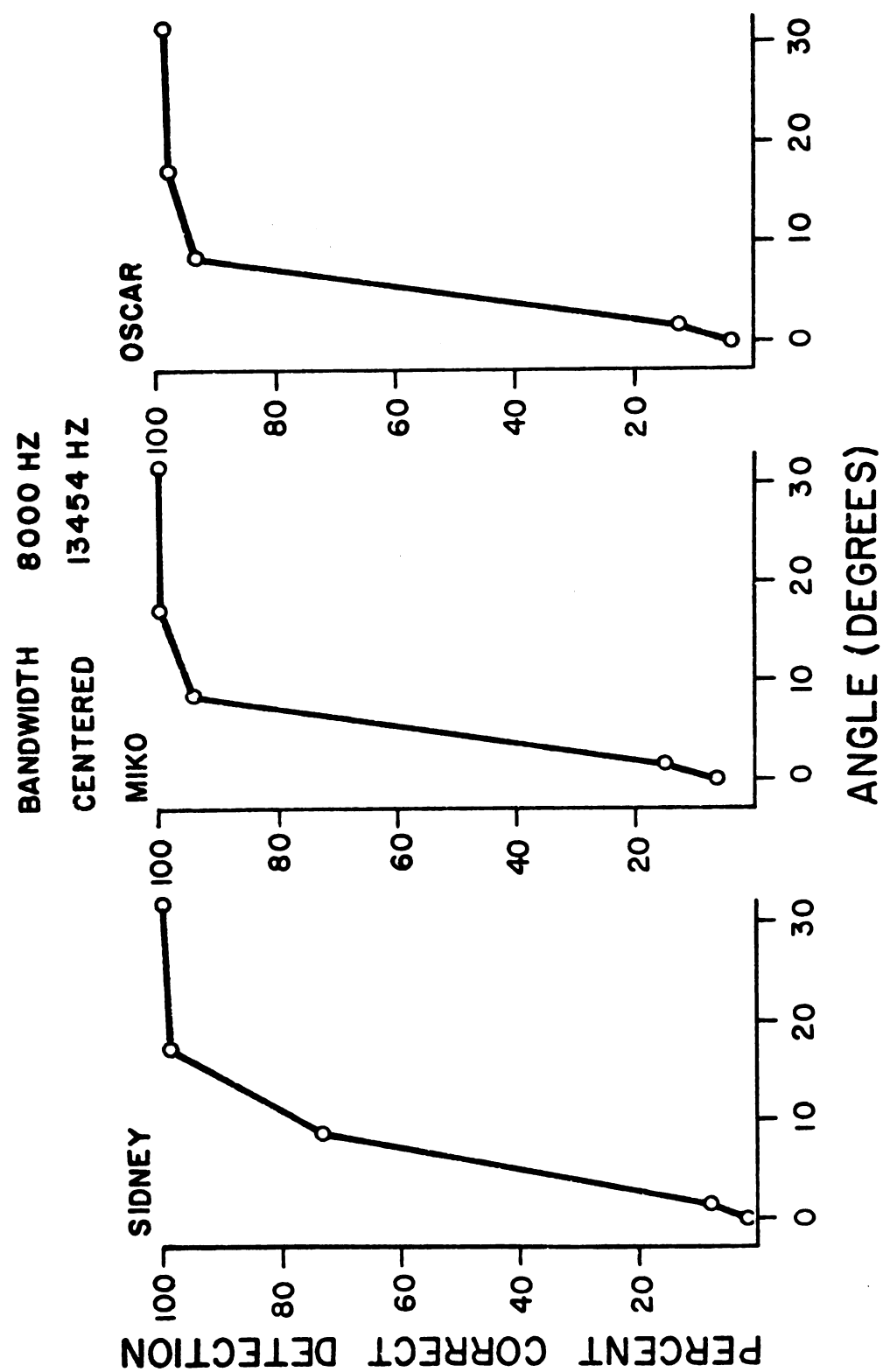

BANDWIDTH 8000 HZ
CENTERED 13454 HZ
SIDNEY
MIKO
OSCAR
PERCENT CORRECT DETECTION
ANGLE (DEGREES)
100
80
60
40
20
0
10
20
30

FIGURE 39

Oscar's functions are non-monotonic. The functions are more similar between bandwidths for the same observer than they are between observers for the same bandwidth.

Figure 39 presents the psychophysical functions for the 8000 Hz bandwidth geometrically centered at 13454 Hz. As may be seen in this figure the functions for all observers were monotonic and steep as is characteristic of the curves generated by wide band stimuli.

The data presented here indicate that at the quarter-octave point between 11200 Hz and 16000 Hz the psychophysical functions for Sidney and Oscar share some of the attributes of the functions obtained at 11200 Hz. That is, changes in the azimuth of narrow band stimuli were difficult to detect. In contrast, the psychophysical functions obtained from Miko resembled those produced by stimuli centered at 16000 Hz. Miko's functions were steep and monotonic and as displayed in the threshold estimations presented in Table 11 the values were similar to those obtained by the corresponding bandwidths at 16000 Hz.

Discussion

The results of Experiments I and II demonstrate that the ability to detect changes in the azimuth of an acoustic source is a function of stimulus bandwidth at any given frequency. This relationship was summarized by the linear regression of threshold on the log of stimulus bandwidth. The correlation coefficient was generally higher for the probit analysis values than for linear interpolation. This is likely a reflection of greater sampling error in linear interpolation. That the correlation coefficient was greater than .90 in 8 of the 9 cases with probit analysis and greater than .8 for the remaining case indicates that bandwidth accounts for a great deal of the variation in threshold.

Interaural Intensity Differences and the Psychophysical Function

The graphs of the psychophysical functions show that, in general, the detectability of a change in azimuth was monotonically related to the magnitude of the change. Six functions, however, showed departures form monotonicity (Figures 18, 20, 34, 36, 37, 38). These nonmonotonic functions were restricted to cases of pure tone, and the 250 or 500 Hz bandwidths centered at 11200 and 13454 Hz. The departures from monotonicity were also observer dependent; different subjects displayed nonmonotonic psychophysical functions at different acoustic parameters.

Both the occurrence of nonmonotonic functions and their observer

dependence are consistent with psychophysical observations of binaural intensity differences. Measurements derived psychophysically (Sivian and White, 1933), by probe microphones (Harrison and Downey, 1970), or from an artificial head (Harris, 1972) indicate that the interaural difference in sound pressure level may not be monotonically related to azimuth, and as a result two or more locations in space may engender identical binaural intensity differences. The shapes of these functions vary with frequency, but are in general highly irregular. A study by Harris (1972; results presented here as Figure 3) demonstrated that interaural intensities are a function of the size of the pinna. One might predict, therefore, that individual differences in the architecture of heads and external ears would produce intersubject differences in binaural intensities.

The Binaural Spectral Difference Hypothesis

In contrast to the functions generated by pure tones and narrow bands of noise, the psychophysical functions engendered by wide band stimuli were consistently steep and monotonic. The effect of stimulus bandwidth on the auditory localization of azimuth is interpreted according to the following working hypothesis:

An acoustical stimulus is not transmitted without modification to an observer's ear. The head and external ear of a subject are acoustically opaque and differentially attenuate the energy within the audio spectrum. The shape of this attenuation, or spectral transfer, function is an expression of two factors: (A) the architecture of an individual's head and external ears; and (B) of the angle of incidence of the wave form on the ear. Because an observer's two ears are spatially

separated the angle of incidence of the wave form will be different for each ear and the resulting spectral transfer functions will differ. The difference between these functions is the binaural difference spectrum which will be unique for each location in space if the following four conditions are satisfied: One, the auditory stimulus must be composed of more than a single frequency. Two, the ear must be capable of discriminating at least two of the frequencies within the stimulus and assess their relative energies. Three, the external ear must differentially attenuate the energy for each frequency within a stimulus. Four, this differential attenuation must be unique for each location in space. Thus according to the working hypothesis if the binaural difference spectrum is unique for each point in space and if the vertebrate ear is sensitive to the frequencies at which this uniqueness is realized then an acoustic event with a defined spectral content could not be changed in locus without the observer detecting that change.

The effect of stimulus bandwidth on detectability is represented in Figure 40. The top panel depicts a rectangular band of noise, the middle panel the spectral transfer function for each ear, and the bottom panel the resulting binaural difference spectrum. The employment of the binaural difference spectrum in localization is easily visualized. For example, in the simplest case if a subject with perfectly symmetrical head and ears is presented with a pure tone at the zero azimuth, identical spectral transfer functions would be produced at both ears and the resulting binaural difference spectrum would be zero. However, if this pure tone is changed in azimuth, this change in location may be detected if the binaural difference spectrum at that

Figure 40

Hypothetical Binaural Difference Spectrum. The top panel represents a rectangular band of noise, the middle panel the spectral transfer functions for each ear, the bottom panel the resulting binaural difference spectrum. See text for details.

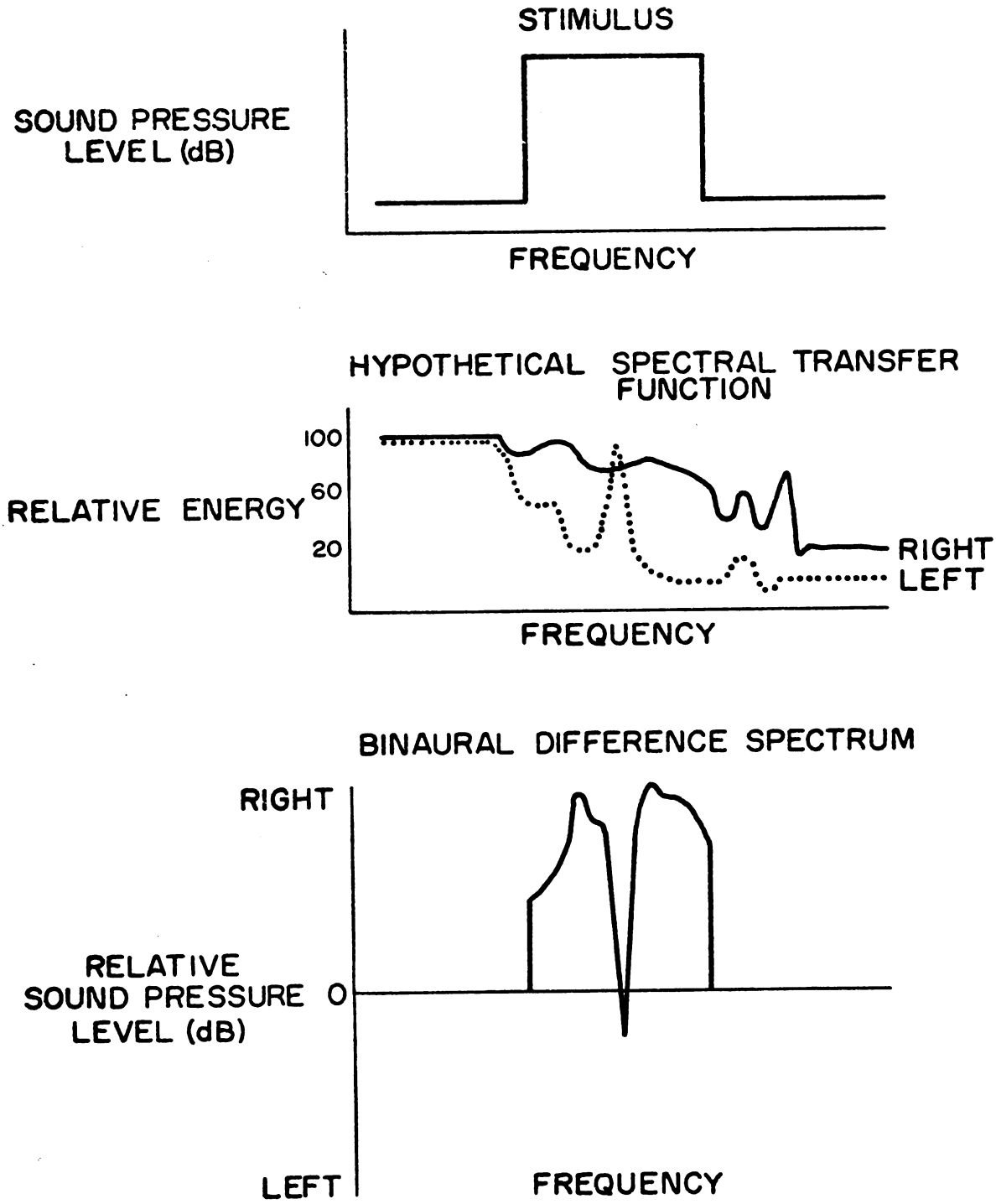

STIMULUS
SOUND PRESSURE LEVEL (dB)
FREQUENCY
HYPOTHETICAL SPECTRAL TRANSFER FUNCTION
100
60
20
RELATIVE ENERGY
RIGHT
LEFT
FREQUENCY
BINAURAL DIFFERENCE SPECTRUM
RIGHT
RELATIVE SOUND PRESSURE LEVEL (dB)
0
LEFT
FREQUENCY

Figure 40

point is discriminable different from that engendered at zero azimuth. If the acoustical stimulus is a band of noise rather than a pure tone, the detectable change in acoustic locus would occur when the binaural differences summed over the frequencies contained in the noise band are discriminably different between the two locations.

The binaural difference spectrum hypothesis at present cannot be rigorously tested because measurements of the spectral transfer function have not been made. However, measurements of interaural intensity differences (Harris, 1972; Harrison and Downey, 1970; Sivian and White, 1933) suggest that the following assumptions are probably true. One, binaural intensity differences are greater for high frequencies than for low frequencies for any locations not in the median plane. Two, the change in binaural intensity differences for any given change in azimuth is greater for high frequency stimuli than for low frequency stimuli. Three, for any give azimuth outside the median plane, interaural intensity differences are greater for wide bandwidth stimuli than for narrow band stimuli or pure tones.

Psychophysical Data in Support of the Binaural Difference Spectrum Hypothesis

The Binaural Difference Spectrum Hypothesis predicts that the threshold for detecting changes in azimuth for wide stimulus bandwidths is less than the corresponding threshold for narrow stimulus bandwidths or for pure tones. The results reported here agree with this prediction. Departures from monotonicity in the psychophysical functions suggest that the binaural difference spectrum may not be

monotonically related to azimuth. Theoretically, these departures will be restrictied to pure tone and narrow band stimuli, a prediction also consonant with the obtained data. The major findings of the research presented here are, therefore, in accordance with the binaural difference spectrum hypothesis.

The functions relating the threshold to stimulus bandwidth may be considered the product of both the binaural difference spectrum and the ability of the binaural neural processor to discriminate changes in the spectrum. Differences in the slope of these functions at any center frequency must, then, indicate either a difference in the ability of the head and ears to generate a binaural difference spectrum or a difference in the ability of the binaural mechanisms to resolve it.

Psychophysical Results Not Predicted by the Binaural Difference Spectrum Hypothesis

The psychophysical functions for the three monkeys include several cases where localization was poorer for wider bands of noise than for narrower bands or for pure tones. For example, compare the proportion of trials detected by Oscar at 7.8° azimuth using a 250 Hz bandwidth stimulus with the proportion detected at the same angle using a 500 Hz bandwidth stimulus (Figures 27 and 28). These results were not predicted from the binaural difference spectrum hypothesis; for as the bandwidth of the binaural difference spectrum increases, so should detectability.

There are two likely exceptions to the above generalization. The first exception may occur if detectability is dependent on the energy level per cycle of the sitmulus. As the bandwidth of the stimulus is increased from a pure tone, the sound pressure level per cycle decreases.

If, as the sound pressure level for the frequency in question approaches the threshold of hearing, the ability to detect binaural intensity differences is degraded, then the change in location of a pure tone may be more easily detected than the same change for a band of noise unless there is a large difference in the binaural difference spectrum for the band of noise at the two locations. In this case, the reduction in sound pressure level per cycle decreases the neural ability to discriminate binaural differences and the decrease is not compensated for by any increase in the difference between the binaural difference spectra. The second exception falls within the complex realm of masking. In general, the detectability of a test frequency is maximally degraded by a masking stimulus composed of frequencies adjacent to the test stimulus (Fletcher, 1940; Scharf, 1970). Therefore, a wider band stimulus may be less localizable than a narrower bandwidth stimulus if the increase in bandwidth effectively masks the region of the spectrum where binaural differences would have been expressed. As in the first case, the degradation in detectability of the wider bandwidth is not compensated for by any increase in the difference between the binaural difference spectra generated at the two test locations. It is interesting to note that low frequency stimuli are better maskers of high frequency stimuli than the converse (Mayer, 1894; Wegel and Lane, 1924); thus any masking that occurs in a band of noise is most likely due to the low frequency components of the noise. Furthermore, the possibility of masking is greater with high frequency bands because the low frequency components of those bands are louder than the high frequency components due to the fall off in sensitivity to high frequencies (Figure 4). However, it is likely that

bands located higher on the frequency spectrum would generate more distinct binaural differency spectra, perhaps offsetting the effects of masking.

The above considerations suggest that the effect of increasing stimulus bandwidth on localization depends on the local features of the difference spectra for specific stimuli. While the data support the general contention that broad band stimuli are more readily localized than narrow band stimuli, this is only true as long as the salience of the binaural difference spectrum increases with bandwidth. Whether this occurs or not is dependent on the frequency of the band and the structural characteristics of the observer's head and ears, as well as upon the ability of the binaural neural processor to appreciate these differences.

Additional Evidence in Support of the Binaural Difference Spectrum Hypothesis

One obvious test of the binaural difference spectrum hypothesis is the comparison of the ability of monaural and binaural observers to localize. The literature consistently reports that binaural localization is superior to monaural, although the magnitude of the binaural advantage varies widely among precedures and laboratories. Gatehouse and Cox (1972) compared localization in normal binaural subjects to localization in subjects with clinically defined severe to profound sensorineural monaural deafness. Binaural subjects localized better than monaural subjects; but the monaural observers did better than chance would predict. These results agree with early clinical observations indicating that, while intersubject variability was high, some

monaurally deafened subjects were nearly as accurate in localization as observers with normal hearing (Angell and Fite, 1901; Pierce, 1901).

In the laboratory Perrott and Elfner (1968) and Elfner, Bothe and Simrall (1970) employed ear plugs to render normal subjects monaural. The central findings of those studies was that subjects could initially localize only using loudness cues. However, after training with appropriate feedback, subjects could localize according to spectral differences generated by the acoustic shadow of the head and the differential attenuation of high frequencies. That is, subjects could be trained to respond to differences in the spectral transfer function for the unoccluded ear.

Butler and Nauton (1967) and Belendick and Butler (1975) have also studied monaural localization in the laboratory. Their data indicate the error in localization is a function of the spectral content of the stimulus. The noise band must contain frequencies greater than 5000 Hz for subjects to display an ability to localize the sound. If the stimulus was a broad band noise, observers were able to localize all azimuths within about 20°. Furthermore, the error of localization was not randomly distributed; the perceived source of the sound was displaced toward the unoccluded ear. The constant error in location displayed by Butler's monaural observers may be subject to reduction by a training program. Freedman and Fisher (1968) have reported that highly trained monaural observers were nearly as accurate at localizing a sound source as were binaural observers.

Despite the difficulties in making empirical comparisons between laboratories (due to differences between the angular positions of speaker arrays, the spectral characteristics of the transducers, and the room acoustics) the results from the studies on the monaural

localization of azimuth support the contention that while the spectral transfer function for a single ear may be employed to localize an acoustic source, binaural processing is always more accurate and less dependent on the spectral content of the stimulus.

Spectral transfer functions may also account for localization in the median plane. Pratt (1930) and Roffler and Butler (1968b) have shown that observers are unable to localize pure tones which differ in elevation in the median plane. Such differences in elevation can, however, be detected using bands of noise (Thurlow and Runge, 1967; Roffler and Butler, 1968a; Butler and Planert, 1976; Hebrank and Wright, 1974a; Gardner and Gardner, 1973). The ability to discriminate changes in location in the median plane can be explained by corresponding changes in the spectral transfer function. If this hypothesis is true, then a noise band with a frequency spectrum adjusted to mimic the spectral transfer function associated with a specific location should evoke that subjective location irrespective of its actual location. This hypothesis has qualitatively been confirmed by Blauert (1974) and Hebrank and Wright (1974b). These two studies differed markedly in the spectral content of the stimulus associated with the apparent location of a sound. It is unclear if these differences may be attributable to differences in the spectral transfer functions generated by the different ears of different observers.

Psychophysical observations of vertical localization demonstrate that the spectrum of the auditory stimulus must contain high frequencies. Roffler and Butler (1968a) reported that accurate localization required frequencies between 7000 and 8000 Hz. Butler and Planert (1976) demonstrated that braod high frequency noise bands were localized more

accurately than narrow noise bands. These results are corroborated by physical measurements of the spectral transfer function. Shaw and Terishini (1968) and Shaw (1974) have reported that the ear performs complex spectral filtering primarily for frequencies greater than 5000 Hz. As a result the differential transmission of acoustic energy is only expressed in that region of the spectrum greater than 5000 Hz. Hebrank and Wright (1974a) have reported that the spectral transfer functions change for different median plane locations for frequencies between 4000 and 16000 Hz.

In the median plane the angle of incidence of the wave front at the right and left ear is identical, consequently binaural differences are at a minimum. However, psychophysical data demonstrate a superiority for binaural over monaural observers in localization within that plane (Gardner, 1973; Butter, 1969; Butler and Planert, 1976; Hebrank and Wright, 1974a). Searle (1973) has reported that in the median plane the spectral transfer functions are asymmetrical. Thus individual characteristics of each pinna would generate a binaural difference spectrum and the localization of sounds in the median plane may in part be a binaural phenomenon. Hebrank and Wright (1974a) have argued that median plane localization is a primarily monaural process. In support of this thesis they showed that trained monaural observers could localize ripple spectrum noise as well as binaural observers could. However, this demonstration did not unequivocally prove that median plane localization is a monaural process because the power spectra of the ripple-spectrum sounds, adjusted to imitate spectral transfer functions, may have masked or removed from the spectrum those frequencies where binaural asymmetries may have been expressed.

This interpretation gains support from the observation that neither monaural nor binaural observers could localize ripple-spectrum noise as accurately as they could white noise. Thus a binaural advantage in median plane localization may only occur when the power spectrum of the stimulus allows for the realization of pinna asymmetries.

The phenomena considered here demonstrate that one advantage of the binaural difference spectrum hypothesis is its ability by extension to account for the fundamental observations of auditory localization in vertical as well as horizontal space.

Duplicity Theory and the Relative Contributions of High and Low Frequency Sensitivity to the Determination of Azimuth

According to classic duplicity theory, the localization of low frequency stimuli depends on binaural phase or temporal differences while localization of high frequency sounds is due to interaural differences in intensity (Stevens and Newman, 1934). The literature on the binaural difference spectrum has considered only the latter case. An important question, then is what are the relative contributions of binaural temporal and intensity differences to the localization of acoustic events at frequencies where both mechanisms may be operative.

Yost, Wightman, and Green (1971) attempted to measure the relative contributions of high and low frequencies to the detection of a lateralized transient. In the lateralization procedure the stimuli are presented through headphones and the acoustic image appears to reside within the observer's head; it is analytically useful because interaural differences in phase and intensity may be precisely controlled. The investigators required their subjects to detect the difference

between synchronously presented transients and transients where the presentation to one ear was delayed. The interaural temporal delay required for 75% detection was measured as a function of the frequency content of the transient. The results indicated that performance depended on the low frequency content of the transient; when only frequencies above 1200-1500 Hz were presented, a greater interaural temporal difference was required for the subjects to discriminate simultaneously presented transients from transients in which the signal to one ear was delayed. These results were interpreted to support the position that the discrimination between lateral images depends primarily on the low frequency content of the stimulus. However, these results do not resolve the question of the relative contributions of binaural phase and intensity differences to auditory localization.

The stimuli were dichotically presented and only binaural temporal differences were introduced. Thus the study only measures the upper frequency limit for the discrimination of interaural temporal differences; their value of 1200 to 1500 Hz agrees well with that obtained by more direct measurements (Yost, 1974).

Banks and Green (1973) repeated the Yost, Wightman, and Green experiment with some modification -- the stimuli had real spatial locations and were not dichotically presented. An anechoic chamber was fitted with three matched and calibrated loudspeakers. The middle speaker, located at the zero azimuth, emitted a continuous wideband noise. The subject was required to identify the location of an acoustical transient presented randomly from either the right or left side of the standard speaker. The observation interval was marked and the subject provided with feedback. The transient signal, a 0.1 msec pulse,

was filtered to emphasize different regions in the stimulus spectrum. Filtering the frequency content of the pulse had little effect; the change in threshold was no greater than 1°, with a range of about .6° to 1.6°. Within that small range, threshold increased as the low frequency content of the signal was attenuated. The results tentatively indicate that in man binaural phase differences are a better clue to azimuth than are binaural intensity differences. These results, however, require two qualifications -- 1) the experiment used a 0.1 msec pulse where most of the energy is below 5000 Hz and a bandpass filter whose upper limit was 6000 Hz. Consequently, the frequency range where the binaural difference spectrum is best expressed was excluded from analysis. 2) Masking noise from the referent speaker may have hindered detection of the higher frequency noise bands. Banks and Green observed that when the sound pressure level of the masking noise was increased, threshold for the high frequency bands was elevated while that for the low pass band was unchanged. Considering these qualifications, additional research is required to fully demonstrate the relative contributions of binaural temporal and intensity differences to the localization of complex stimuli.

Auditory Localization in an Evolutionary Perspective

Masterton contends that the mammalian attribute of an expanded sensitivity range to high frequency stimuli is a consequence of selection for a superior capability to localize acoustic sources (Masterton, Heffner, and Ravizza, 1969; Masterton and Diamond, 1975; Masterton, 1974). If high frequency hearing is an adaptation for auditory localization then its contribution to a spatial sense should be so expressed. In a

restricted context this hypothesis may be tested by the research presented here. The detection of a change in azimuth may be facilitated by high frequency sensitivity. That is, for a given stimulus bandwidth the binaural difference spectrum may lead to greater spatial acuity for high frequency bands than for low frequency bands. Thus selection may have operated to evolve an external ear and neural binaural processor for the optimization of spatial acuity. One way to examine this hypothesis is by the construction of a binaural efficiency quotient. It is generally recognized for any given stimulus bandwidth the number of sensory cells encompassed in that band, (or alternatively, the area on the basilar membrane) decreases as the center frequency of the band is increased (von Bekesy and Rosenblith, 1951; Scharf, 1970). Thus the frequency scale is compressed and higher frequencies are subserved by a smaller proportion of the neural substrate than are lower frequencies. This compression is approximately expressed by a logarithmic scale. A behavioral consequence of this comparison is that the just detectable differences in frequency between two tones increase as the frequency of the stimuli is increased. The just discriminable difference in frequency or frequency difference threshold (Δ f) has been determined for the macaque. Stebbins (1973) reported that the frequency difference threshold was approximately 50 Hz, 90 Hz, and 200 Hz for referent frequencies of 8000 Hz, 11200 Hz, and 16000 Hz respectively. These values may serve as an approximate index of the relative density of the neural represnetation at each frequency. The relative efficiency (E) of the binaural difference spectrum may be arbitrarily defined as the ratio of the threshold for any given stimulus bandwidth to the frequency difference threshold for the same center frequency. The

efficiency quotient for the binaural difference spectrum for the mean threshold of the three monkeys for the 250 Hz and 500 Hz stimulus bandwidths for each center frequency are given in Table 12. Though this quotient is rough and approximate it demonstrates that at 16000 Hz the detection of a change in azimuth for narrow stimulus bandwidths is mediated by relatively less cochlear tissue than at lower frequencies. In this context the results of this research are consistent with the hypothesis that high frequency sensitivity is an adaptation for sound localization. The binaural difference spectrum efficiency quotient does not, however, differentiate between the relative contribution of the magnitude of the interaural spectral differences or of the acuity of the neural processor. Thus selection may have operated either centrally or peripherally. In addition the contribution of high frequency sensitivity to auditory localization may be more dramatically expressed in the determination of elevation in the median plane. Consequently this research only partially demonstrates the role of high frequency sensitivity in the localization of acoustic events.

Auditory Localization in the Bioacoustical Context

Marler (1965) has observed that throughout the class mammalia alarm calls and distress calls share many acoustical features across species. That is, alarm calls are characterized as shrill narrow band barks, while distress calls are typically wide band screeches and screams. Marler (1955, 1957) has made similar observations regarding the vocalizations of many birds and has speculated that the acoustical features of a call may render it more or less readily localized. This proposition was experimentally explored by Konishi (1972) who found

TABLE 12

Binaural Difference Spectrum Efficiency Quotient [a]

	Center Frequency (Hz)			
	8000	11200	16000	Stimulus Bandwidth
Probit	.25	.24	.06	250 Hz
Linear Interpolation	.24	.22	.045	
Probit	.21	.21	.06	500 Hz
Linear Interpolation	.21	.19	.04	

[a] The smaller the quotient the greater the relative efficiency.

that barn owls would strike more accurately at an acoustic prey as the bandwidth of the stimulus was increased. The research presented here corroborates Konishi's results and supports Marler's contention. As a first approximation species specific vocalizations may be described by their bandwidth and dominant frequency; and high frequency, narrow band, more tonal stimuli are harder to localize than are wide band noisier stimuli. These results are consistent with the proposition that the natural variation in the acoustical features of a species's vocal repertoire may be tailored to minimize or exploit location cues as appropriate for the social context.

APPENDIX A

Appendix A

Acoustical Calibration

All measurements were made in an anechoic chamber. The acoustical signal for noise bands and for pure tones was measured in the following manner: A Bruel and Kjaer 1/2 inch free-field microphone (4133) was mounted on a microphone stand 10 cm from the transducer on the speaker's axis. The response of the microphone was measured by a Hewlett Packard (3590 A) wave analyzer. The wave analyzer was adjusted to measure the sound pressure in a 100 Hz bandwidth "window" which was slid along the frequency axis. The acoustic spectrum of the stimulus measured by the wave analyzer was concurrently recorded by a Moseley (135C) X-Y plotter. Figure 41 presents the acoustic measurements for noise bands centered at 16000 Hz. The ordinate is sound pressure level as recorded by the wave analyzer in the 100 Hz bandwidth window. The abscissa is audio frequency represented on a logarithmic scale. The power spectra presented here are for noise bands which were attenuated to maintain a constant sound pressure level of 93 dB re 20 μPa at 10 cm. As a result, as the stimulus bandwidth was increased the sound pressure level per cycle decreased. As may be seen in Figure 41 the narrow bands of noise were essentially rectangular in shape while the wider bandwidths were less regular in shape and the shoulders of the curves were not as steep. The degradation of the stimulus for the wider bandwidths was largely due to

Figure 41

Acoustical Calibration at 16000 Hz. The ordinate is relative sound pressure level as measured by the wave analyzer in a 100 Hz bandwidth window. The abscissa is audio frequency represented on a logarithmic scale. The power spectra were recorded from stimulus bandwidths of 250, 500, 1000, 2000, 4000, 8000 Hz respectively. The high and low cutoff points for each bandwidth are indicated above the corresponding power spectrum.

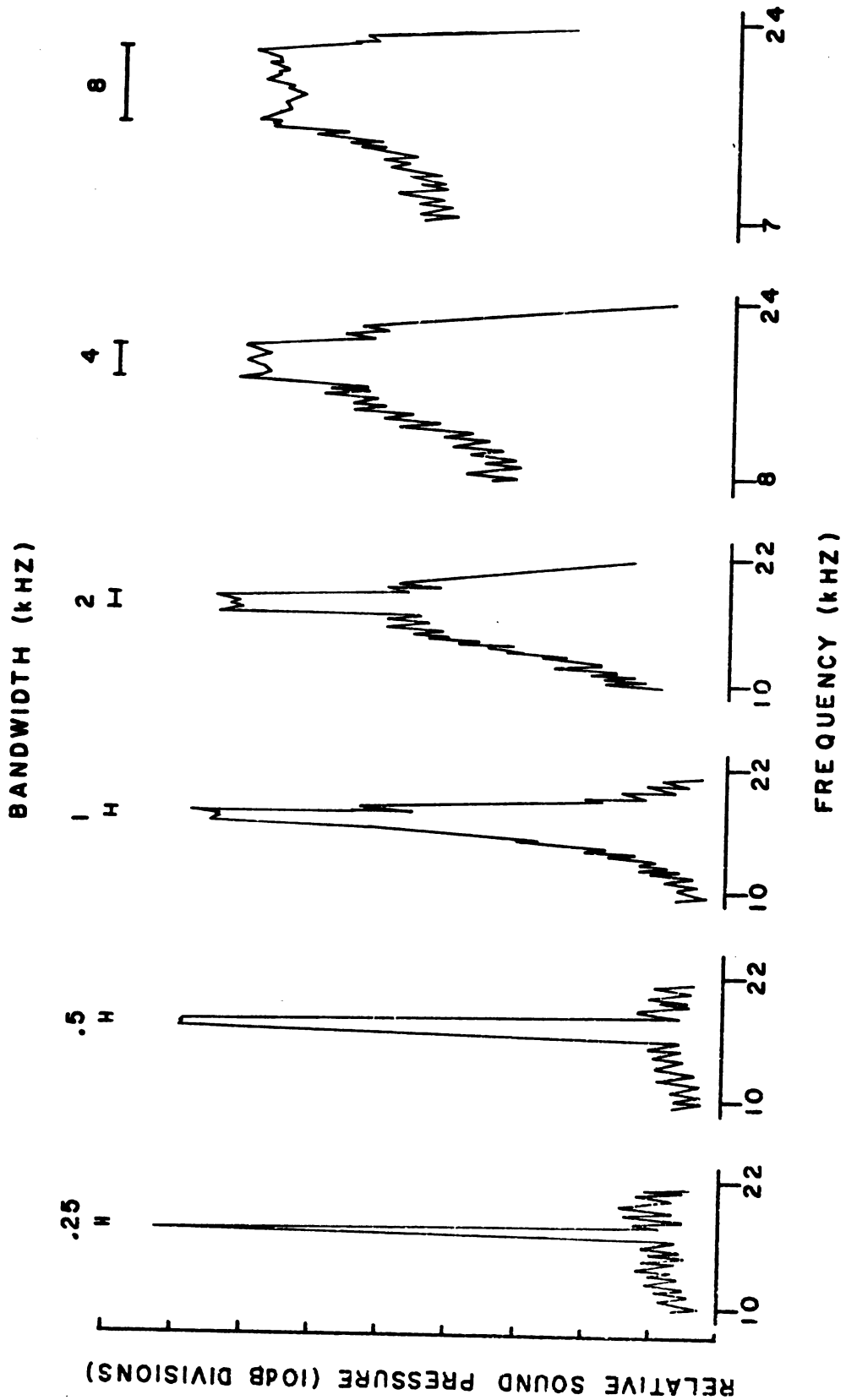

RELATIVE SOUND PRESSURE (10dB DIVISIONS)
BANDWIDTH (kHZ)
.25
.5
1
2
4
8
10
22
8
24
7
FREQUENCY (kHZ)

FIGURE 41

an increase in the noise feedthrough from the analog audio multiplier as the bandpass of the Allison filter was increased. The high and low frequency cutoff points for the noise bands as presented in Table 1 are represented in Figure 41 above the corresponding power spectrum. The sound pressure level for the widest bandwidth, 8000 Hz, was 26 dB down at one octave out from the cutoff points. The slopes for the narrow bandwidths were much steeper and the sound pressure level fell off as much as 75 dB per octave to the ambient noise level. Corresponding acoustical measurements for stimuli centered at 8000, 11200, and 13454 Hz were made. The acoustic spectra for these signals are not reproduced here. These signals were generated by simply changing the oscillator carrier frequency to the appropriate value. As a result, the major difference between the curves generated at 16000 Hz from those centered at other frequencies was their corresponding location on the frequency axis. Acoustical measurements of pure tones (not reproduced here) demonstrated that harmonic distortion was at least 60 dB down from the fundamental, and electrical measurements indicated that most of the signal recorded at harmonic intervals was generated by the oscillator.

Equating Transducers

As previously stated it was important to minimize the contribution of speaker differences to the detection of a change in acoustic locus. The matching of speakers is largely opportunistic and the relevance of an acoustical difference between two speakers must ultimately be determined by the bahavior of the subject - do they sound different? As a result, the speakers were initially matched by the ear of the

Figure 42

Acoustical Measurements of 5 Transducers for the 8000 Hz Stimulus Bandwidth Centered at 11200 Hz. The ordinate is relative sound pressure level as measured by the wave analyzer in a 100 Hz bandwidth window. The abscissa is audio frequency represented on a logarithmic scale. The response characteristic for each transducer is shifted 20 dB with respect to one another.

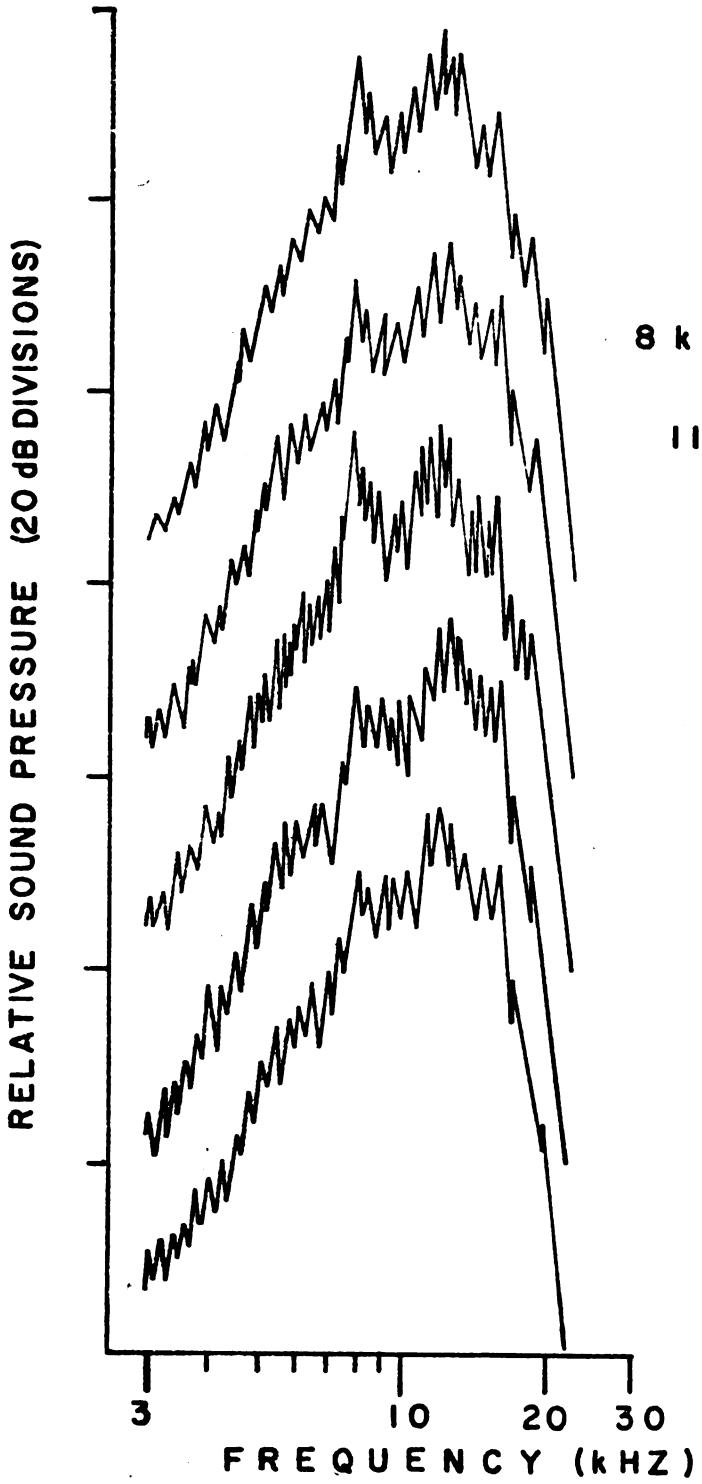

RELATIVE SOUND PRESSURE (20 dB DIVISIONS)
8 kHZ BAND
at
11200 HZ
3
10
20
30
FREQUENCY (kHZ)

FIGURE 42

experimenter and this match was subsequently confirmed or rejected by the behavior of the subjects. Figure 42 presents the acoustical measurements for five speakers for the 8000 Hz bandwidth stimulus centered at 11200 Hz. The curves are shifted 20 dB with respect to one another. The intensity of the signal between transducers was subsequently equated within 1 dB. This was performed by mounting the microphone in the sound field of the transducer. Measurements made by this system were easily reproduced and the sound pressure levels for each speaker were adjusted by Daven (PT 324-M) attenuators.

APPENDIX B

Appendix B

The Proportion of Trials Detected at Each Azimuth

TABLE 13

Ratios of Correct to Total Responses for Bandwidths Centered at 8000 Hz

	Angle (degrees)				
	0.0	2.9	8.6	17.2	28.6
			1 Hz Bandwidth		
Sidney	16/445	47/805	299/657[a]	473/622	722/776
Miko	96/765	195/904	475/727	622/716	786/813
Oscar	97/822	188/830	247/605	510/604	717/760
			250 Hz Bandwidth		
Sidney	27/704	70/1290	290/826[a]	706/991	1158/1256
Miko	140/1141	166/1129	377/930	695/921	1103/1186
Oscar	89/1053	121/966	328/780	613/782	949/973
			500 Hz Bandwidth		
Sidney	24/783	67/1438	483/1035[a]	948/1131	1284/1345
Miko	116/907	180/958	378/775	618/744	810/836
Oscar	121/1374	201/1231	413/1101	884/1056	1274/1282

TABLE 13 (cont'd.)

		1000 Hz Bandwidth			
Sidney	11/551	62/1092	430/687[a]	679/761	976/1097
Miko	140/1170	231/1119	535/970	814/853	1048/1052
Oscar	71/1035	144/919	404/814	674/708	887/888
		2000 Hz Bandwidth			
Sidney	16/527	112/1035	461/703[a]	676/824	956/998
Miko	104/960	214/954	469/778	758/784	957/966
Oscar	58/1179	136/1077	554/888	833/840	1047/1048
	0.0	2.9	8.6	17.2	L
		4000 Hz Bandwidth			
Sidney	7/200	82/549	239/376	518/520	25/337
Miko	53/400	149/373	293/319	360/360	54/315
Oscar	38/390	193/426	375/383	436/436	34/353
		8000 Hz Bandwidth			
Sidney	7/239	77/522	294/385	551/552	19/486
Miko	92/563	192/390	332/348	396/396	44/341
Oscar	26/428	204/410	367/369	439/440	32/366

[a] Sidney tested at 12.0° rather than at 8.6°.

TABLE 14

Ratios of Correct to Total Responses for Bandwidths Centered at 11200 Hz

	Angle (degrees)				
	0.0	1.3	7.8	15.5	29.5
		1 Hz Bandwidth			
Sidney	35/602	47/591	196/662	260/536	301/502
Miko	140/1098	86/248	128/558	228/533	308/457
Oscar	153/905	25/101	87/274	220/390	267/320
		250 Hz Bandwidth			
Sidney	32/511	10/370	83/595	93/468	320/478
Miko	138/1030	38/278	188/620	260/503	268/469
Oscar	178/1244	65/439	155/534	270/506	408/458
		500 Hz Bandwidth			
Sidney	17/531	9/428	70/500	171/399	306/423
Miko	134/1101	46/332	159/487	296/444	221/394
Oscar	115/799	43/315	175/424	165/382	346/361
		1000 Hz Bandwidth			
Sidney	23/541	15/381	101/524	218/417	390/485
Miko	97/784	24/297	171/409	299/372	304/362
Oscar	96/858	64/324	115/362	150/303	252/286

TABLE 14 (cont'd.)

		2000 Hz Bandwidth			
Sidney	17/608	25/704	258/590	405/540	645/667
Miko	58/680	39/399	254/375	291/297	351/352
Oscar	83/608	50/327	216/332	277/311	321/340
		4000 Hz Bandwidth			
Sidney	17/616	19/623	328/591	437/454	510/510
Miko	51/637	46/428	349/388	303/303	298/298
Oscar	32/584	52/465	362/371	350/350	423/423
		8000 Hz Bandwidth			
Sidney	3/412	14/428	270/353	345/351	369/370
Miko	69/905	132/615	510/548	502/512	569/576
Oscar	32/790	163/751	614/627	569/570	701/701

TABLE 15

Ratios of Correct to Total Responses for Bandwidths Centered at 16000 Hz

	Angle (degrees)				
	0.0	1.3	7.8	15.5	29.5
			1 Hz Bandwidth		
Sidney	15/693	9/323	166/711	272/655	334/508
Miko	71/824	124/634	286/638	428/471	486/488
Oscar	82/694	130/536	310/493	294/409	347/437
			250 Hz Bandwidth		
Sidney	24/546	23/570	181/610	282/482	388/461
Miko	35/510	66/548	352/544	292/368	395/395
Oscar	57/537	66/468	349/472	312/393	372/414
			500 Hz Bandwidth		
Sidney	18/577	44/626	315/566	341/450	454/490
Miko	49/834	79/749	352/715	503/548	522/525
Oscar	74/808	127/683	396/698	408/537	375/463
			1000 Hz Bandwidth		
Sidney	13/475	25/493	192/500	364/405	363/366
Miko	26/488	36/458	323/452	331/338	351/351
Oscar	49/680	81/514	472/537	394/405	384/401

TABLE 15 (cont'd.)

2000 Hz Bandwidth					
Sidney	8/555	20/439	258/438	335/343	343/346
Miko	37/611	39/509	356/460	377/385	424/429
Oscar	24/614	42/523	517/538	421/421	405/405
4000 Hz Bandwidth					
Sidney	1/434	10/430	238/399	318/323	327/327
Miko	33/669	45/614	534/581	470/471	428/430
Oscar	18/397	41/411	374/380	279/280	301/302
8000 Hz Bandwidth					
Sidney	4/458	9/479	339/490	351/359	370/372
Miko	22/411	26/432	382/410	333/334	310/310
Oscar	24/617	63/469	507/517	403/403	383/383

TABLE 16

Ratios of Correct to Total Responses for Bandwidths Centered at 11200 Hz: Replication

	Angle (degrees)				
	0.0	7.8	15.5	29.5	46
	250 Hz Bandwidth				
Sidney	10/407	58/386	147/392	164/297	172/213
Miko	19/146	15/133	51/132	50/96	27/105
Oscar	78/775	201/572	224/551	386/420	315/316
	500 Hz Bandwidth				
Miko	11/131	18/132	64/116	75/90	83/104

	Angle (degrees)				
	0.0	1.3	7.8	15.5	29.5
	8000 Hz Bandwidth				
Sidney	2/368	6/377	216/351	277/278	301/303
Miko	4/267	8/239	164/202	188/188	174/174
Oscar	14/268	31/194	205/208	132/132	164/164

TABLE 17

Ratios of Correct to Total Responses for Bandwidths Centered at 13454 Hz

	Angle (degrees)				
	0.0	1.3	7.8	15.5	29.5
			1 Hz Bandwidth		
Sidney	16/576	53/559	370/635	245/553	185/500
Miko	44/543	57/405	160/576	216/410	383/421
Oscar	62/500	301/536	333/523	209/400	162/405
			250 Hz Bandwidth		
Sidney	13/640	30/522	238/676	234/591	321/565
Miko	67/580	154/639	319/584	365/480	426/448
Oscar	76/680	263/584	293/519	271/434	222/435
			500 Hz Bandwidth		
Sidney	12/649	27/398	174/647	186/517	296/518
Miko	37/487	79/382	245/479	347/413	400/415
Oscar	94/680	254/695	356/669	185/493	294/525
			8000 Hz Bandwidth		
Sidney	10/584	42/558	426/584	505/513	479/480
Miko	29/444	77/521	507/539	395/396	395/396
Oscar	25/687	73/595	578/620	462/474	447/454

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