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LATERALIZATION OF AUDITORY STIMULI IN MONKEYS

by

DIRK HOUBEN

A dissertation submitted to the Graduate
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1977

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7/20/77
date

George Gourevitch
Chairman of Examining Committee

7/22/77
date

Florence L. Denmark
Executive Officer

Prof. George Gourevitch

Prof. Eric Heinemann

Prof. Harry Levitt
Supervisory Committee

The City University of New York

Abstract

LATERALIZATION OF AUDITORY STIMULI IN MONKEYS

by

Dirk Houben

Adviser: Professor George Gourevitch

The ability of one species of monkey, M. nemestrina, to discriminate small interaural time and intensity differences was investigated at various frequencies. In one of the three experiments animals were trained to report which ear received the more intense stimulation from a dichotic tone pulse. A diotic reference pulse and the dichotic comparison pulse were presented via earphones at 60 dB SPL. Various interaural intensity differences were presented in a forced-choice, constant stimuli procedure. In a second experiment the same procedure was used to train monkeys to report which ear received the leading signal in a phase shifted comparison pulse.

In both experiments the measured thresholds varied as a function of frequency. The monkeys were maximally sensitive to interaural intensity differences at 250 Hz and 500 Hz, and least sensitive at 8,000 Hz; thresholds varied from 3.6 dB to 7.2 dB over this range. Unlike man, the sensitivity to interaural time differences of all three monkeys extended up to 2,000 Hz. Thresholds were about 50 μsec for frequencies above 750 Hz, higher at 250 Hz and 500 Hz.

In a third experiment the effect of combining phase and intensity information was investigated. Results from all three experiments indicate that the monkey is different from man in his ability to discriminate small interaural disparities. Predictions about the monkey's ability to localize actual sound sources were based on the time difference thresholds measured in this study. These predictions are well supported by previously reported measures of localization ability.

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Introduction

The auditory system of an animal not only can alert him to an acoustic event of possible consequence, but can also locate its source. This characteristic of hearing is largely binaural, and depends on the occurence of non-identical acoustical signals at the two ears, from which direction of the sound is extracted. Much of the research on auditory localization has attempted to identify the variables underlying this function and to specify their relative contribution to the accuracy of localization.

Since these variables usually occur together, another experimental arrangement is necessary to isolate their separate effects on localization. This is achieved in lateralization experiments in which separate acoustic signals are delivered through earphones to each ear, and controlled independently. In this way only one variable at a time can be investigated while the others are held constant.

Almost all of the research done in this area has been conducted on man. Without a doubt, his ability to localize sound and his sensitivity to interaural cues as examined individually, are impressive indeed.

Since few studies have been conducted on animals, the present research is directed at measuring the sensitivity of one species of monkey (M. nemestrina) to interaural phase and intensity differences in an attempt to examine whether animal localization resembles human localization, and whether the latter can serve as a model for the former.

Binaural Acoustic Variables

If we assume that the human or monkey head is roughly a sphere we can analyze how this sphere interacts with a plane wave front. Woodworth (1938) proposed an analysis which is reproduced in modified form in Figure 1. For sound sources greater than 1 meter from the sphere the wave front at the sphere may be considered a plane surface. In Figure 1, the page represents the horizontal plane extending from the ears. In this plane sounds originating at angles other than 0° azimuth (directly ahead) and 180° azimuth (directly behind), will have to travel a distance d to the nearer ear and a distance $d + \Delta d$ to the farther ear. The extra distance, Δd, is the sum of the straight line segment, $r \sin \theta$, and the arc, $r\,\theta$; it can be expressed as

$$\Delta d = r\,(\theta + \sin\theta)$$

where r is the radius of the sphere in centimeters, and θ is the angle of the sound source in radians.

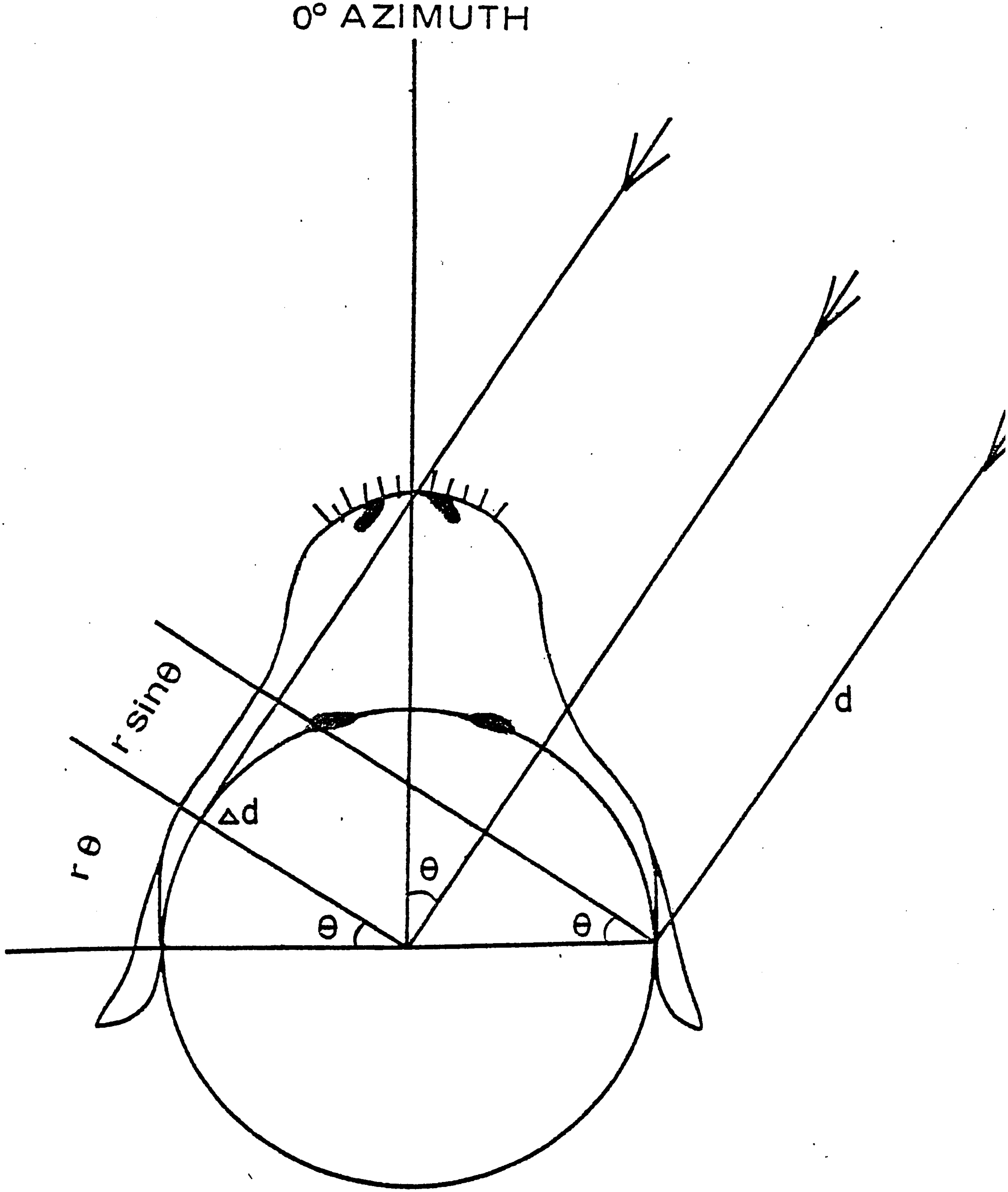
Since sound speed is approximately 340 m/sec in air, the elapsed time per unit length of travel is 29 μsec/cm $[340 \times 10^2 \text{ cm/sec}]^{-1}$. The temporal difference at the two ears can be simply expressed as

$$\Delta t = \Delta d\,(29)$$

where t is in μsec and d is in cm.

Figure 1

The additional path to the distal ear travelled by a sound originating to one side of the animal. The biaural distance difference, Δd, is the sum of the straight line segment labelled $r \sin \theta$, and the arc labelled $r \theta$. Adapted from Woodworth (1938).



0° AZIMUTH
r sinθ
d
Δd
rθ
θ
θ
θ

The physical arrangement shown in Figure 1 suggests immediately cues that can serve the organism in localization. It is apparent that since sound originating to the side of the monkey must travel further to the distal ear, a difference in time of arrival of the signal wave front at the two ears results. This transient time difference is especially well deliniated with impulsive sounds, and may serve as a cue to the direction of the source. For continuing sounds, such as maintained sinusoids, an on-going phase difference between the ears exists, which can also serve as a localizing cue. Finally, an intensity difference across the ears may occur, and serve as directional information. This happens when the dimensions of an object in a sound field are large compared to the wave length of the tone. The sound shadow is negligible at low frequencies since the wavelengths of such tones are long relative to the object and refract around it. In practice, this simple relationship is complicated by the azimuth of the sound source. Feddersen, Sandel, Teas, & Jeffress (1957) measured directly the intensity difference at the ears of human subjects at various frequencies and for different azimuths. They found that intensity differences depended in a complex way on frequency and azimuth. For example, they observed approximately a 20 db intensity difference for a 6 kHz tone originating at 90° azimuth; but a similar difference was also seen at 60°, 100°, and 110° azimuth.

For humans and many smaller animals the arrangement depicted in Figure 1 is the same. However, because the head size of the animal may be a fraction of the human, the time difference cues are much smaller. Similarly, for a given frequency, the sound shadow cast by small animals will be smaller than for man. Harrison and Downey (1970) measured intensity differences at the ears of squirrel monkeys, rats, bats, as well as humans. They found that, in general, the difference in intensity for a particular frequency originating at a given azimuth decreased with head size. Again, as in humans, the interaural intensity disparities they observed in animals depended in a complex fashion on frequency and azimuth.

Human Studies

Wallach, Newman, & Rosenzweig (1940) performed a series of experiments that showed that the difference in time of arrival at the two ears of a human subject was a powerful determinant of where a sound was perceived to originate. Two speakers were placed in front of the subject such that the angle between the speakers and the subject was 60°, and the speakers were equi-distant from the subject. Under these conditions, with both speakers emitting equal intensity in-phase clicks, the subject reported the sound to be emanating from a point half-way between the speakers. When one of the speakers was moved 30 cm closer to the subject, he reported that all the sound appeared to originate from the closer speaker. This amounted to a 30° shift in the perceived location of the sound source. Since the speed of sound is 340 m/sec, moving one speaker 30 cm closer resulted in a 1 msec difference in the time of arrival of the clicks at the subject's ears. In addition, since the speakers were originally located 3 m from the subject, a 10% decrease in distance, according to the inverse square law, would result in a 1 dB increase in intensity from the nearer speaker.

To show that it was the difference in time of arrival, and not the difference in intensity, that was responsible for the perceived shifts, the authors once again placed the speakers equi-distant from the subject and this time electrically introduced a 1 msec delay between the click of one speaker and the click of the other. Both clicks were now equally intense but the sound was still perceived to be coming from the speaker that presented the leading click. Comparable results were obtained using clicks presented via earphones, a procedure that was presumed to allow a more precise control over intensity and interaural delay. The threshold for judgments of "left" or "right" when the click led or lagged in the left ear was found to be around 45 μsec. The authors emphasized that for clicks the "precedence effect" was the major determinant of localization.

Another approach to localization was proposed by Jeffress & Taylor (1961). They presented binaurally two second noise bursts delivered by earphones and asked their subjects to turn on one lamp in a spatially distributed set of lamps, corresponding to the location of the perceived direction of the acoustic image. The location of the image was varied by introducing interaural delays ranging from 0 to 657 μsec. These time differences had previously been observed for sounds originating at azimuth positions between 0° and 90° (Feddersen, Sandel, Teas, & Jeffress, 1957). The subjects were able to assign external angular locations quite accurately and the authors suggested that the distinction between localization and lateralization be based on what the subject is asked to do, rather than how the sound is presented. It was only in 1968 that the distinction between localization (free-field sound presentation) and lateralization (binaural earphone sound presentation) was suggested (Sone, Ebata, and Nimura, 1968). This convention has been followed in the subsequent literature, as it is here.

Time disparity which may serve as a cue in localization has often been called "phase difference" and "time difference", leading to some confusion as to whether the terms refer to the transient arrival time difference of the initial wave front, or to the on-going time difference that lasts for the duration of periodic sounds. The convention that appears to have been adopted in the recent literature allows time and phase to be used interchangeably when referring to on-going differences. Arrival time differences are now usually referred to as onset, or transient disparities.

The contribution of these transient disparities to lateralization was the subject of a study by Perrott & Baars (1974). Binaural noise bursts of various durations were presented to subjects who were required to detect either interaural onset or offset disparities. Thresholds for identifying the direction of the onset or offset differences were inversely proportional to burst duration. For all pulse durations the direction of the onset disparities was easier to detect than the direction of the offset disparities. Transient thresholds ranged from 180 µsec for onset of 1 msec noise pulses, to 3.2 msec for offset of 1 sec noise pulses. The results indicate that transient image shifts are effective cues for lateralization only when the signal duration is brief. For longer duration signals the ongoing stimulation determines the location of the image.

One of the most extensive experiments on auditory localization was performed by Mills (1958). He noted that prior to his study, investigators of localization measured the absolute error of localization by asking a subject to point toward a hidden sound source and noting the difference, in degrees, between the indicated and the actual location of the speaker. Mills was interested in the resolving power of auditory localization and, by analogy with the concept of minimum visual angle, he defined the minimum audible angle as "... the smallest detectable difference between the azimuths of two identical sources of sound" (Mills, 1958, p. 237).

Subjects were seated in an anechoic chamber. A speaker suspended from the ceiling could be rotated about the subject's head while always maintaining the same distance from the head. The stimuli were 13 different frequencies, ranging from 250 to 10,000 Hz, presented at 50 dB SPL. The psychophysical method was a forced-choice variation of the method of constant stimuli. A trial consisted of a standard 1 sec tone burst followed 1 sec later by a 1 sec tone burst from the speaker which had been displaced either to the left or to the right during the interpulse interval. Left and right displacements were randomized across trials, and the amount of displacement was varied according to the method of constant stimuli to yield a complete psychophysical function. The subjects were asked to indicate whether the second tone burst was to the left or to the right of the reference burst and were told to guess if they were not sure. The minimum audible angle was defined as half the distance between the 25% and 75% points for saying "right".

Mills found that the minimum angle was smallest when the azimuth of the reference tone was straight ahead (0^{o}), and greatest when the azimuth of the reference tone was to the extreme right (90^{o}). Regardless of the azimuth of the reference, the minimum angle function decreased between 250 Hz and 1,000 Hz, increased rapidly near 2,000 Hz, and then decreased again, reaching a second minimum between 3,000 and 8,000 Hz. The smallest observed minimum audible angle was for a 750 Hz tone at 0° azimuth, and was less than 1°. For high frequencies originating from extreme lateral positions, the minimum angles were estimated to be greater than the available 40° rotation of the speaker.

To establish the relative contributions of interaural phase and interaural intensity differences, Mills measured these directly by replacing the human subject with a dummy head that had a condenser microphone fitted in each artificial ear where normally the tympanum would be. Phase measurements were made as a function of azimuth and frequency, only up to 1,500 Hz. In general, as azimuth increased, so did phase difference. Above 750 Hz the phase difference for lateral azimuths actually exceeded 180° that is, the phase at the proximal ear lagged the phase at the distal ear. When the phase differences were converted to time differences, a plot of minimum audible angle as a function of frequency showed that the time difference required to localize a sound near the midline reached a minimum of 10 µsec at about 800 Hz, and rose rapidly at higher frequencies. Mills concluded that the upper frequency limit for phase discrimination is about 1,400 Hz and that at higher frequencies intensity differences become the primary cue.

In an experiment in which equal intensity tone pulses were delivered through earphones, Zwislocki & Feldman (1956) found that the just noticeable interaural phase difference changed with frequency in the same way as reported later by Mills (1958) for free field stimulation. The excellent agreement between these two functions extended up to 1,250 Hz, which they determined as the frequency limit for lateralization of pure tones by humans. Similar findings were reported by Klumpp & Eady (1956).

Another significant finding in the lateralization study by Klumpp & Eady (1956) was that their subjects could detect interaural time differences in high frequency band-limited noise. Recently, a renewed interest has emerged in this time cue provided by complex waveforms with energy only at high frequencies. Henning (1974;a) and McFadden & Pasanen (1976) used as stimuli two-tone complexes composed of a high frequency carrier and a low frequency modulator. Both investigators used an intense low-pass noise to mask out any possible difference tones. Henning's results indicate that the threshold for interaural time differences is the same whether the stimulus is a 300 Hz pure tone, a 3,900 Hz carrier modulated by a 300 Hz sine wave, or a two tone complex in which only the modulating frequency is delayed. The last condition provides a signal in which only the envelope, not the entire waveform, is delayed. In their experiment, McFadden & Pasanen presented two-tone complexes centered around 4,000 Hz. The frequency difference between the tones of the complex ranged from 25 to 550 Hz. Threshold for interaural delay using these complexes decreased as the frequency separation increased, up to about 250 Hz. For separation greater than 275 Hz the lateralization threshold increased. Here, as in Henning's study, the threshold for lateralization of complex tones approached the thresholds reported in the literature for low frequency pure tones.

The same investigators (Henning, 1974, b; McFadden & Pasanen, 1976) also measured lateralization thresholds for noise stimuli with interaural delays. Henning presented bands of noise centered at 3,900 Hz; no systematic change in threshold was found as a function of bandwidth. Both observers in this study had thresholds of about 10 μs for the 600 Hz band and greater thresholds for bandwidths ranging from 100 to 2,500 Hz. McFadden & Pasanen used two different center frequencies for the band-limited noise bursts presented in their experiment. For the low frequency noise (500 Hz center frequency) no improvement in lateralization performance was found as the bandwidth was increased from 1 (pure tone) to 100 Hz. In contrast, lateralization of high frequency noise centered about 4,000 Hz improved with increases of noise bandwidth from 50 Hz to 800 Hz.

These studies do not contradict the previous findings that for pure tones above 1,500 Hz human subjects cannot utilize on-going interaural time differences for lateralization judgments. They do indicate, however, as has been suggested by McFadden & Pasanen, that the so-called duplex theory of sound localization, based as it is on pure tone data, is limited to a rather small class of acoustic stimuli. McFadden & Pasanen also suggested that it might be useful to distinguish three distinct time related cues: onset-time difference, on-going time difference, and envelope time differences in complex stimuli.

Mills (1960) using a psychophysical technique similar to the one he applied in an earlier paper (Mills, 1958), measured interaural intensity thresholds by requiring his subjects to report whether a test tone appeared to the right or left of a fixed tone pulse. He investigated frequencies from 250 Hz to 10,000 Hz and found that the threshold ranged from a low of 0.5 dB at frequencies above 1,000 Hz, to 1.0 dB at about 1,000 Hz. Mills also plotted the interaural intensity differences produced by actual sources. Between 1,500 Hz and 5,000 Hz this function almost overlays the function obtained using dichotic stimuli, lending support to the hypothesis that for human subjects intensity is the basis for localization of pure tones above 1,500 Hz.

A recent study has attempted to validate the experimental approach of using earphone simulation to investigate the parameters of free-field localization (Molino, 1974). Molino calculated, based on speed of sound and distance traversed, the interaural time difference that would be expected at the ears of a subject if speakers were placed at 20 azimuths in an open field. For each of these 20 azimuths in the first quadrant he also obtained empirical estimates of interaural intensity differences from the literature. These intensity differences and time differences were presented via earphones using a psychophysical procedure similar to Mills' (1958); the minimum audible angles were determined for each of four reference azimuths at three frequencies. The functions relating frequency and just noticeable differences in azimuth closely followed those of Mills, and supported the assumption that at least some of the variables under free-field conditions can be duplicated by presenting stimuli via earphones.

Animal Studies

Few of the studies on localization and lateralization in animals have attempted to establish the precision with which animals localize; nor have they been concerned with systematic examination of pertinent acoustic cues such as interaural intensity and time differences. Most investigations have been concerned with the anatomy of the brain underlying localization and lateralization; that is, they ascertained whether removal of specific cortical or subcortical areas produced deficits in these auditory functions. Typically, the psychophysical and behavioral methods used were quite crude. For example, Neff, Fisher, Diamond, & Yela (1956) trained cats to obtain food by walking toward one of two goal boxes behind which a buzzer had sounded. The goal boxes were separated by 25° or more; normal cats could readily learn this discrimination. Cats with large bilateral auditory cortex lesions did not retain the discrimination, nor could they be retrained. They could, however, perform the task when visual cues were substituted, thus ruling out an overall performance deficit.

To avoid the potentially contaminating effects of behavior deficits caused by large lesions, Thompson & Welker (1963) used the orienting reflex (head turning toward the sound source) of a cat as the indicator of localization. Although cortical ablation modified the orienting responses, no accurate measure of auditory spatial resolving ability was obtained.

In a series of lateralization studies with cats (Masterton & Diamond, 1964; Masterton, Jane, & Diamond, 1967, 1968) Clicks were delivered through earphones mounted on helmets worn by the animals. They were trained in a double-grill shuttle box to avoid shock by moving to the alternate compartment during the "warning signal". The "safe signal" consisted of a dichotic click train in which the click to one ear led the other by 0.5 msec. The "warning signal" was the reverse. Again, in these experiments lesions were made at various sites in the auditory pathway and the performance assessed. In only one study was an interaural time difference threshold determined and this was only done on one intact cat (Masterton et al., 1967). The threshold was stated to be between 50 and 100 μsec.

In their study Ravizza & Masterton (1972) reported minimum audible angles in the normal and ablated opossum. They used a conditioned suppression technique in which the safe signal was a series of noise bursts presented to the left of the midline, and the warning signal was a series of noise bursts presented to the right of the midline. The angular separation between the safe and warning signals was diminished symmetrically about the midline to determine the threshold. Unfortunately, the ordinate of the discrimination function was expressed in terms of a lick-suppression ratio and no mention was made of a criterion for suppression. For the purpose of comparing normal animals to ablated animals this reporting was adequate; but all that could be seen in the graphs was that the ratio was 0 (no suppression) when the angular separation was 0°, and that by the time the angular separation was 30° the suppression ratio had reached 0.80.

Finally, two additional studies demonstrated that monkeys and rats will readily learn to localize a sound source when they are permitted to move toward it (Beecher & Harrison, 1971; Harrison, Downey, Segal, & Howe, 1971).

Only recently have a few animal studies appeared that have investigated systematically some of the parameters of localization and lateralization. Casseday & Neff (1973) reported the minimum audible angle for cats in a free field using a method similar to that of Neff et al. (1956). Cats were trained to leave a starting box when a tone sounded behind one of two goal boxes. If the cat approached the correct box it was rewarded with the food that had been placed inside. If the cat made an incorrect response, both boxes were locked and no reinforcement was given. The speakers were 3 feet from the starting box. The separation of the speakers was changed in a decreasing method of limits. Threshold for inter-speaker azimuth difference was defined as that angular separation which resulted in 75% correct responding. Tones of six different frequencies, at octave steps from 250 Hz to 8,000 Hz, were presented at about 50 dB above the published threshold for the cat. The signal to be localized had a rise-decay time of 100 msec and was presented five times for each trial with duration 1 sec on, 1 sec off.

Curves of angular separation thresholds as a function of frequency for eight cats are quite similar. The average threshold curve shows a slight decrease from 11° minimal angle at 250 Hz to 8° minimal angle at 2,000 Hz. At 4,000 Hz the threshold is up to 25° and at 8,000 Hz it is back down to about 18°. Human observers were also tested in this study to provide an anchoring point for the cat data. Observers placed their heads at the position of the starting box and made at least 100 judgments per frequency using the same decreasing method of limits. The average curve for five human observers shows a steady rise in minimum audible angle between 250 Hz and 2,000 Hz (from about 5° to 18°). At 4,000 Hz the threshold drops to about 12° and remains approximately the same at 8,000 Hz. One difference in the cat and human data appears at 250 Hz, where the human observers appear to be more sensitive. The other major difference is in the point of worst performance. Human subjects are least sensitive at 2,000 Hz, while in the cat the least sensitive frequency is 4,000 Hz. The general shape of the minimum audible angle curve for human observers agrees well with that published by Mills (1958), except that it seems to be shifted upward by at least 6°.

Casseday & Neff (1973) made no attempt to restrain head movement so that the animal could presumbly maximize the cues by both head and pinna orientation. A lateralization study by Wakeford & Robinson (1974) examined the sensitivity of the cat to interaural phase and intensity differences. In a shuttle-box avoidance situation, cats were trained to move to another compartment whenever the on-going interaural disparity favoring one ear was shifted to the other ear. For the interaural intensity study 500 msec tone bursts at 70 dB SPL were presented. The warning stimulus consisted of three pulses in which the signal intensities at the two ears were reversed. The interval between pulses was 1.17 sec, rise-decay time was 50 msec. Thresholds, defined as $P(C) = 0.80$, were found to vary as a function of the three frequencies investigated. For three cats the intensity difference threshold decreased monotonically from 500 Hz to 3,000 Hz. The highest threshold was about 2 dB at 500 Hz and the lowest was 0.5 dB at 3,000 Hz. The cat is about 1 dB less sensitive at 500 Hz than are humans, but almost identical at 1,000 Hz and 3,000 Hz, when compared to the data of Mills (1960). The interaural time difference threshold was obtained at four frequencies, using the same procedure. Average thresholds for 500 Hz and 1,000 Hz were about 25 μsec ($P(C) = 0.75$), and increased to about 90 μsec at 2,000 Hz. None of the three cats could utilize temporal cues at 3,000 Hz.

Over the range of frequencies tested, these data indicate that the cat is almost as sensitive to interaural intensity differences as man. However, with respect to the time difference cue the cat appears to be quite different. Cats are able to utilize time difference cues to lateralize tones up to at least 2,000 Hz, whereas man is unable to lateralize beyond 1,500 Hz. Also, the time difference thresholds for the cat at 500 Hz and 1,000 Hz are about twice as large as those reported for man (Zwislocki & Feldman, 1956). These larger time difference thresholds, coupled with the smaller interaural distance for cats, lead to the prediction that the cat cannot localize low frequency pure tones as accurately as man. When the localization function for cats (Casseday & Neff, 1973) is compared to the function obtained for humans by Mills (1958), this prediction is verified. However, if we instead compare the cat localization function to the minimum audible angles Casseday & Neff (1973) obtained for their human subjects, the prediction is not verified. At 1,000 Hz and 2,000 Hz the cats used in that study had smaller minimum audible angles than the human subjects tested with the same apparatus.

Kelly (1974) investigated the precedence effect in rats and has also obtained estimates of the rat's sensitivity to interaural time delays. The animals were first trained to make a simple left-right discrimination in a conditioned suppression paradigm according to which rats drinking water from a spout were given at times an acoustic signal which was always terminated with an electric shock. The safe signal consisted of 1/sec clicks from a speaker located at 270° azimuth; for the five second warning interval the clicks were shifted to a speaker located at 90° azimuth. Each speaker was located 18 inches from the water spout.

After the animals reliably suppressed licking in the presence of the warning signal, the monaural clicks were replaced by delayed binaural click pairs. For delay between 0.5 msec and 4 msec, performance was relatively unaffected by the change in stimulus conditions. This indicated that the left-right discrimination task and the delayed binaural click task were similar. The animals responded as though the sound were emanating from the speaker with the leading click, which is consistent with the belief that the precedence effect is a determinant in sound localization in animals.

Kelly also trained five of the rats to discriminate smaller interaural time delays. Threshold for detecting the reversal in click pairs was between 31 µsec and 62 µsec, depending on the criterion for a threshold suppression ratio. Although the speakers were located 18 inches from the animals' head, the results were similar to click lateralization thresholds for the cat (Masterton et al., 1976). As pointed out by Kelly, the size of the rat's head limits time difference cues to 113 µsec maximum. It is therefore, unlikely that phase information alone would allow the rat to localize sounds as accurately as animals with larger heads.

Localization in monkeys has been studied by Brown, Beecher, Moody, & Stebbins (1975, 1976), both as a function of frequency and as a function of noise bandwidth.

The monkeys (*Macaca*) were trained to release a response disk when a series of acoustic pulses was switched from a speaker located at 0° azimuth to one of four other locations on the observer's right . The minimum audible angle function for pure tones, averaged across the three subjects, reaches a minimum of 4° at 1,000 Hz. At lower frequencies localization ability deteriorates rapidly; at 250 Hz the threshold is up to 21°. Above 1,000 Hz threshold increases gradually up to 11,200 Hz, where it reaches 18°; at 16,000 Hz, the highest frequency tested, the threshold declines somewhat to about 12°.

An interesting feature of the data presented by Brown, et al. (1976) concerns the role of noise bandwidth. In general, as the bandwidth of a noise centered at various frequencies increases, the minimum audible angle decreases. This relationship holds for stimuli centered at 250, 4,000, 8,000 and 11,200 Hz, and less clearly at 16,000 Hz. However, increasing bandwidth for intermediate stimuli centered at 500, 1,000, and 2,000 Hz brings little or no improvement in minimum audible angle, indeed, at 1,000 Hz the best performance is obtained for a pure tone. These results suggest that a different cue appears at low frequencies, which is in accord with the duplex theory of localization.

The first lateralization study on monkeys was reported by Don & Starr (1972). Click trains were presented to squirrel monkeys via condenser microphones positioned so that they just touched the tragus of each ear. The monkey was required to press the right lever when the click to the right ear was leading or more intense, and the left lever when the signal to the left ear was leading or more intense. The 250 µsec duration clicks were presented at a repetition rate of 32/sec. The monkey's response terminated the clicks and the trial; correct responses were rewarded by food, incorrect responses were followed by a 10 sec time-out. The three intensity levels used were 40, 50, and 60 dB above the experimenter's threshold. Interaural disparity was varied using a block up-down method with step sizes of 20 µsec for the time difference and 2 dB for the intensity difference.

Using a threshold level of 85% correct, (apparently two of the four monkeys refused to work at stimulus disparities that produced less than 78% correct) yielded threshold estimates for interaural time difference ranging from 60 to 180 µsec depending on the monkey and the intensity level. Although not all monkeys were tested at all levels, time difference thresholds tend to be lower for more intense stimuli. The two monkeys that yielded no data points below 78% gave very shallow psychometric functions that barely rose above 85% even at 200 μsec.

The interaural intensity difference functions were more orderly and complete, suggesting that this was an easier task for the monkeys, a point that was also raised by the authors. Thresholds for the four monkeys ranged from 6 to 10 dB, and there did not seem to be an overall intensity effect. The click time difference thresholds were higher than the 11 μsec reported by Klumpp & Eady (1956) for human subjects, but compared favorably with the 50 to 100 μsec reported for cats by Masterton et al. (1967).

As part of a whole series of tasks to assess the effect of ablation on localizing ability, Heffner (1973) used a two-lever task very similar to the one used in the study by Don & Starr (1972). He reported measurements on only one intact monkey who was able to discriminate 27 μsec time differences and 2.25 dB intensity differences in dichotic 3/sec click trains. These thresholds were lower than those reported by Don & Starr (1972), which may have been due to Heffner's choice of the 75% correct rather than 85% correct level to define threshold.

Interaural time and intensity thresholds for the same genus, <u>Macaca</u>, investigated in this study, have been published by Wegener (1974). Only 1,000 Hz pure tones were presented and the monkeys were trained to indicate on one of two levers which ear had been stimulated by the more intense, or leading, tone. The mean threshold (nine monkeys) for intensity differences was 2.7 dB, and the mean threshold for time differences was 53 µsec.

Research Objectives

A number of physiologists and psychologists proceed under the assumption that animals that respond to sound, can also localize sound accurately (Erulkar, 1972). If this assumption is accepted and if a further assumption is made, i.e., that it is important for a monkey to localize as accurately as a human, then several predictions are possible about the results of a lateralization experiment using monkeys as subjects.

The duplex theory of pure tone localization states that in man, at frequencies below 1,500 Hz, interaural time difference is the cue for perceiving the direction of a sound source. As described earlier, a geometric analysis of the path covered by a wave front from a distant source indicates that the extra distance traversed in reaching the distal ear is a function of the radius of the sphere. For any azimuth position, smaller radii produce smaller distance difference cues. To be able to localize low frequency pure tones as accurately as humans, monkeys would need to have lower interaural time difference thresholds than those reported for humans. If, on the other hand, monkeys were not more sensitive than humans to ongoing time differences, then their ability to localize based on time cues would have to diminish in proportion to the ratio of the radius of the monkey head to the radius of the human head.

The intensity difference measured directly at the ears of squirrel monkeys is less than 0.5 dB when free-field tonal stimuli below 4 kHz originate within an arc of 30° of the midline (Harrison & Downey, 1970). The magnitude of this cue below 4 kHz is presumably insufficient for accurate localization. A similar argument applies to *M. nemestrina* with the difference that the somewhat larger head of this monkey would begin to produce detectable intensity differences at a lower frequency, probably in the neighbor~~g~~hood of 3 kHz. Below this frequency the monkey would have to be able to utilize time difference cues.

At all frequencies the monkey head will produce a smaller "sound shadow" than will a human head. Reasoning along lines similar to the above analysis of time difference cues, predictions can be made that either the monkey will be more sensitive than man to intensity differences at corresponding frequencies, or that its ability to localize will be poorer than man's.

Since the phase and intensity differences will be smaller for organisms with small heads, these animals might still localize successfully by relying on the combined effects of time and intensity disparities which would always occur together in free-field stimulation.

The purpose of this study was to determine for monkeys the effectiveness of two of the cues that are available for localization. Since the acoustic variables involved could be precisely controlled using earphone stimulation, a lateralization task was used. Two experiments were conducted to determine the threshold for interaural time and intensity differences, both as a function of frequency. In a third experiment an attempt was made to investigate the effect of simultaneously presenting time and intensity differences, also as a function of frequency.

EXPERIMENT I

Discrimination of interaural intensity difference as a function of frequency

Method

Subjects

Three female pig-tailed monkeys (Macaca nemestrina) served as subjects. All subjects were obtained from an animal importer and had been acclimated to the animal quarters for at least one year before they were introduced to the experimental conditions. Two of the subjects, B.F. and No Name, were adults. They were maintained at weights of 3.0 and 3.8 kg throughout the experiment. The other subject, Mimi, was a juvenile with a weight range from 2.7 to 3.6 kg.

B.F. had previously served as a subject in a signal detection task designed to measure the monkeys' ability to discriminate interaural onset time differences (Houben & Gourevitch, 1974). The other two subjects were experimentally naive at the beginning of training.

The subjects were housed individually in stainless steel primate cages in a small, climate-controlled, colony room. An automatic water delivery system provided free access to water between 7 p.m. and 1 p.m. Water was not available to any colony member during the remaining six hours to restrict their intake at feeding time and prevent gastric distension. The three subjects were weighed daily and received enough Purina monkey chow after each daily experimental session to maintain a relatively constant weight. The diet was supplemented with 250 mg vitamin C pills given weekly and with Beechnut Junior applesauce which was earned in the experimental sessions.

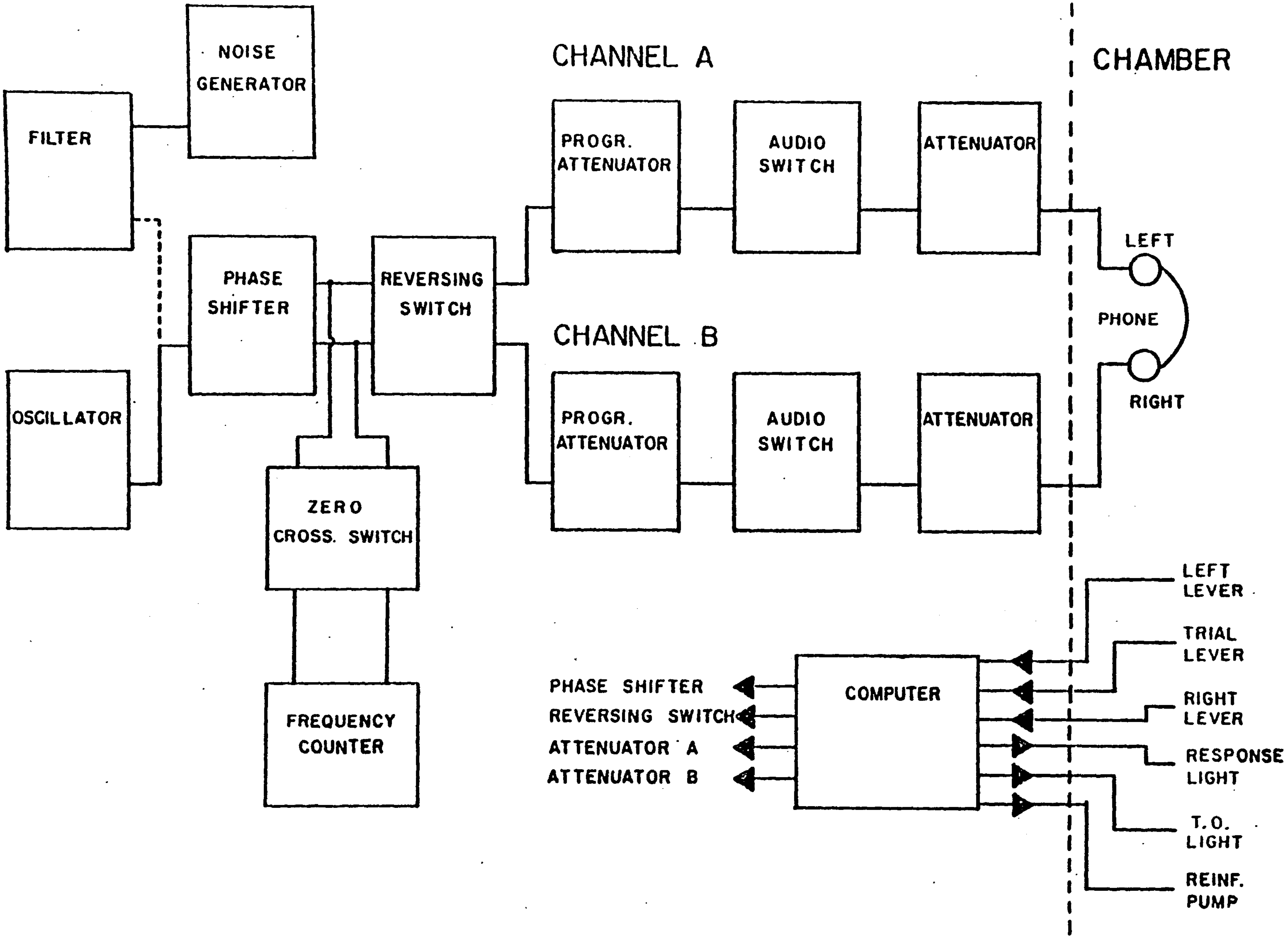
Apparatus

The equipment used for generating, controlling, and presenting stimuli and recording responses is shown in Figure 2. Tones were generated by a General Radio model 1309-A oscillator. Low-pass (cut-off at 10 kHz) noise was generated by a General Radio model 1381 noise generator and a Krohn-Hite model 2242 filter. The output of the oscillator or filter was buffered and split into two identical signals by the phase shifter which is described in Experiment II. From this point to the earphones there were two independent channels, channel A and channel B. Each channel could be independently attenuated and gated.

The programmable attenuators were custom built with minimum step sizes of 0.8 dB over the range 0 to 100 dB and could be computer controlled. The random crossing audio switches were also custom built; an important feature of these switches was the greater precision of rise-decay

Figure 2

Block diagram of the apparatus used to generate acoustic stimuli and record the monkey's responses. The components are described in the text. For the intensity difference study the phase shifter was set to deliver in-phase signals and the reversing switch was inactive. A noise generator and filter replaced the oscillator when noise signals were required.


NOISE GENERATOR
FILTER
CHANNEL A
CHAMBER
PROGR. ATTENUATOR
AUDIO SWITCH
ATTENUATOR
LEFT
PHASE SHIFTER
REVERSING SWITCH
PHONE
CHANNEL B
OSCILLATOR
PROGR. ATTENUATOR
AUDIO SWITCH
ATTENUATOR
RIGHT
ZERO CROSS. SWITCH
LEFT LEVER
TRIAL LEVER
COMPUTER
PHASE SHIFTER
REVERSING SWITCH
RIGHT LEVER
ATTENUATOR A
ATTENUATOR B
FREQUENCY COUNTER
RESPONSE LIGHT
T.O. LIGHT
REINF. PUMP

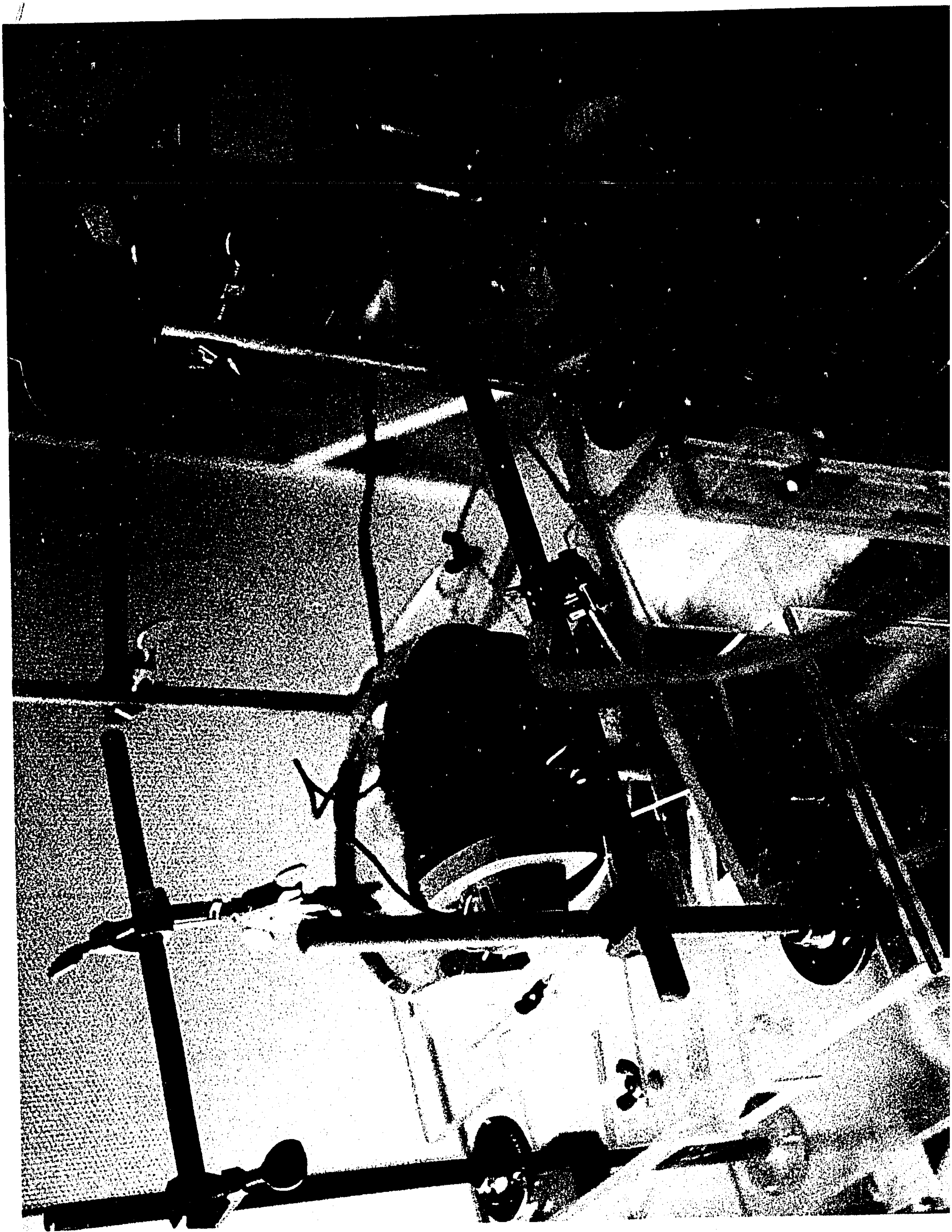
time they offered compared to commercial units. Thus they could be gated simultaneously without introducing interchannel delays at any point on the onset or offset ramp. The final attenuators (Hewlett-Packard model 350D) were used to change overall intensity during preliminary testing but remained fixed during final testing.

Stimuli were presented to the subjects via Fisher HP-100 high fidelity earphones with foam cushions. These earphones were chosen because they did not require a good acoustic seal, a difficult task on small furry heads, to produce a relatively flat response across the frequency range used in this experiment. The calibration procedures and frequency response curves are shown in Appendix A.

Testing was conducted in a double-walled isolation chamber, Industrial Acoustics model 1200. The monkey was seated in a custom built acrylic primate chair, with the head restrained by a nose bar and a plate against the back of the head (Figure 3). The lamp slightly above the monkey's line of sight served as a session light and also as an indicator of incorrect responding. A center knob and the two side levers were used to record the monkey's responses. Reinforcement was delivered directly to the subject's mouth via a feeding tube clamped to the chair. During early training with two of the subjects, B.F. and

Figure 3

One of the subjects, B.F., seated in the test chair. Headphones and reinforcement delivery tube are in place.



No Name, shock was used briefly to punish incorrect responses.

All stimuli and responses were controlled and recorded by a PDP-12 laboratory computer.

Procedure

The choice of psychophysical procedure for an animal discrimination study is a difficult one. The ideal procedure would be one chosen from the literature on human psychophysics; it would combine efficiency with low, stable, bias-free threshold estimates. Unfortunately, animals cannot respond to verbal instructions, nor are they capable of giving direct introspective reports. Our inability to communicate directly with animals is circumvented by training them to respond differentially to two or more classes of events and in this way inform the experimenter as to what categories of stimuli they can identify. This is often achieved by means of operant conditioning techniques (Stebbins, 1970).

A great concern in selecting the appropriate testing method is time efficiency; that is, the rapidity with which the method allows threshold determination. Quick estimates of threshold avoid the effects of time dependent variables such as fatigue, satiation, etc. In man, highly efficient procedures are the tracking method and the block up-down method. However, when these methods have been applied to animal discrimination studies they have lost much of their efficiency. This comes about because of modifications that must be made in this procedure to maintain the discrimination and to give sufficient access to reinforcement. Dewson & Burlingame (1975), for example, interspersed testing with sessions of clearly discriminable, untitrated signals. Moreover, they overtrained their monkeys in the basic discrimination task. Such manipulations decrease sizably the efficiency of the up-down method.

Another approach to discrimination in animals defines the task as one of detection; that is, the animal simply reports a change in stimulation rather than identifying the direction of the stimulus change. Wakeford & Robinson (1974), for example, required their cats to signal when the disparity in a sequence of tone pulses shifted from one ear to the other. There are two problems with this approach. The first concerns the false alarm rate which in such a situation reflects the subject's criterion and response bias and not the criterion alone. The second problem with the detection method is that typically lateralization and localization are defined as tasks that require identifying the location of the sound, whereas this procedure does not.

For the reasons stated above, a single interval, forced-choice procedure with stimuli presented according to the method of constant stimuli was adopted. The method of constant stimuli provides for the presentation of clearly supra-threshold stimuli that serve to maintain the animal's learned responses. In a two-alternative forced-choice procedure the effect of response bias, if any, can be estimated from the probability correct for each of the two alternatives (Green & Swets, 1966). An added benefit of the use of this paradigm is that it is very similar to the procedure used by Mills (1960) with human subjects, and therefore the results of the two studies should be more directly comparable than if another method had been used.

Training procedure. The training of the desired discrimination proceeded through six separate stages. The monkeys were deprived to 80% of their free-feeding weight and were placed in the primate chair to acclimate them to physical restraint. During the one to two weeks of daily chairing, feeding was limited to pellets presented whenever the monkey sat quietly without struggling. At this point actual training was begun. The earphones were placed on the monkey's head and a continuous tone was presented to the right ear. The right lever only was mounted on the response panel, and any pull of sufficient force to activate a micro-switch resulted in the delivery of a small amount of applesauce which could be licked off the tube placed at the monkey's mouth. The response was shaped using traditional operant conditioning techniques. Once the right lever response was established the left lever was mounted instead, and the tone was now presented to the left ear only. The left lever response was shaped as described above.

After responding had been established on both levers the center key was added to the response panel and both the left and right levers were installed. The monkeys now had to press the center key to initiate a trial. A press on the center key resulted in a tone to either the left or the right ear and the tone was terminated when the monkey pulled either choice lever. Pulling the lever on the same side that had received the tone resulted in the delivery of applesauce, responses on the opposite side resulted in a six second time out (T.O.) which was signalled by extinguishing the session light. Responses on any of the three manipulanda during the T.O. reset the duration to six seconds so that the session light would not go on until six response-free seconds had elapsed.

Reaching this stage of training required from six to twenty sessions for training the choice lever responses, and another two to twelve sessions for training the center key response. During this shaping phase sessions varied in length from one hour to four hours, depending on whether the monkey was active or inactive, and on how quickly the monkey was satiated. The variability in training time was not consistent for the four monkeys shaped in this way. Two monkeys, B.F. and Mimi, required more than 15 sessions to learn the left and right lever responses but quickly learned the response chain of pressing the center key followed by a choice lever. No Name was just the opposite, she quickly learned to pull both levers but required twelve sessions to learn the center key response.

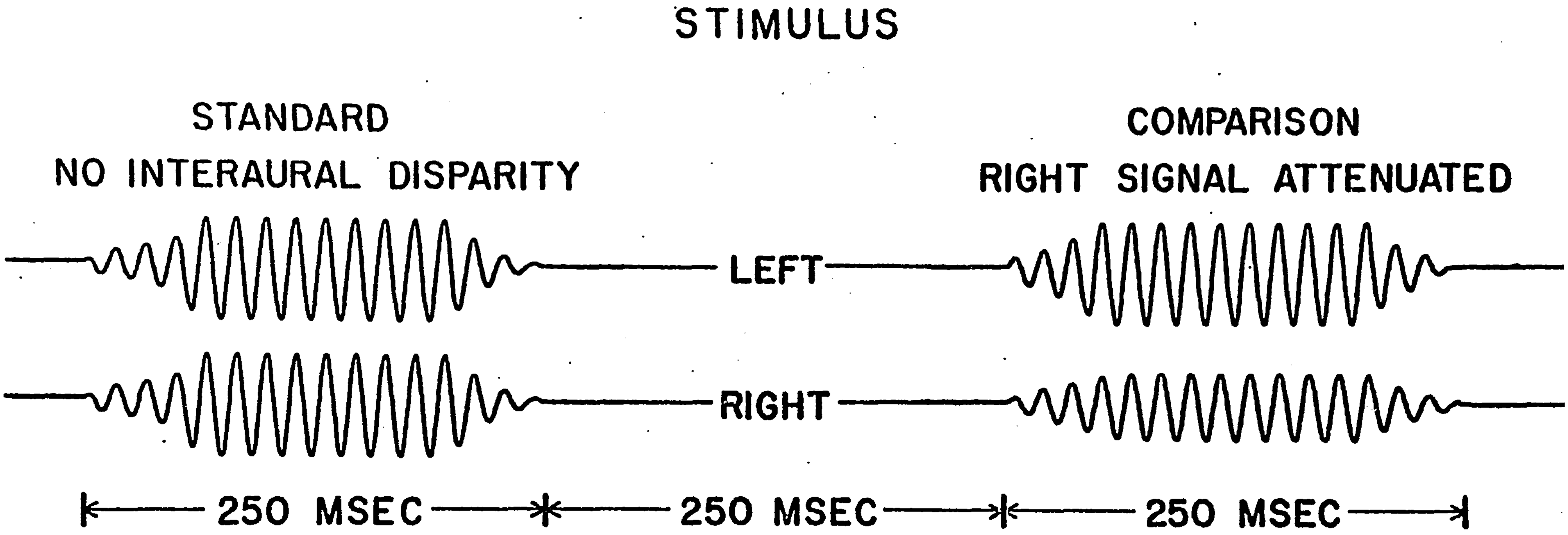
The monkeys were less variable in learning the left-right discrimination. All four required fifty or more sessions to begin to respond correctly on better than 50% of the trials. To speed up the training of the discrimination several modifications were tried. The frequency of the tone to be lateralized was changed from session to session, as was the intensity of the tone. The last monkey to be trained, Mimi, was given noise stimuli during this part of the training and she learned fastest. To eliminate position bias a correction procedure was added; the left-right sequence of stimulus presentations was varied randomly unless an incorrect response was made. Following an incorrect response the same stimulus was repeated on subsequent trials until it was identified correctly, then the random procedure was reinstituted. For two of the four monkeys this correction procedure had to be alternated with completely random sessions since they learned to respond on one lever exclusively unless they had received a time out. After a time out they switched to the other lever for one trial and, if the correction procedure was in use, they would be 100% correct on trials following incorrect trials. Compound stimuli have sometimes been used to train animals to make difficult discriminations and this approach was also tried. In addition to the left or right auditory stimulus, a light was turned on above the correct choice lever. The hope was that the visual component could be faded out and that the auditory discrimination would remain. The attempt failed. Within one session of adding the cue lights the monkeys were responding 100% correctly. After two 100 trial sessions of perfect discrimination the lights were faded in two ways; the intensity was lowered, and the duration was shortened. As the visual discrimination became more difficult, the monkeys, instead of relying on the auditory information which was presumably easily discriminable, kept looking for the cue light. Eventually, they reverted to a position preference.

The four monkeys ultimately learned to respond correctly close to 100% of the time in daily sessions ranging from 100 to 400 trials each. Choice responding occurred with a very short latency and the auditory stimulus was shortened to a fixed duration of 250 msec. The final stage of training involved the addition of a standard, "centered" stimulus which preceded the left or right stimulus on every trial. This standard stimulus was presented to both ears simultaneously with equal intensity (diotic). The standard was also 250 msec in duration and the interval between the standard and comparison stimuli was 250 msec. Rise/fall time for both bursts was 10 msec. This completed the training of the desired discrimination.

Testing procedure. Figure 4 shows the stimulus conditions and response consequences for the psychophysical testing. The interaural intensity disparity of the comparison tone was produced by attenuating the signal in one ear, relative to the intensity of the standard tone.

Figure 4

Stimulus conditions and response consequences for Experiment I. On every trial the standard stimulus shown on the left side of the top panel was followed by the comparison stimulus. In the comparison stimulus either the left or the right signal was attenuated relative to the intensity of the standard. Rise/fall time of the signals was 10 milliseconds. The bottom panel shows the possible outcomes of a trial. Responding on the correct lever was rewarded with a drop of applesauce. Incorrect responses were followed by a six second time-out during which no new trials could be initiated.



	RIGHT LEVER RESPONSE	LEFT LEVER RESPONSE
RIGHT STIMULUS MORE INTENSE	REINF.	6 SEC T.O.
LEFT STIMULUS MORE INTENSE	6 SEC T.O.	REINF.

The top panel of Figure 4 shows the stimulus conditions for a single trial in which the comparison signal to the right ear was attenuated. As may be seen in the bottom panel, left lever responses were reinforced when the comparison signal was more intense in the left phone, and right lever responses were reinforced if the comparison signal was more intense in the right phone. Incorrect responses resulted in a six second time out, same as during training.

The intensity of the diotic standard pulse and the unattenuated comparison pulse was 60 dB SPL. This intensity assured that at all frequencies tested, the sensation level of the stimuli would be at least 40 dB above the published threshold for old world monkeys (Stebbins, 1973). No attempt was made to measure the absolute thresholds of the subjects used in this study.

A daily test session consisted of 400 or more trials at one frequency. From trial to trial the location (right vs. left ear) of the more intense of the signal pair was randomized in blocks of 20 trials. Similarly, five interaural intensity differences used in the method of constant stimuli were randomized in blocks of 20 trials. Thus, in these blocks each intensity difference was presented four times, twice favoring lateralization to the left, and twice favoring lateralization to the right. The range of constant stimulus values was determined for each monkey, at each frequency, during preliminary testing. Four psychometric functions at one frequency were obtained in a single day. These functions were based on 100 trials each.

These measurements were repeated with seven frequencies ranging from 125 Hz to 8 kHz in octave steps, and with a 10 kHz low-pass noise. The order of testing at the various frequencies was randomized for each of the monkeys. Each animal was tested daily, six days per week; an experimental session lasted from one to three hours depending on the level of performance. The performance of the task did not transfer readily across frequencies, especially if the frequency to be tested was widely separated from the previous one. As many as thirty daily sessions were required to establish the appropriate range of constant stimulus values for a new frequency. In training the animals to perform at a new frequency it was sometimes necessary to train at intermediate frequencies to help affect the transfer.

Results

The data in a constant stimulus procedure are in the form: p (correct) as a function of stimulus magnitude. In this experiment, each of the five values of interaural intensity difference has associated with it a probability of correct left-right identification. These probabilities range from 0.5 to 1.0, a consequence of the two-alternative, forced-choice procedure. Since the direction of the disparity was varied randomly, with an equal probability of left and right, even random responses have a probability of 0.5 of being correct.

The monkey's performance in discriminating interaural intensity difference at each frequency was measured over four blocks of 100 trials each. The 100 trial blocks were separated by a two-minute break, the time required to punch a trial by trial record on paper tape. Performance over such a large number of trials could conceivably have shown systematic changes due to practice, or, deterioration due to fatigue or other factors. Combining trials at different performance levels would have resulted in a threshold estimate that reflected added variability. A way to check the validity of combining data was to do an analysis of variance on subsets of the data to test for significant changes over successive blocks. The results of this analysis are shown in Table 1. For the two extreme frequencies, 125 Hz and 8,000 Hz, the data were analyzed in blocks of 100 trials, and in blocks of 200 trials. The probabilities were first corrected for chance by the formula: $p_c = 2\ (p - .5)$, which had the effect of changing the range from 0.5 - 1.0 to 0 - 1.0 (Guilford, 1954, Pg. 146). The corrected probabilities were then transformed by the arc-sine transform ($X = \sin^{-1} \sqrt{p_c}$) before being submitted for analysis. None of the analyses summarized in Table 1 were significant with respect to the blocks variable, therefore, the hypothesis that there were no systematic changes in performance could not be rejected. As a consequence, all subsequent analyses of the data were based on the combined 400 trials.

Figures 5 through 12 depict psychometric functions obtained from three monkeys at each of the test frequencies. Individual curves are based on 400 trials, 80 trials at each of the five stimulus valued indicated on the abscissa. The ordinate represents the percent correct lateralization, uncorrected for chance responding. At most frequencies, the five particular intensity differences used were the same for the three monkeys. Exceptions were for Mimi at 500 Hz and under low-pass noise stimulation and for No Name at 1,000 Hz. As already mentioned, the

TABLE 1

Analysis of Variance for Experiment I: Proportion Correct at two Frequencies as Function of Stimulus Disparity and Blocks of Trials

	Blocks of 200 Trials						Blocks of 100 Trials				
	125 Hz				8,000 Hz		125 Hz			8,000 Hz	
Monkey	Source	df	MS	F	MS	F	df	MS	F	MS	F
B.F.	Stimulus(A)	4	3.14	10.39*	2.14	5.65*	4	3.14	17.70*	2.14	5.65*
	Block(B)	1	2.25	7.45	1.96	5.17	3	0.75	1.92	0.71	1.87
	A X B	4	0.63	2.09	0.24	0.64	12	0.49	2.76	0.39	1.01
No Name	Stimulus(A)	4	2.45	4.75*	4.82	9.56*	4	2.45	4.43*	4.28	11.15*
	Block(B)	1	0.25	0.48	0.11	0.24	3	0.24	0.43	0.59	1.53
	A X B	4	0.54	1.05	0.55	1.24	12	0.51	0.92	0.53	1.37
Mimi	Stimulus(A)	4	4.23	15.08*	1.19	3.29	4	4.23	11.84*	1.19	2.65
	Block(B)	1	0.03	0.10	0.11	0.31	3	0.04	0.10	0.07	0.14
	A X B	4	0.27	0.97	0.50	1.37	12	0.19	0.53	0.31	0.70

*$p < .01$

range of stimuli used was determined for each monkey in preliminary testing. In almost all the testing conditions the chosen range of interaural intensity differences yielded a fairly complete psychometric function extending from below 60% to above 90% correct.

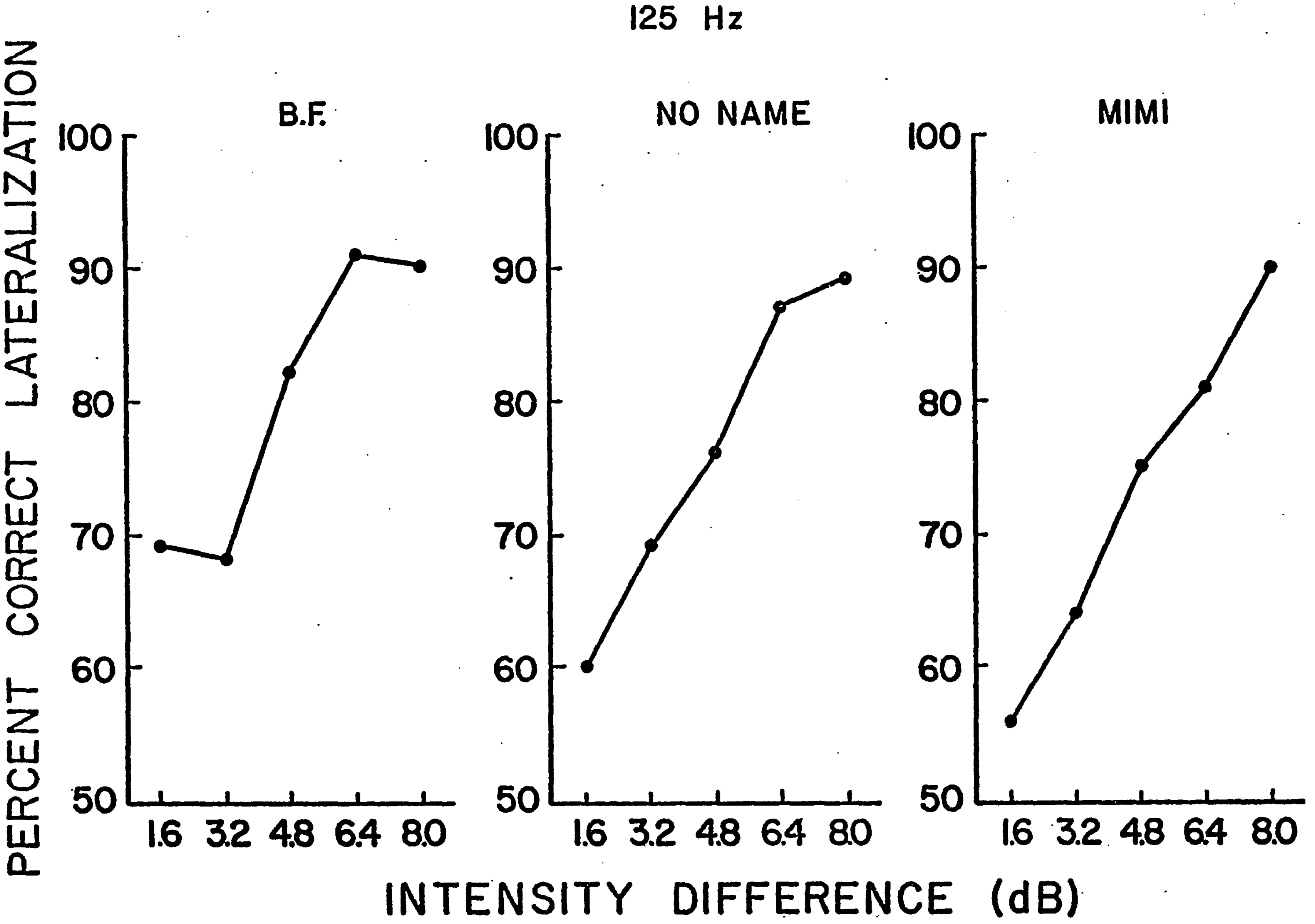
Not all the individual psychometric functions are monotonic. Thus, a shallow reversal appears in B.F.'s function at 125 Hz.

Mimi's psychometric functions are slightly irregular at 250 Hz and 2,000 Hz; at 4,000 Hz and 8,000 Hz deep reversals occur in her functions. However, in no case do these aberrations take place within the 70% to 80% correct range. Finally, two of No Name's psychometric functions are non-monotonic. One, at 250 Hz, had a small reversal; the other, for the noise signal, is located at the center of the function, within the range of 70% to 80% correct lateralization.

There are several procedures by which a threshold can be estimated from a psychometric function. The simplest procedure, and the one requiring the fewest assumptions, is the one of linear interpolation (Guilford, 1954). The threshold is defined as the point falf-way between chance performance and perfect discrimination. In a two-alternative procedure this would be the 75%

Figure 5

Psychometric lateralization functions of interaural intensity difference for three monkeys at 125 Hz. Each function is based on a total of 400 trials.



125 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
1.6
3.2
4.8
6.4
8.0
INTENSITY DIFFERENCE (dB)

Figure 6

Psychometric lateralization functions of interaural intensity difference for three monkeys at 250 Hz. Each function is based on a total of 400 trials.

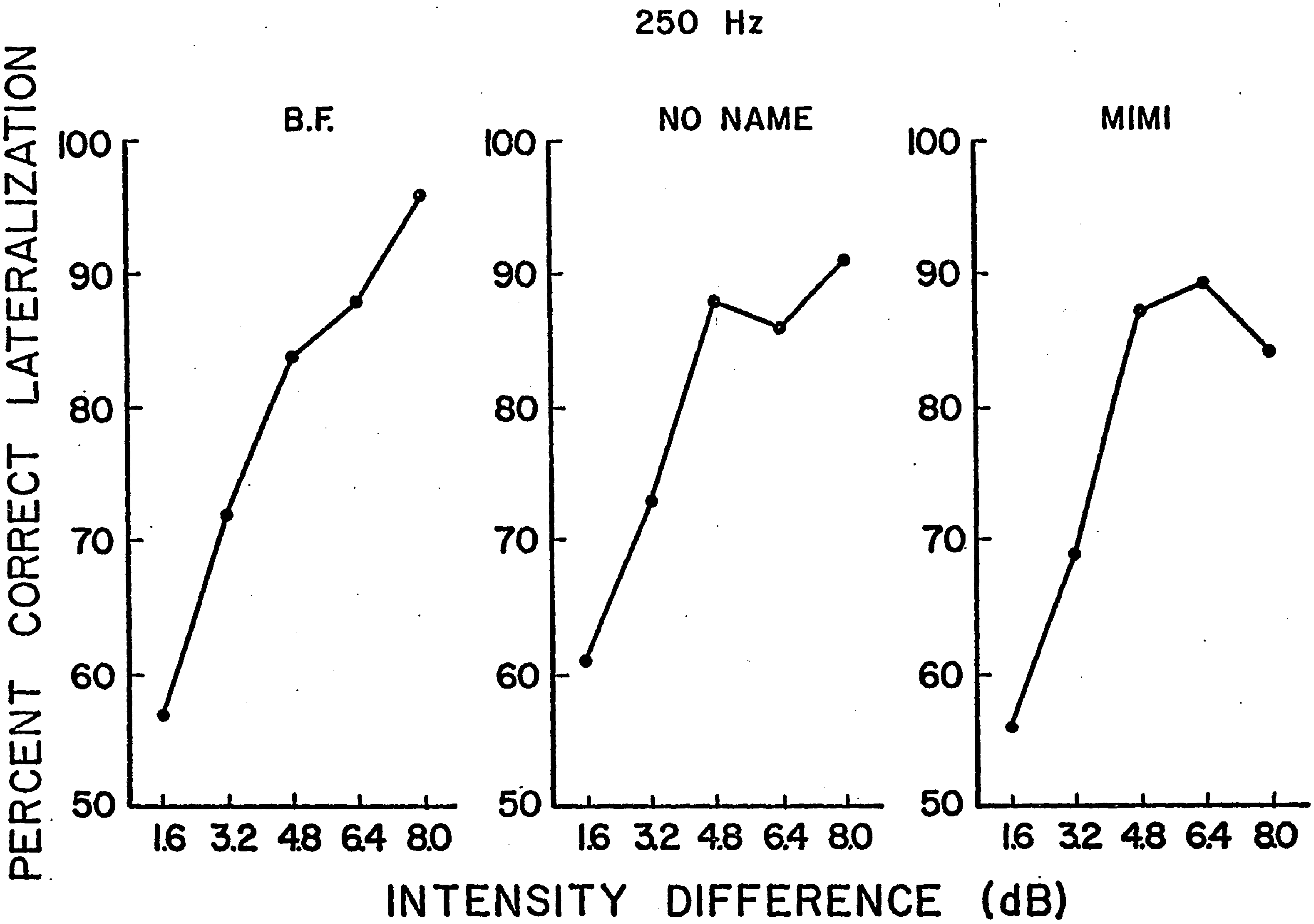

250 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
1.6
3.2
4.8
6.4
8.0
INTENSITY DIFFERENCE (dB)

Figure 7

Psychometric lateralization functions of interaural intensity difference for three monkeys at 500 Hz. Each function is based on a total of 400 trials.

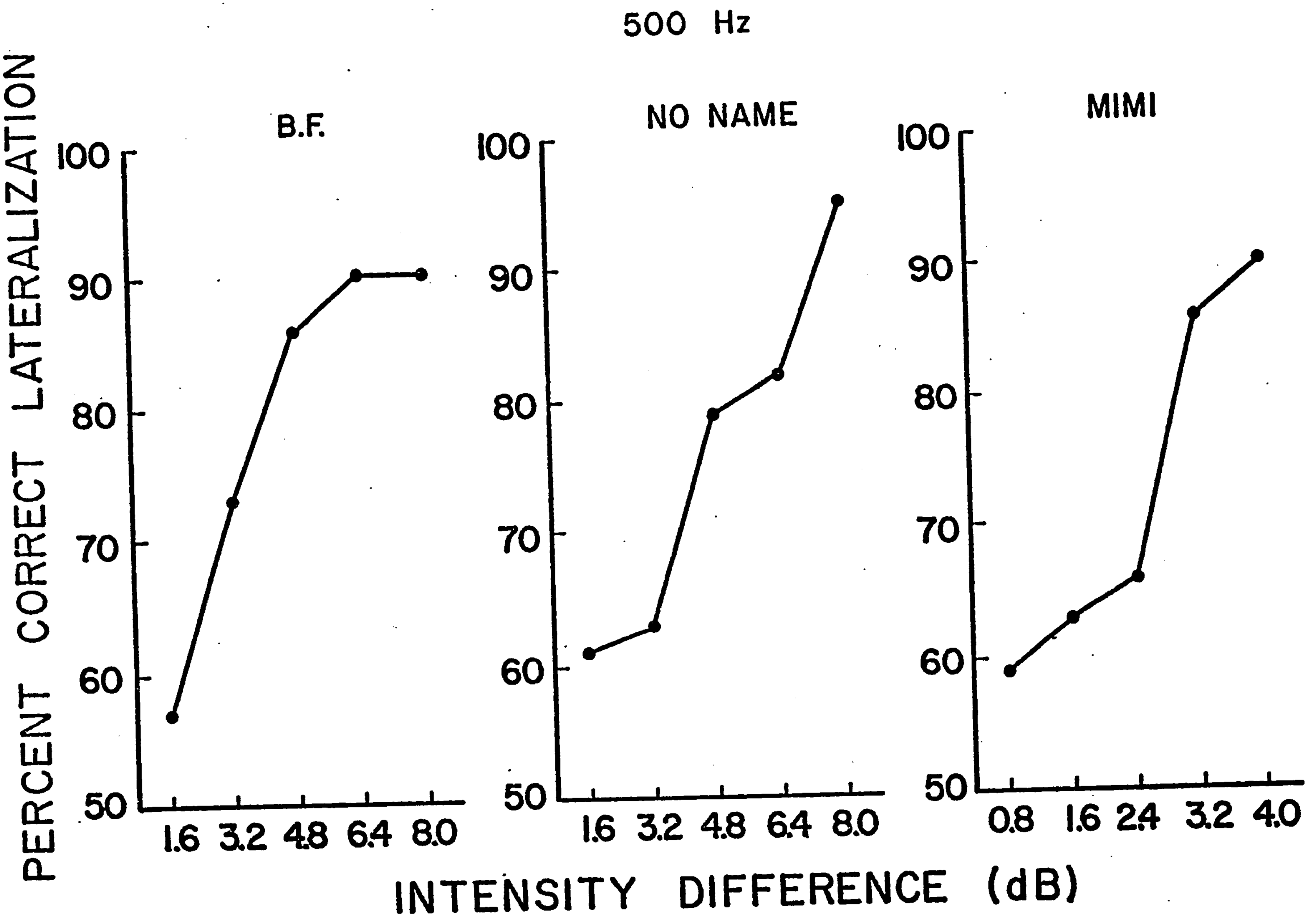
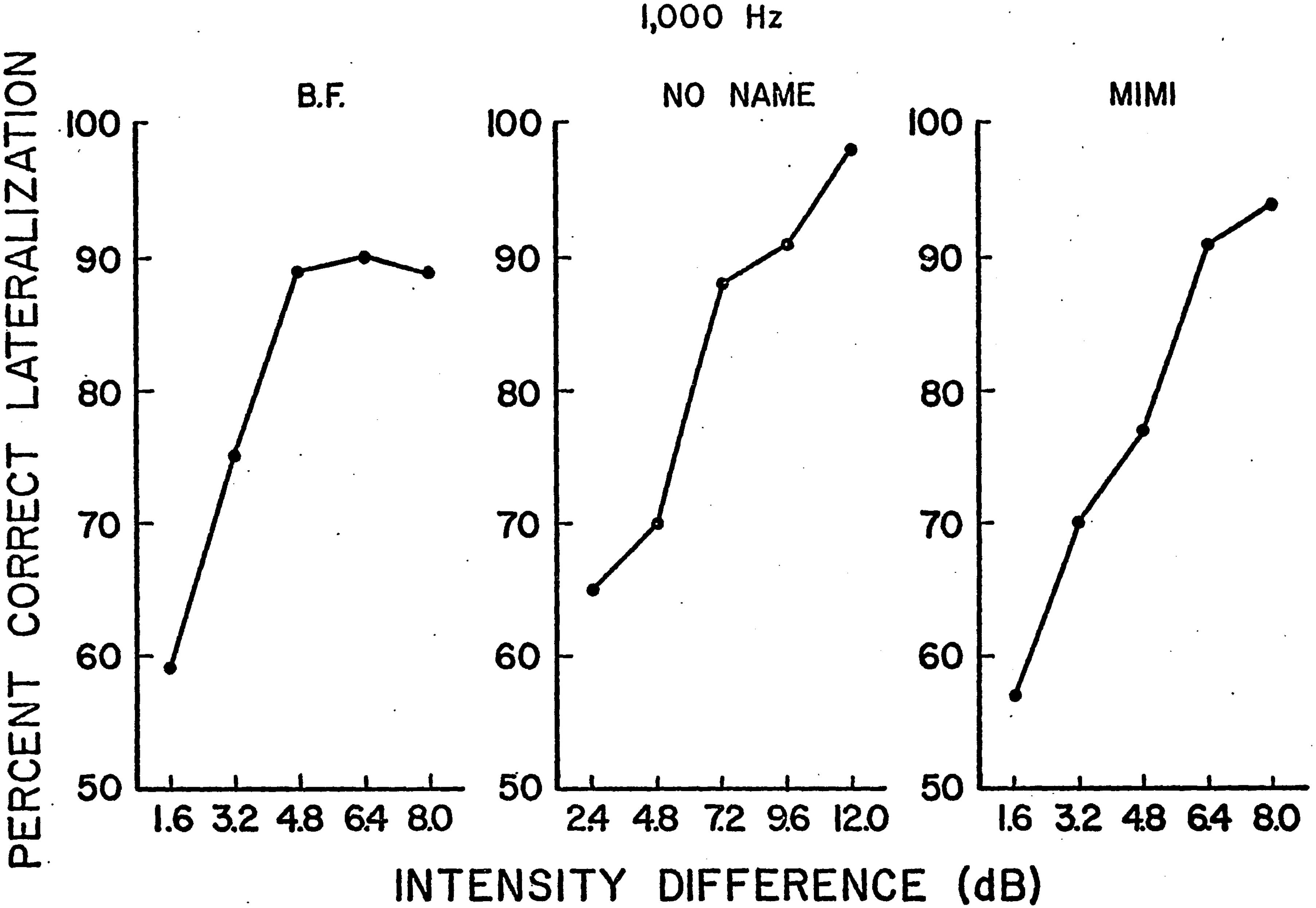

500 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
1.6
3.2
4.8
6.4
8.0
0.8
1.6
2.4
3.2
4.0
INTENSITY DIFFERENCE (dB)

Figure 8

Psychometric lateralization functions of interaural intensity difference for three monkeys at 1,000 Hz. Each function is based on a total of 400 trials.



1,000 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
1.6
3.2
4.8
6.4
8.0
2.4
4.8
7.2
9.6
12.0
INTENSITY DIFFERENCE (dB)

Figure 9

Psychometric lateralization functions of interaural intensity difference for three monkeys at 2,000 Hz. Each function is based on a total of 400 trials.

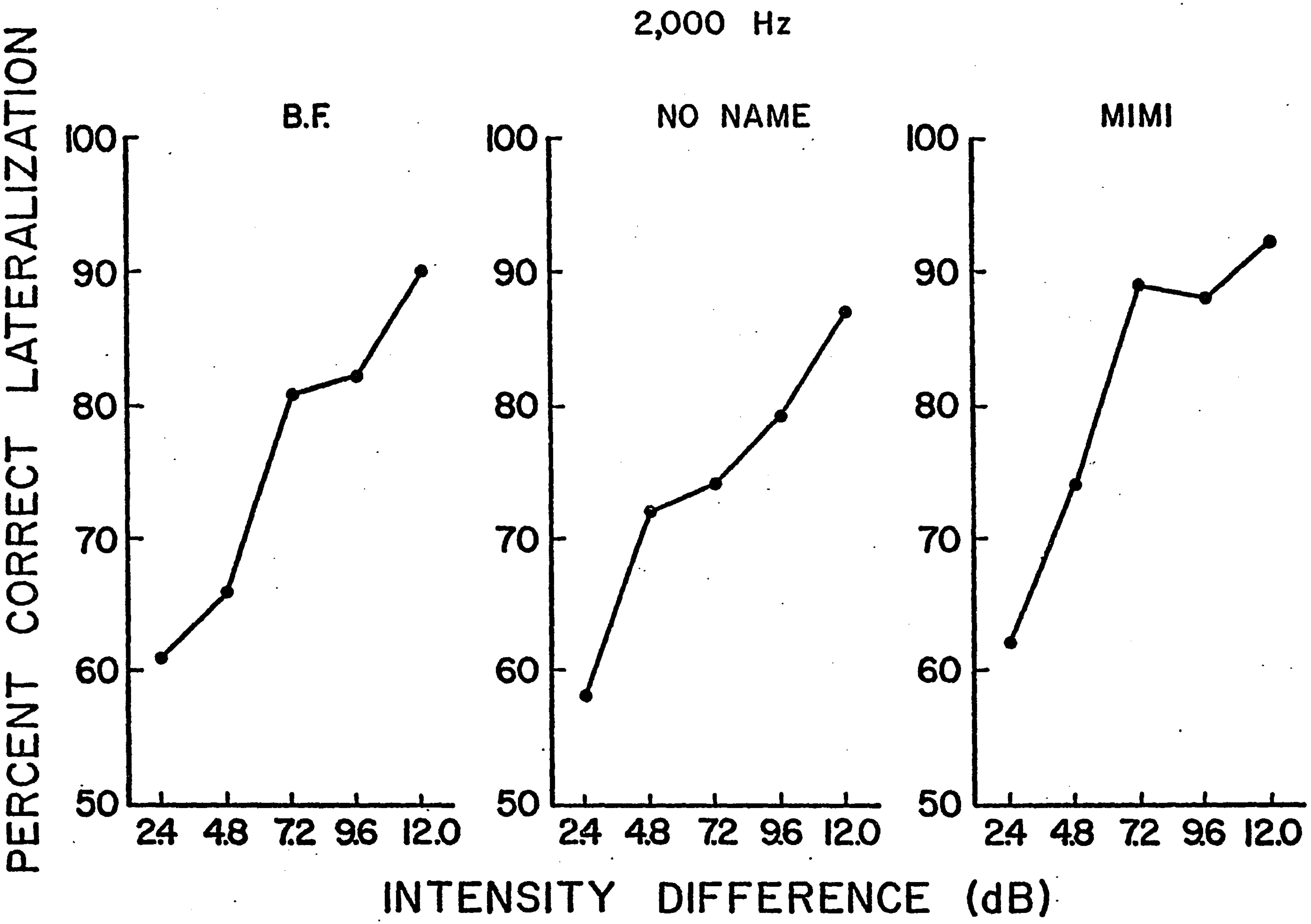

2,000 Hz
PERCENT CORRECT LATERALIZATION
B.F.
NO NAME
MIMI
100
90
80
70
60
50
2.4
4.8
7.2
9.6
12.0
INTENSITY DIFFERENCE (dB)

Figure 10

Psychometric lateralization functions of interaural intensity difference for three monkeys at 4,000 Hz. Each function is based on a total of 400 trials.

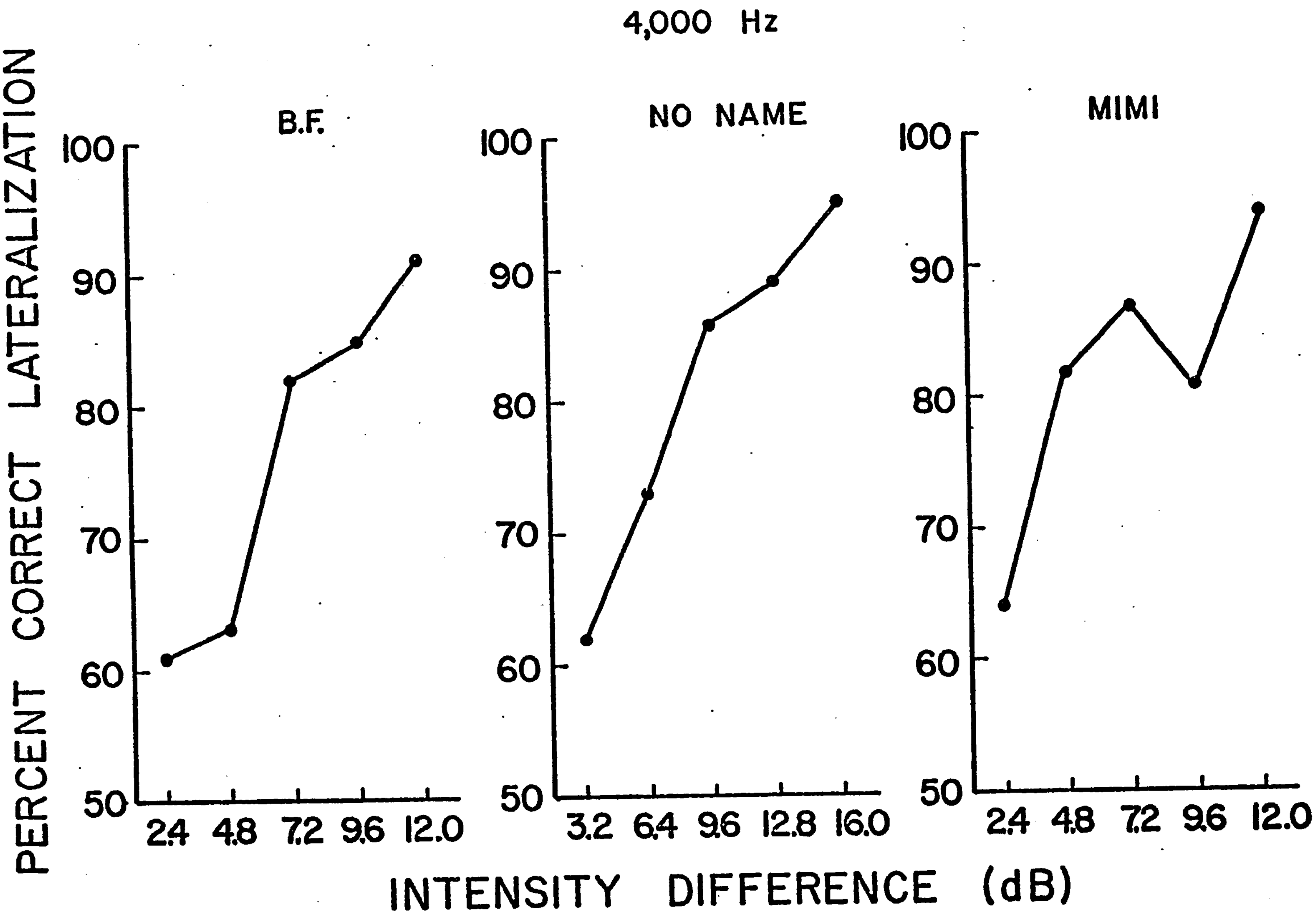

4,000 Hz
PERCENT CORRECT LATERALIZATION
B.F.
NO NAME
MIMI
100
90
80
70
60
50
2.4
4.8
7.2
9.6
12.0
3.2
6.4
9.6
12.8
16.0
INTENSITY DIFFERENCE (dB)

Figure 11

Psychometric lateralization functions of interaural intensity difference for three monkeys at 8,000 Hz. Each function is based on a total of 400 trials.

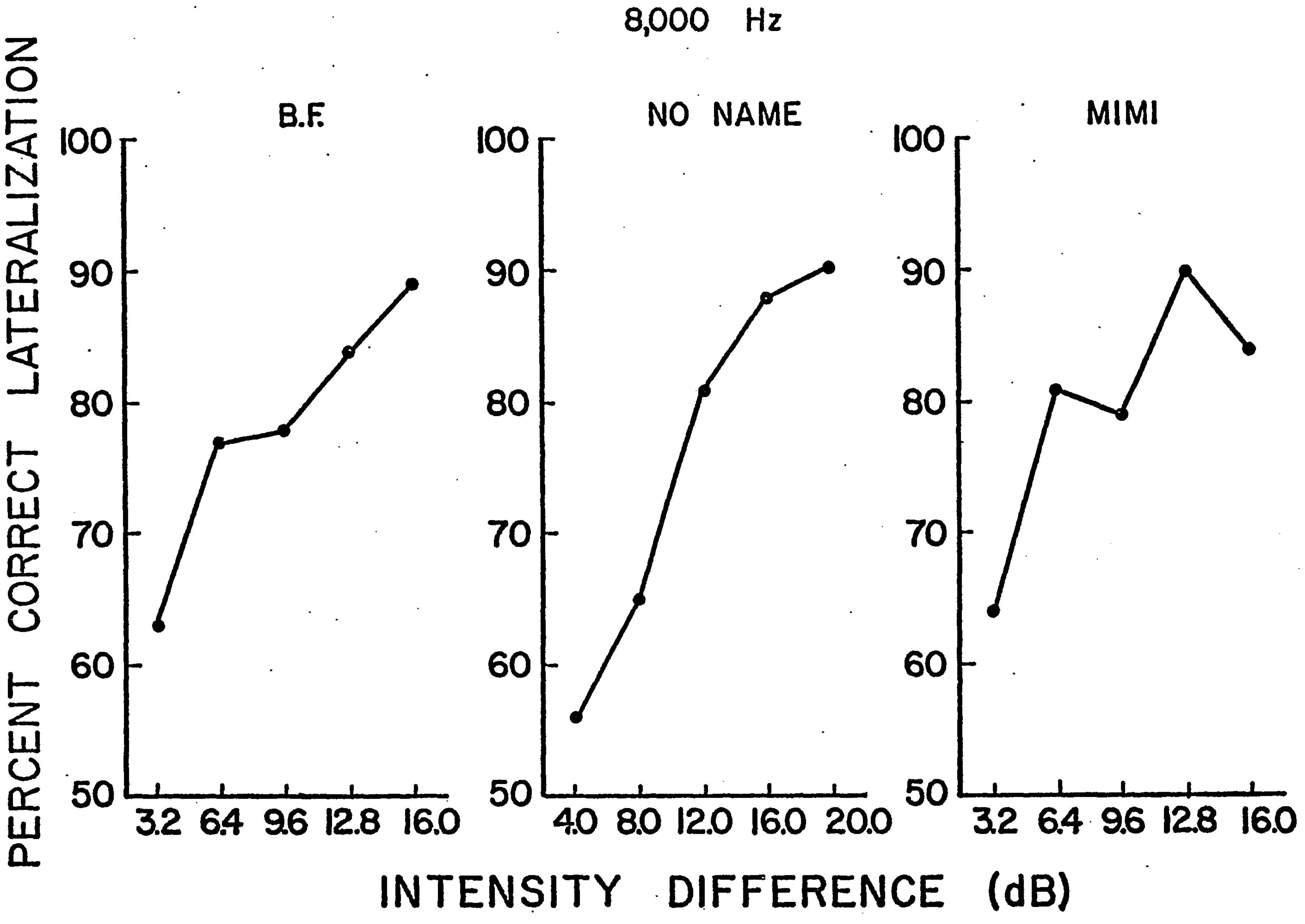
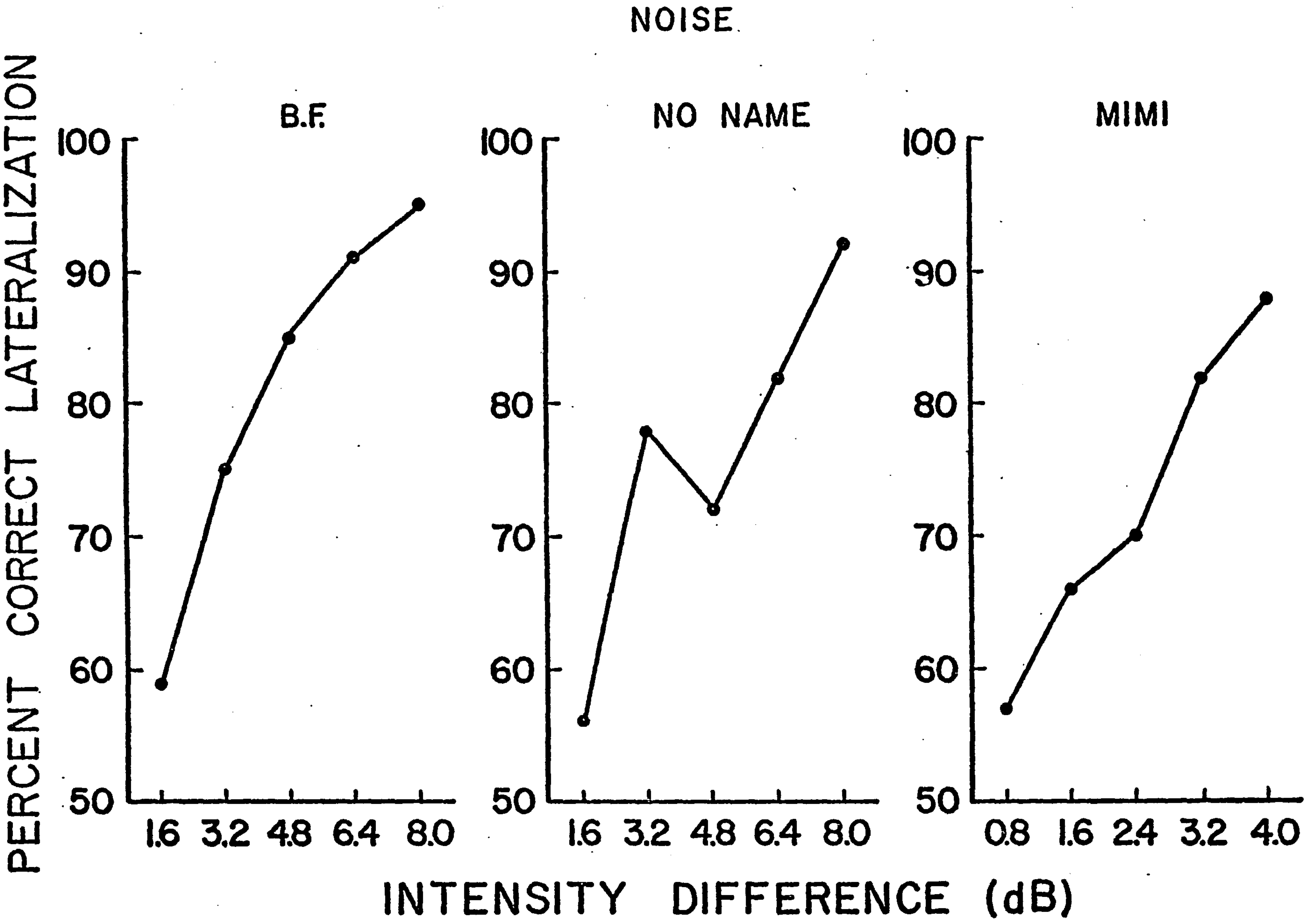

8,000 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
3.2
6.4
9.6
12.8
16.0
4.0
8.0
12.0
16.0
20.0
INTENSITY DIFFERENCE (dB)

Figure 12

Psychometric lateralization functions of interaural intensity difference for three monkeys for noise. Each function is based on a total of 400 trials.


NOISE
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
1.6
3.2
4.8
6.4
8.0
0.8
1.6
2.4
3.2
4.0
INTENSITY DIFFERENCE (dB)

correct level, since the 50% level represents chance performance. Linear interpolation does have its drawbacks; the procedure ignores all but two of the data points on the psychometric function, and assumes that the function is linear between the two points that bracket 75% correct. The first drawback is mainly one having to do with efficiency. The second criticism, which involves the assumption of linearity, is in practice not too serious since functions are typically quite steep in the region of the threshold.

Other procedures for estimating thresholds from psychometric functions involve curve fitting and assumptions about the shape of the function. Two of these procedures are probit analysis and z-transformation. Both procedures assume that the function has the shape of the normal ogive and involve rules for generating the best-fitting ogive to the obtained data points. Probit analysis also assigns weights that give relatively less importance to extreme probabilities, and incorporates the maximum likelihood technique to calculate the best-fitting curve (Finney, 1971).

There are very few extreme probabilities in the data presented here and therefore a procedure that weights extreme scores less than mid-range scores was deemed unnecessary. Furthermore, the correction for chance reduces the number of extreme scores that do occur. These considerations led to the choice of the least-squares z-score technique. Z-values were assigned to each corrected proportion and a straight line was fitted to these values by the least-squares method. Thresholds calculated by this procedure appear in Table 2 for each of the subjects, at each frequency. The threshold estimates based on linear interpolation are also shown in the table. In most cases the estimates from the two procedures are in close agreement; major differences occur at 8,000 Hz for all three subjects.

One of the advantages of using curve fitting techniques is that the goodness of fit can be checked by subjecting the deviations of the observed and expected proportions to a chi-square test. The results of these tests are also shown in Table 2. Half of the tabled chi-square values exceed 7.8, which demarcates the 0.05 significance level. This significant deviation from normality was the reason for adopting the linear interpolation thresholds for subsequent graphing and discussion.

One of the problems which arises when the psychometric function is non-monotonic in the region of the threshold, is that more than one stimulus value is

TABLE 2

Interaural Intensity Difference Thresholds in dB for Seven Frequencies and for Noise

	Frequency (Hz)							
	125	250	500	1000	2000	4000	8000	Noise
				BF				
Linear Interpolation	4.0	3.6	3.4	3.2	6.2	6.3	5.9	3.2
Least Squares Z	3.4	4.0	4.1	3.7	6.8	6.9	7.9	3.7
Chi-Square[1]	9.65*	4.82	18.4.*	23.01*	4.49	7.8*	4.67	4.30
				No Name				
Linear Interpolation	4.6	3.4	4.4	5.5	7.7	6.9	10.5	3.0
Least Squares Z	4.5	3.7	4.5	5.0	7.6	7.1	11.6	4.7
Chi-Square[1]	2.62	10.72*	8.85*	4.60	5.61	2.99	7.81*	22.84*
				Mimi				
Linear Interpolation	4.8	3.7	2.8	4.3	5.0	3.9	5.3	2.7
Least Squares Z	5.2	4.5	2.6	4.3	5.2	4.5	6.6	2.7
Chi-Square[1]	1.56	32.84*	8.63*	3.11	10.58*	21.03	18.42*	1.06

[1] The chi-square associated with the deviation of the observed probabilities from normality.

* The starred entries exceed the tabled value (7.8) for a significance level of 0.05 (df = 2)

associated at the 75% level. In the present experiment such a reversal occurred only in No Name's noise function (Figure 12). The rule adopted for handling such cases was that the threshold would be defined by the point at which the function first crossed the 75% level.

Individual interaural intensity difference threshold functions are shown in Figure 13. Each point on the graph was derived by linear interpolation from the psychometric function. At the lower frequencies and with noise stimulation, the agreement among the thresholds is quite good; they are no more than ± 1 dB apart. Variability increases somewhat from 1,000 Hz, where the thresholds are within ±1.2 dB of each other to 8,000 Hz where they are within ±2.6 dB. For each monkey the intensity difference threshold for noise stimulation is equal to or slightly less than the lowest threshold obtained with tones.

The mean interaural intensity difference function for the three monkeys is plotted in Figure 14. Between 125 Hz and 1,000 Hz the function is relatively flat, exhibiting only a slight bow. At higher frequencies, intensity difference thresholds are all more elevated, the highest threshold occurring at 8,000 Hz.

The interaural intensity threshold obtained with

Figure 13

Interaural intensity difference thresholds for tones and for a 10 kHz low-pass noise in three monkeys.

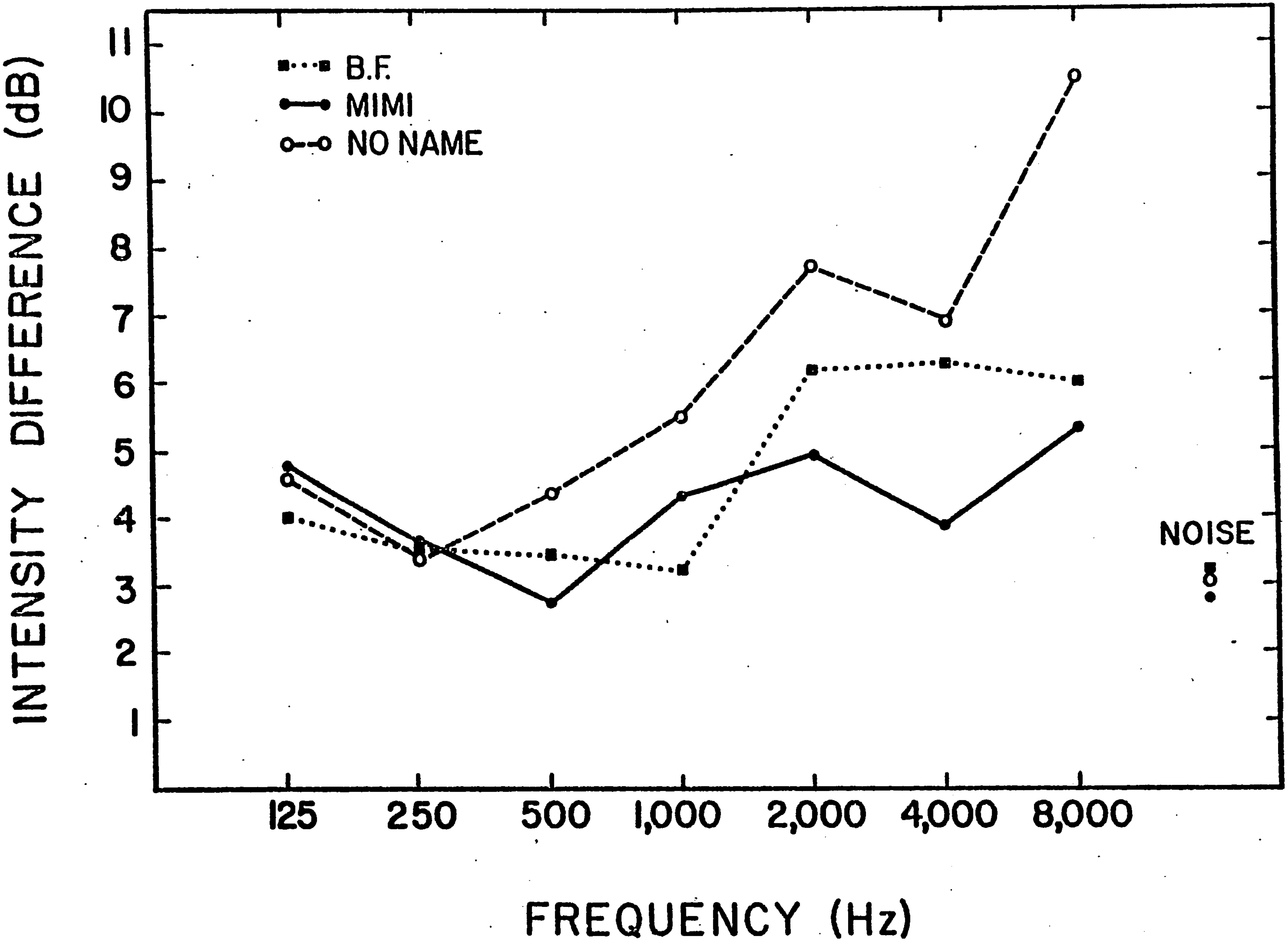
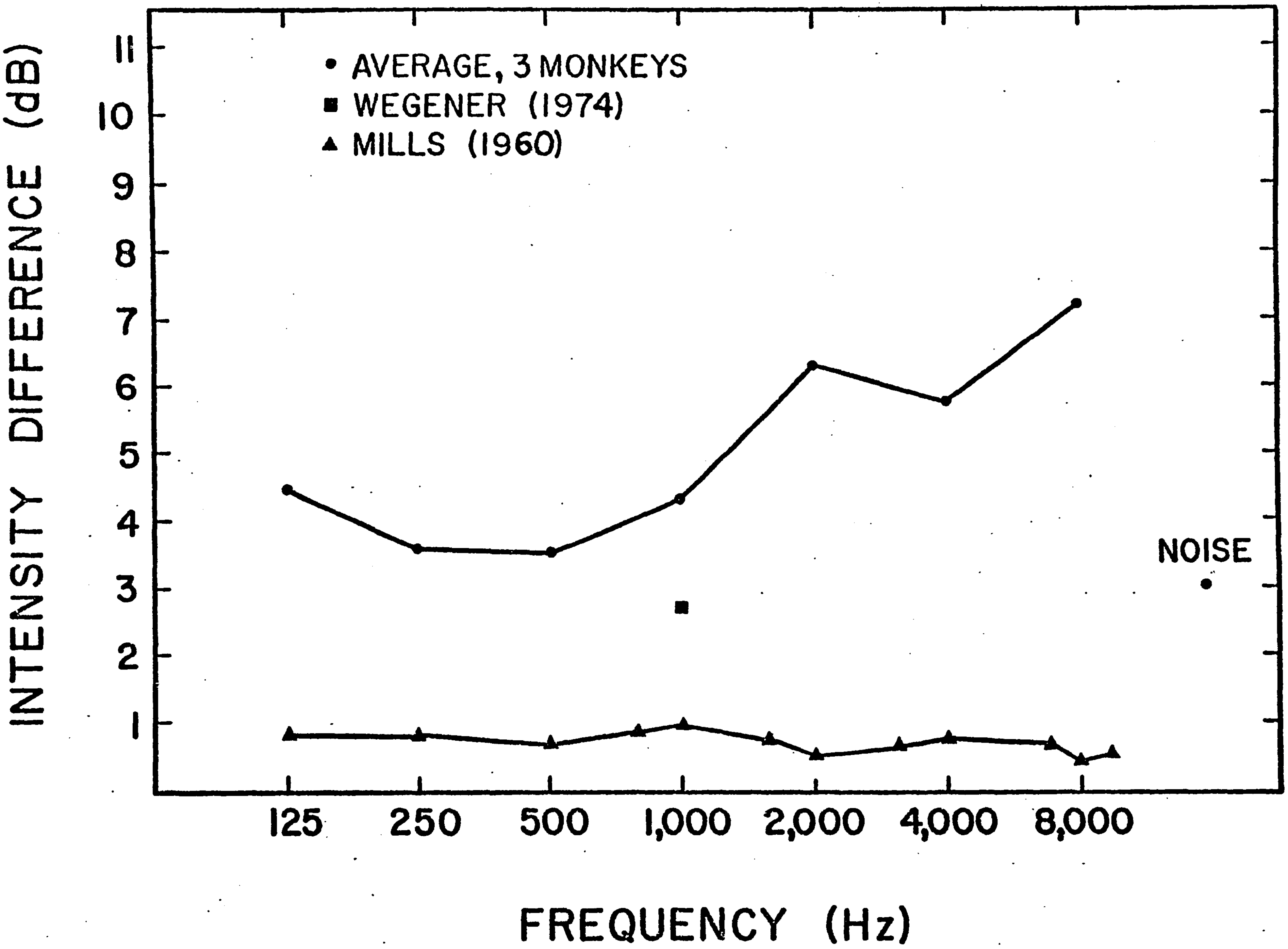

B.F.
MIMI
NO NAME
INTENSITY DIFFERENCE (dB)
11
10
9
8
7
6
5
4
3
2
1
NOISE
125
250
500
1,000
2,000
4,000
8,000
FREQUENCY (Hz)

Figure 14

Mean interaural intensity difference thresholds for three *M. nemestrina*, determined under tone and noise stimulation. ■ , Intensity difference thresholds for *M. mulatta* (Wegener, 1974); ▲, Human intensity difference thresholds (Mills, 1960).



● AVERAGE, 3 MONKEYS
■ WEGENER (1974)
▲ MILLS (1960)
NOISE
INTENSITY DIFFERENCE (dB)
11
10
9
8
7
6
5
4
3
2
1
125
250
500
1,000
2,000
4,000
8,000
FREQUENCY (Hz)

10 kHz low-pass noise, also shown in Figure 14, is 0.5 dB lower than the lowest intensity difference threshold obtained with tonal stimuli.

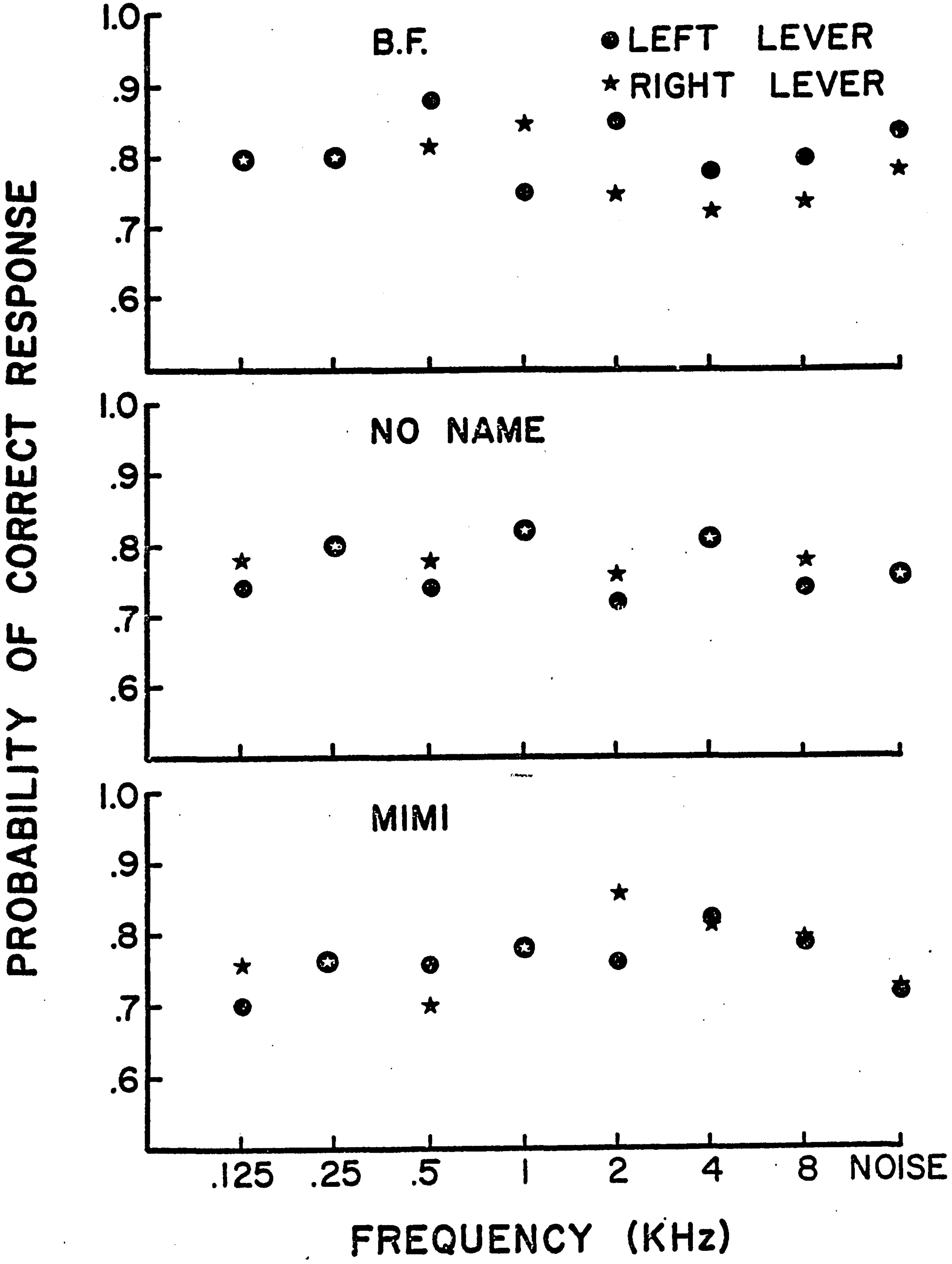
Only a single mean interaural intensity threshold has been reported for _M_. _mulatta_ (Wegener, 1974). It is plotted in Figure 14 and is approximately 1.5 dB below measurements made in the present study.

Human interaural intensity thresholds are also shown in Figure 14 (Mills, 1960). The function is essentially flat over the frequency spectrum from 125 Hz to 10,000 Hz. Between 125 Hz and 1,000 Hz the monkey function is about 3 dB above the human function. At higher frequencies the human and monkey functions diverge, reaching a separation of approximately 7 dB at 8,000 Hz.

The usual procedure for determining response bias in a multiresponse task involves plotting the probability of one of the responses as a function of stimulus magnitude. Another way of looking at response bias is to examine the proportion of correct responses as a function of response category. If, as in this experiment, the a priori probabilities of left and right stimuli are equal, then completely unbiased responding would be indicated by equal percent correct responding on the two choice levers. These equal percentages would hold regardless of the level of the performance. For example, if the overall performance on the task indicates 80% correct responding, then the probability of a correct response on the left lever should be 0.8, and the probability of a correct response on the right lever should also be 0.8. Any large deviation from equal probability indicates that there was a bias toward the choice associated with the lower probability correct. Figure 15 shows the probability of a correct response on the two levers as a function of frequency. Of the three subjects only B.F. exhibited a consistent preference for the right lever response. The other two subjects either showed no evidence of bias or small non-systematic shifts in bias.

Figure 15

Probability correct for left and right choices for each frequency. The points represent the data reported in Experiment I. The circles indicate the proportion of left lever responses that were correct; the stars represent the proportion of right lever responses that were correct. Any large disparity between plotted points at a frequency indicates a bias for the choice associated with the lower probability.


PROBABILITY OF CORRECT RESPONSE
B.F.
● LEFT LEVER
★ RIGHT LEVER
NO NAME
MIMI
1.0
.9
.8
.7
.6
.125
.25
.5
1
2
4
8
NOISE
FREQUENCY (KHz)

Experiment II

Discrimination of interaural time difference as a function of frequency

Method

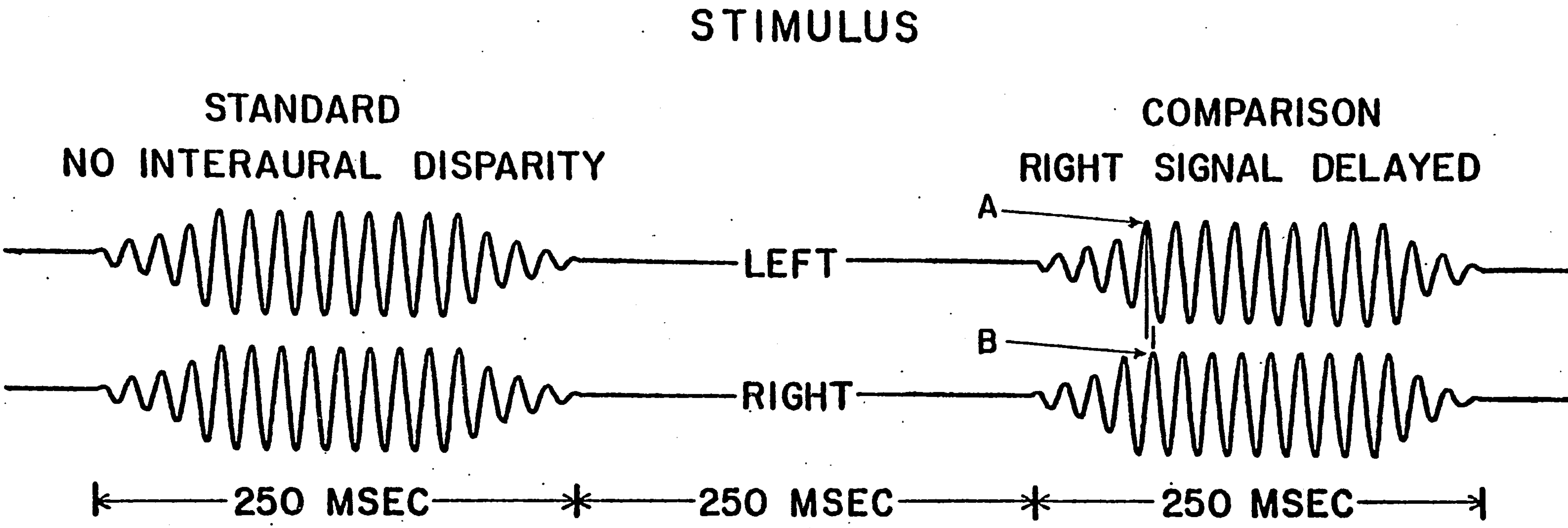
Subjects and apparatus. The subjects and apparatus were the same as in Experiment I. The programmable attenuators were set for zero attenuation. The custom built phase shifter shown in Figure 2, was capable delaying an incoming sine wave by any of five pre-selected phase angles. Regardless of the amount of phase shift, the amplitudes of the buffered input signal and the shifted output signal were identical. The five pre-selected delays could be switched under computer control; so could the double-pole, double-throw relay which served to switch the delayed signal from one audio channel to the other. For calibration of the delays, the shifted and un-shifted signals were led to a custom designed zero-crossing switch. This switch provided 1.0 μsec pulses whenever the incoming signals crossed zero potential in the positive direction. These pulses in turn gated a Hewlett-Packard model 5325B counter. In this way the interval between corresponding portions of the undelayed and delayed signals could be monitored continuously with 1.0 μs resolution.

Procedure. After the completion of Experiment I interaural intensity difference measurements at 1,000 Hz were repeated for each monkey. When performance on the intensity difference task had stabilized, the stimulus conditions for the comparison tone were switched to those shown in the top panel of Figure 16. It can be seen that corresponding points A and B on the waveforms did not exist together, B occurring later in time; this same time difference was maintained for all other corresponding points. Thus, in the comparison tone the waveform to the right ear was delayed, while in the standard tone the left and right signals were in unison. Less obviously depicted in this figure is the fact that the standard and comparison tones in both channels were gated simultaneously. This means that there were no onset or offset disparities, only on-going phase differences.

As in Experiment I, the direction of the disparity (left leading vs. right leading) was randomized in blocks of 20 trials. Similarly, the five values of delay for the constant stimulus procedure were randomized in blocks of 20. Since at the beginning of Experiment II it was not known over which range the monkeys could discriminate interaural time differences, the order of testing was systematic. All three monkeys were tested first at 1 kHz, then at 500 Hz, 250 Hz, and 125 Hz.

Figure 16

Stimulus conditions and response consequences for Experiment II. On every trial the standard stimulus shown on the left side of the top panel, was followed by the comparison stimulus. In the comparison stimulus drawn here, the signal to the right ear is delayed relative to the signal going to the left ear. The envelopes of the signals are gated simultaneously with a 10 millisecond rise/fall time. The bottom panel shows the possible outcomes of a trial. Responding on the correct lever was rewarded with a drop of applesauce. Incorrect responses were followed by a six second timeout during which no new trials could be initiated.



	RIGHT LEVER RESPONSE	LEFT LEVER RESPONSE
RIGHT STIMULUS LEADING	REINF.	6 SEC T.O.
LEFT STIMULUS LEADING	6 SEC T.O.	REINF.

Whenever the frequency was lowered to 125 Hz, the performance of the monkeys broke down, regardless of the delays used. Thus the lowest frequency for which psychophysical functions were obtained is 250 Hz. At this point performance at 1 kHz was re-examined and then 1,500 Hz, 1,750 Hz, and 2 kHz were tested. As at the low frequency end, attempts to measure interaural time difference thresholds at 2,250 Hz led to a complete break-down of performance. Over each of the next ten daily sessions reliable performance at 2,000 Hz was verified and was immediately followed by testing of the 2,250 Hz tone. In every session, the performance under the 2,250 Hz tone was random. Thus, the highest frequency at which time difference thresholds were obtained was 2,000 Hz.

In all, thresholds were measured at eight frequencies extending from 250 Hz to 2,000 Hz in 250 Hz steps. The other details of the procedure were identical with those outlined in Experiment I.

Results

The data obtained in this experiment were analyzed as in Experiment I. An analysis of variance was performed to check for systematic variations in performance as a function of blocks of 100 and 200 trials. The summary for this analysis at the two extreme frequencies, 250 Hz and

2,000 Hz, is shown in Table 3. Performance is not significantly different across blocks for any of the three subjects. Consequently all of the subsequent analyses are based on the combined 400 trials that were presented at each frequency.

Psychometric functions determined on all the subjects at the eight test frequencies appear in Figures 17 through 24. Each point plotted in these figures represents percent correct lateralization based on 80 trials.

As was the case in Experiment I, most, although not all of the psychometric functions in Experiment II were monotonic. Some of the reversals were minor ones as seen for B.F. at 250 Hz and 2,000 Hz, and for Mimi at 1,750 Hz. In other instances a greater departure from the standard shape of the psychometric function took place. These irregularities did not occur in the neighborhood of the 75% correct level except for Mimi's function, at 1,250 Hz, which crossed the 75% level twice. As in Experiment I, the threshold was taken at the first crossing.

It should be pointed out that in order to generate these functions different ranges of interaural time differences, individually selected for the particular monkey, were required. It does not seem that a favorable choice was made in two instances, which could account for the ab-

TABLE 3

Analysis of Variance for Experiment II: Proportion Correct at two Frequencies as Function of Stimulus Disparity and Blocks of Trials

		Blocks of 200 Trials					Blocks of 100 Trials				
		250 Hz			2,000 Hz		250 Hz			2,000 Hz	
Monkey	Source	df	MS	F	MS	F	df	MS	F	MS	F
B.F.	Stimulus(A)	4	3.60	8.83*	3.30	13.58*	4	3.60	7.34*	3.30	13.35*
	Block(B)	1	0.17	0.42	1.27	5.22	3	0.61	1.23	0.62	2.57
	A X B	4	0.27	0.67	0.39	1.60	12	0.16	0.32	0.28	1.11
No Name	Stimulus(A)	4	1.40	7.15*	1.67	6.47*	4	1.40	5.93*	1.67	5.09*
	Block(B)	1	0.08	0.38	0.75	2.90	3	0.09	0.40	0.26	0.81
	A X B	4	0.37	1.91	0.09	0.36	12	0.20	0.86	0.13	0.38
Mimi	Stimulus(A)	4	1.68	6.80*	2.05	5.69*	4	1.68	6.00*	2.05	4.47*
	Block(B)	1	0.13	0.51	0.80	2.22	3	0.10	0.35	0.60	1.31
	A X B	4	0.62	2.51	0.12	0.32	12	0.35	1.23	0.09	0.20

*p<.01

Figure 17

Psychometric lateralization functions of interaural time difference for three monkeys at 250 Hz. Each function is based on 400 trials.

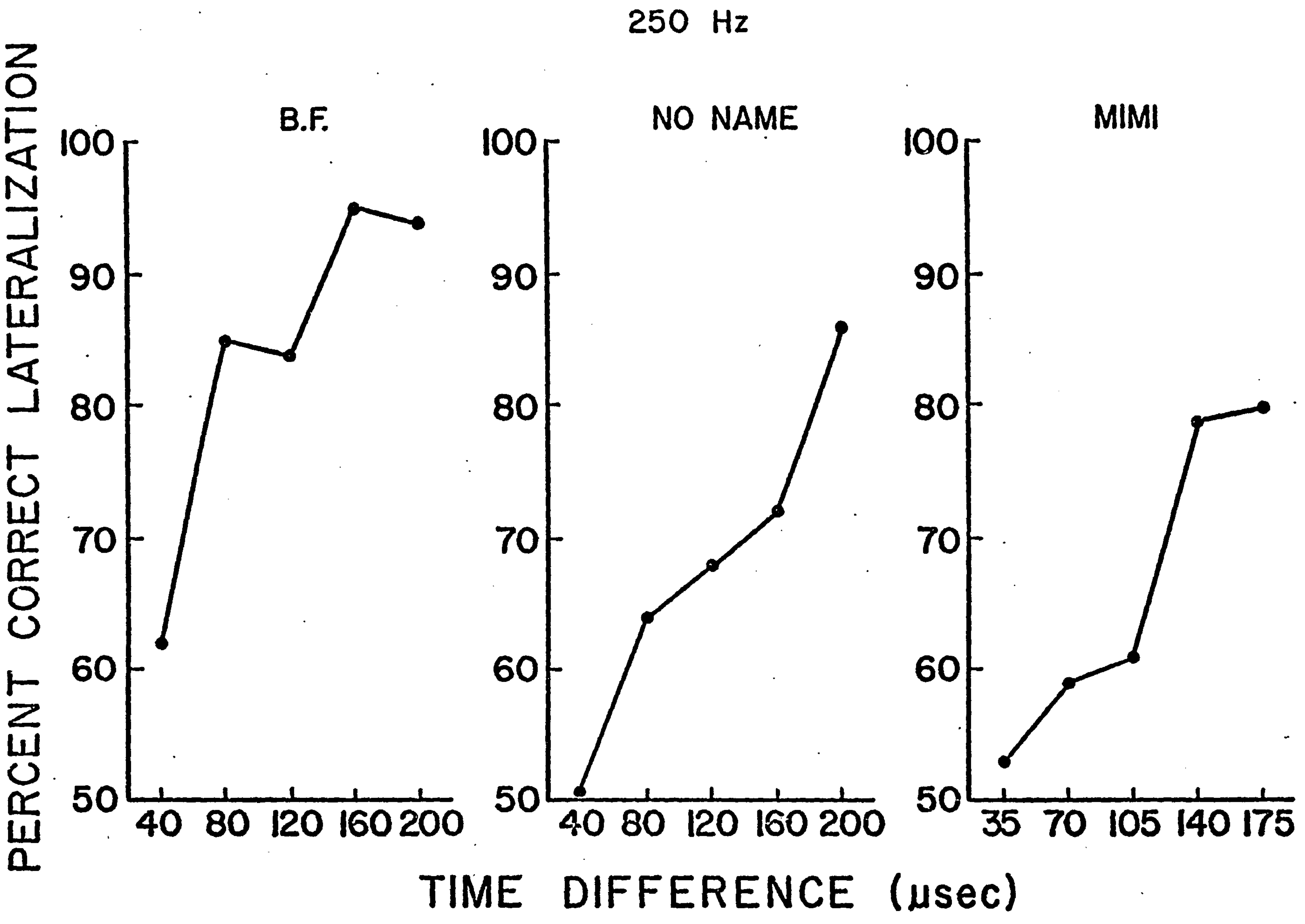

250 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
40 80 120 160 200
40 80 120 160 200
35 70 105 140 175
TIME DIFFERENCE (µsec)

Figure 18

Psychometric lateralization functions of interaural time difference for three monkeys at 500 Hz. Each function is based on 400 trials.

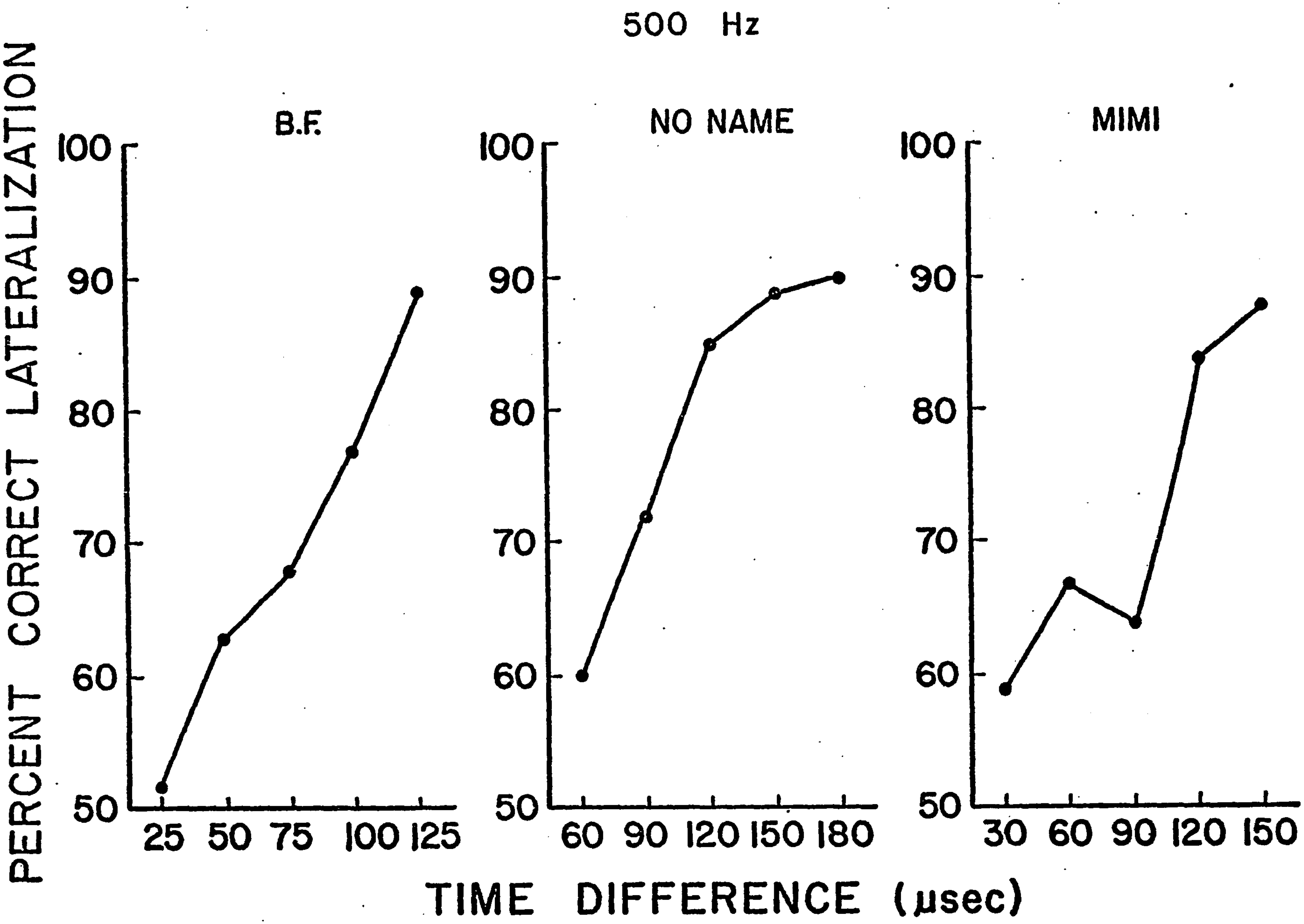

500 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
25 50 75 100 125
60 90 120 150 180
30 60 90 120 150
TIME DIFFERENCE (μsec)

Figure 19

Psychometric lateralization functions of interaural time difference for three monkeys at 750 Hz. Each function is based on 400 trials.

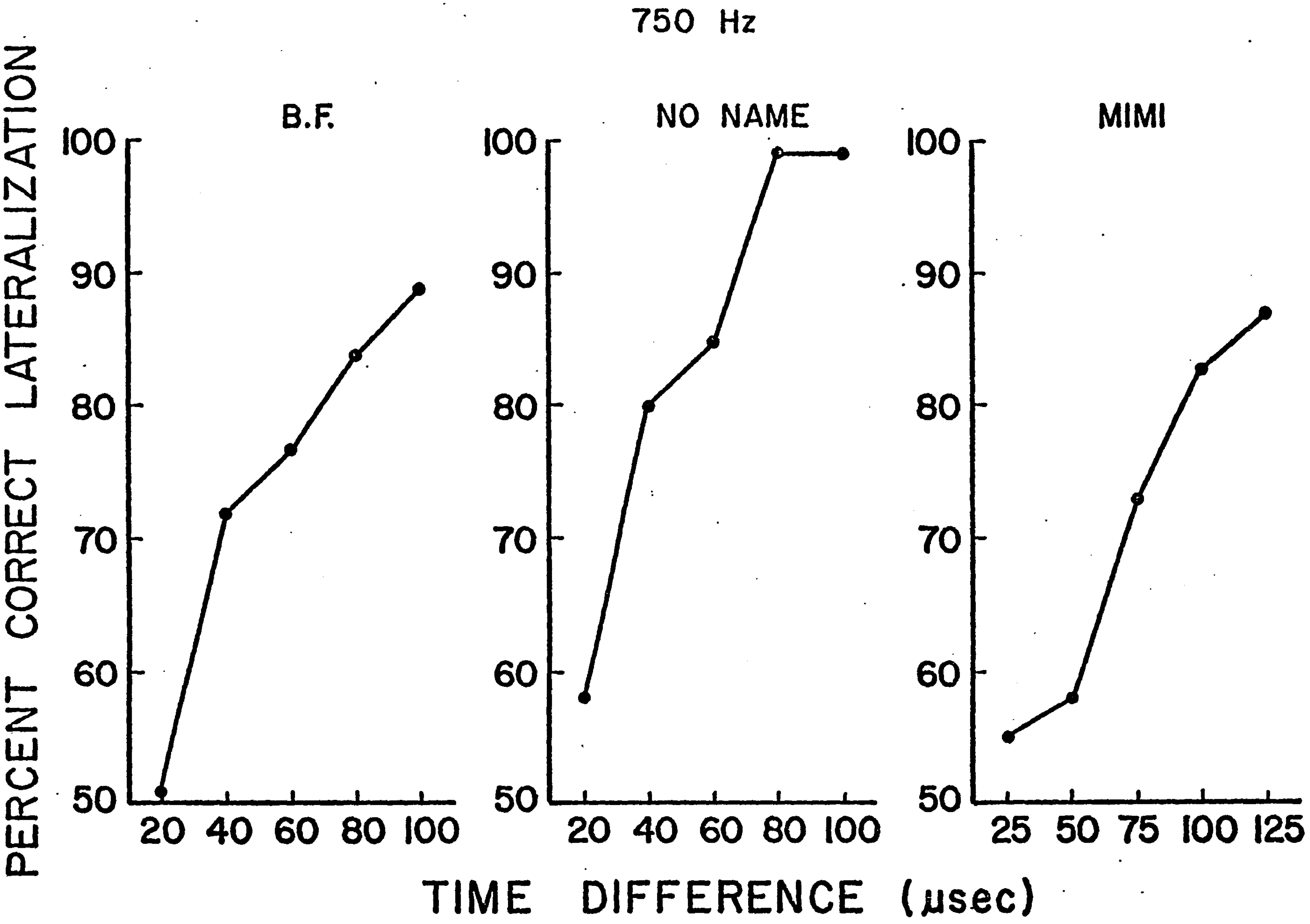

750 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
20
40
60
80
100
25
50
75
100
125
TIME DIFFERENCE (µsec)

Figure 20

Psychometric lateralization functions of interaural time difference for three monkeys at 1,000 Hz. Each function is based on 400 trials.

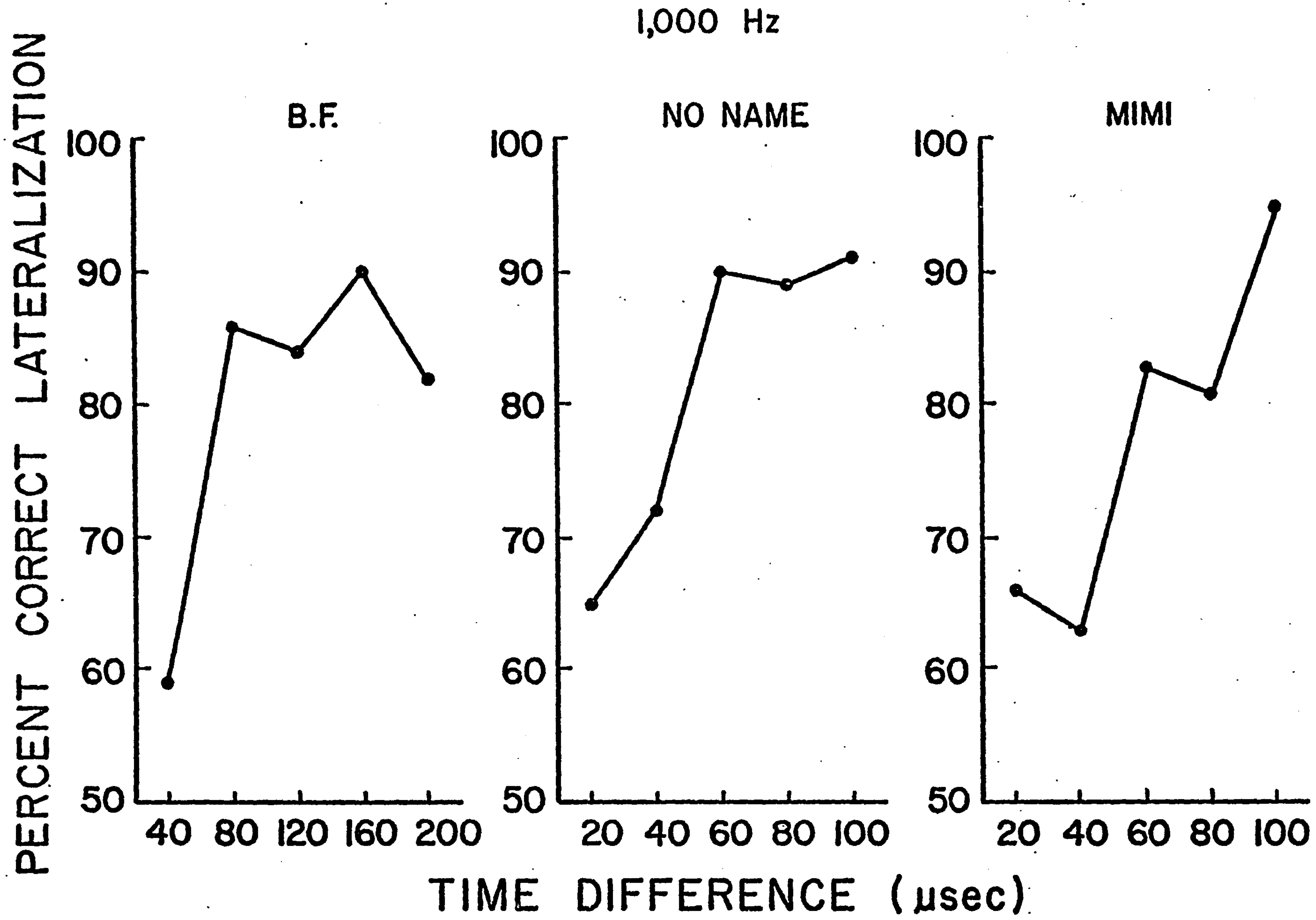

1,000 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
40
80
120
160
200
20
40
60
80
100
TIME DIFFERENCE (μsec)

Figure 21

Psychometric lateralization functions of interaural time difference for three monkeys at 1,250 Hz. Each function is based on 400 trials.

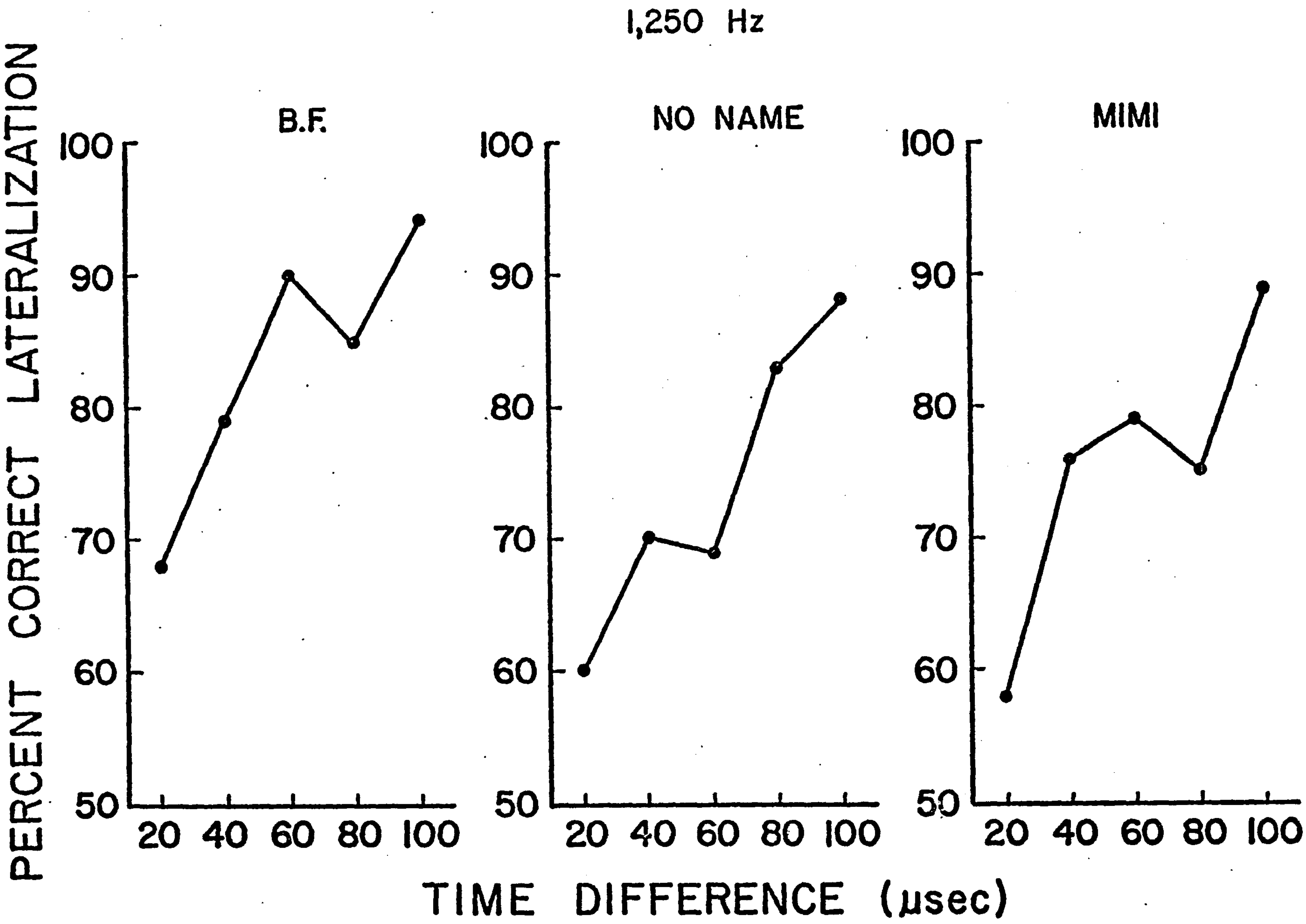
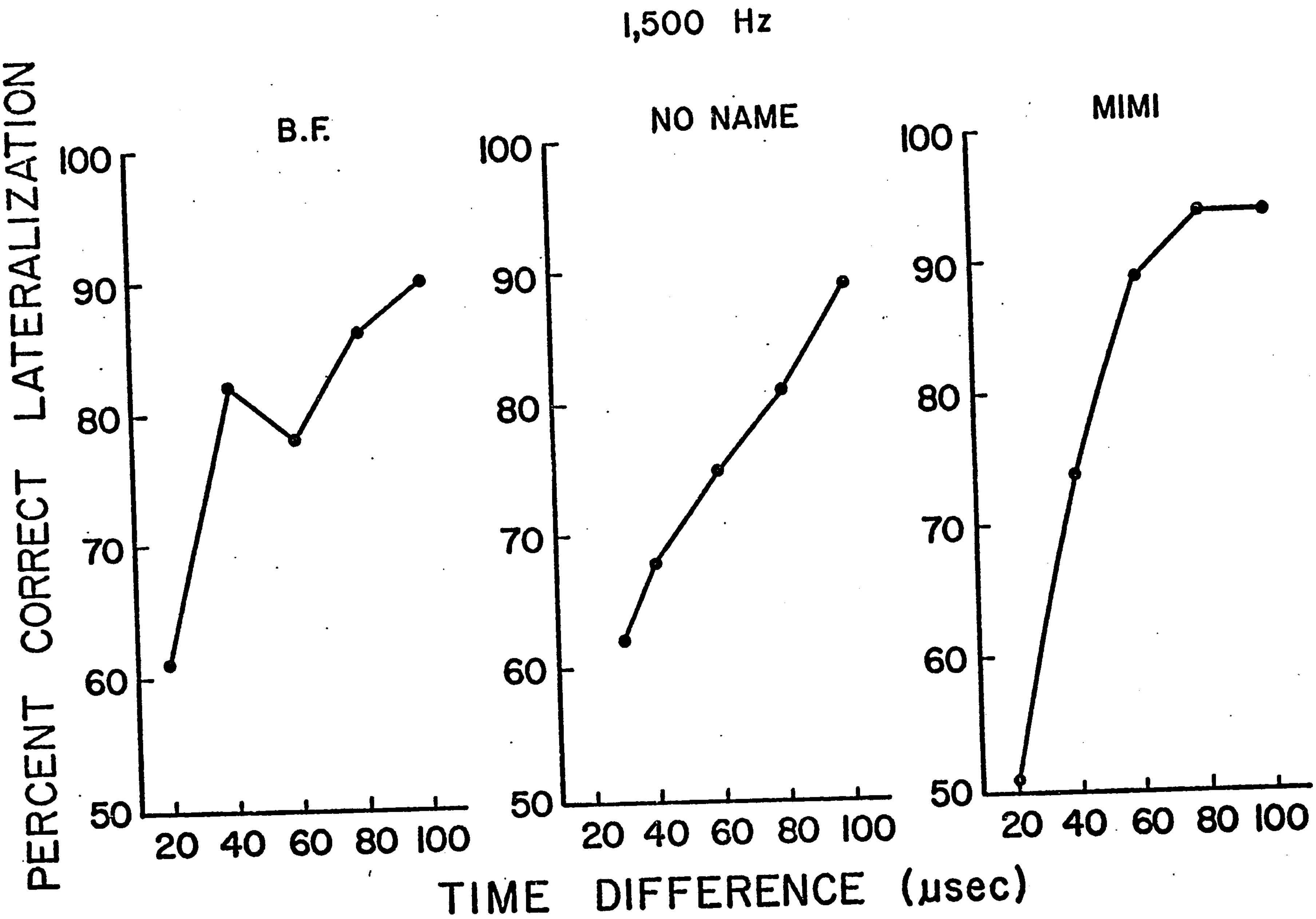

1,250 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
20
40
60
80
100
TIME DIFFERENCE (µsec)

Figure 22

Psychometric lateralization functions of interaural time difference for three monkeys at 1,500 Hz. Each function is based on 400 trials.



1,500 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
20 40 60 80 100
TIME DIFFERENCE (µsec)

Figure 23

Psychometric lateralization functions of interarual time difference for three monkeys at 1,750 Hz. Each function is based on 400 trials.

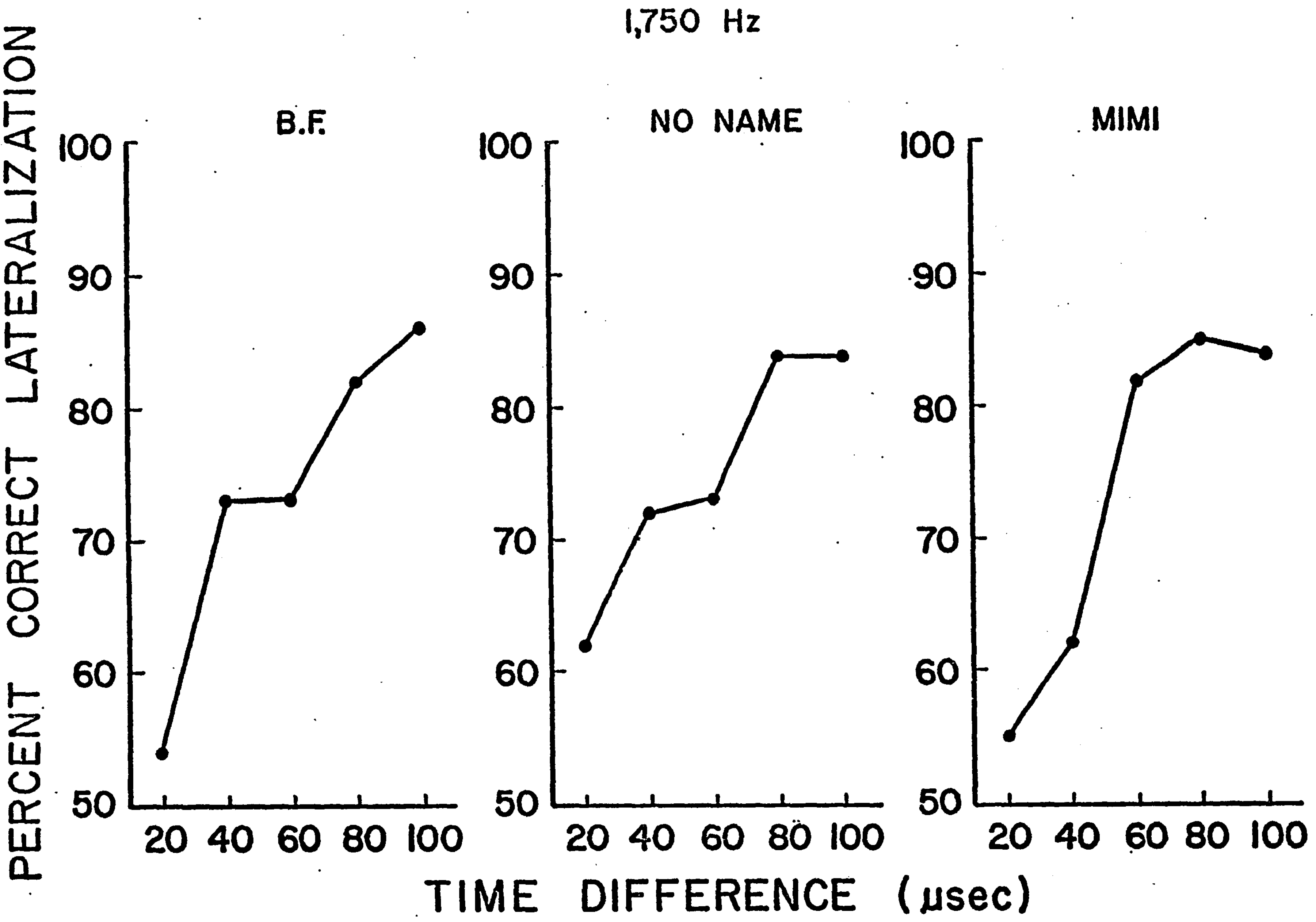
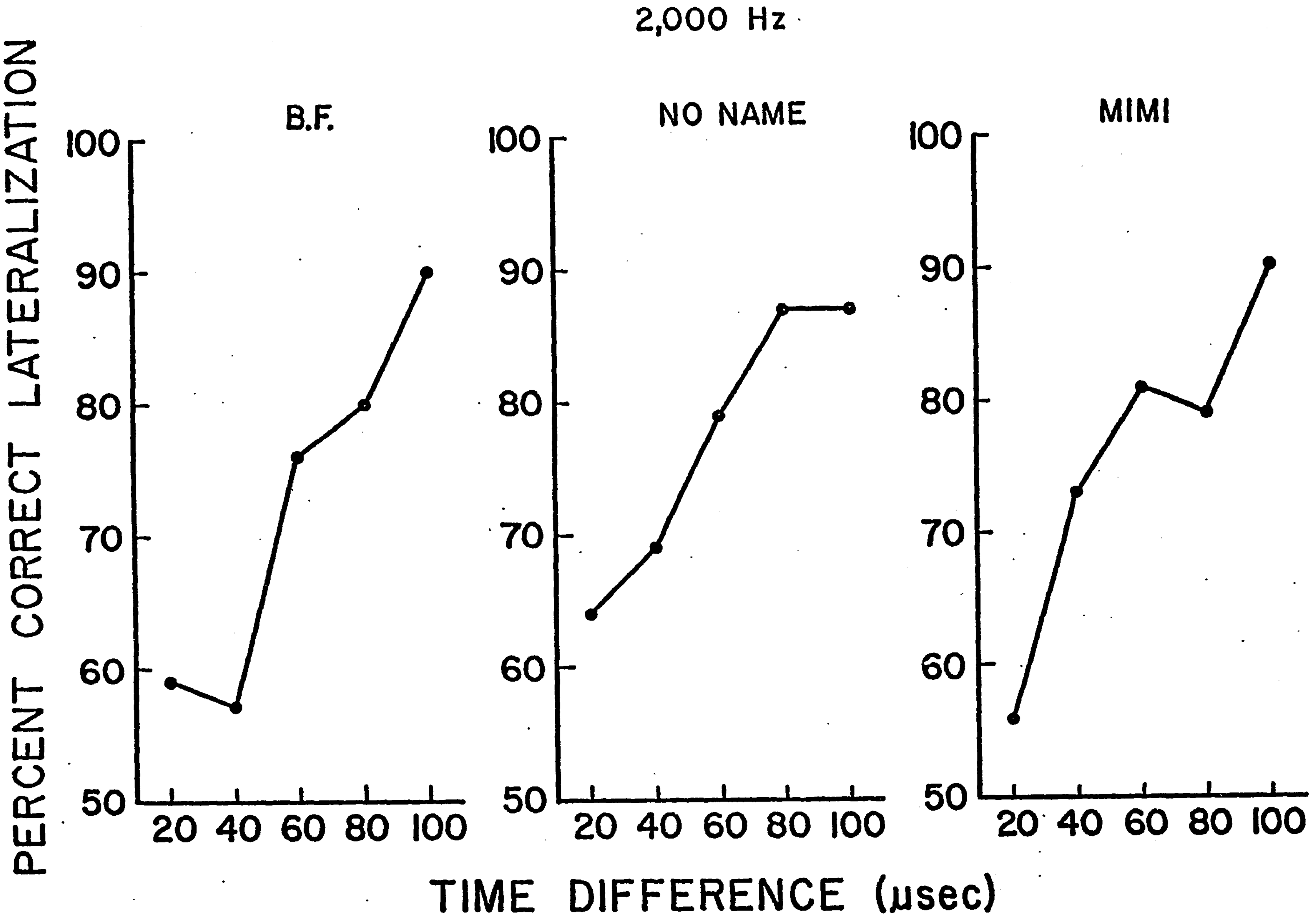

1,750 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
20 40 60 80 100
TIME DIFFERENCE (μsec)

Figure 24

Psychometric lateralization functions of interaural time difference for three monkeys at 2,000 Hz. Each function is based on 400 trials.


2,000 Hz
B.F.
NO NAME
MIMI
PERCENT CORRECT LATERALIZATION
100
90
80
70
60
50
20
40
60
80
100
TIME DIFFERENCE (µsec)

normalities of those psychometric functions. Thus, at 250 Hz, the best performance exhibited by Mimi was around the 80% correct level. Perhaps use of the same range of interaural time differences as with the other two monkeys would have extended her performance level.

Another example of this problem is visible in B.F.'s psychometric function at 1,000 Hz. The interaural time differences used with B.F. were twice as long as those presented to the other two monkeys. The steep ascent of the function between 40 µsec and 80 µsec suggests that the step size of the stimulus was too coarse. Moreover, the oscillations in the psychometric function for greater time differences may indicate that the range of these time delays was excessive and produced a less coherent sound image. It is noteworthy that other ranges and step sizes of interaural time differences were tried with this animal, including those used with the other two monkeys. Yet, when long delays were not available, B.F.'s performance deteriorated completely.

Table 4 shows the linear interpolation threshold estimates based on the functions discussed above. Also entered in the table are threshold estimates based on a z transformation. As in Experiment I, this transformation was made on the percent correct responses. By means of

TABLE 4

Interaural Time Difference Thresholds in μsec for Eight Frequencies

	Frequency (Hz)							
	250	500	750	1000	1250	1500	1750	2000
BF								
Linear Interpolation	62.6	94.4	46.7	63.7	32.7	33.3	64.4	58.9
Least Squares Z	72.7	91.6	65.7	80.9	31.4	45.9	65.7	66.7
Chi-Square[1]	18.28*	6.41	39.32*	44.72*	11.23*	14.98*	17.07*	9.41*
No Name								
Linear Interpolation	168.6	96.9	35.5	43.3	69.6	60.0	63.6	52.0
Least Squares Z	154.7	103.6	40.4	40.6	64.1	60.2	60.0	53.0
Chi-Square[1]	15.86*	9.59*	10.40	11.25*	4.35	0.10	3.61	3.8
Mimi								
Linear Interpolation	132.3	106.5	80.0	52.0	38.9	41.3	53.0	45.0
Least Squares Z	145.1	99.8	87.3	51.5	60.2	54.1	65.2	58.8
Chi-Square[1]	7.10	11.56*	4.97	17.03*	19.58*	41.48*	19.05*	15.55*

[1] The chi-square associated with the deviation of the observed probabilities from normality.

* The starred entries exceed the tabled value (7.8) for a significance level of 0.05 (df = 2)

the least-squares technique a straight line was fitted to the z scores and a threshold derived from this line.

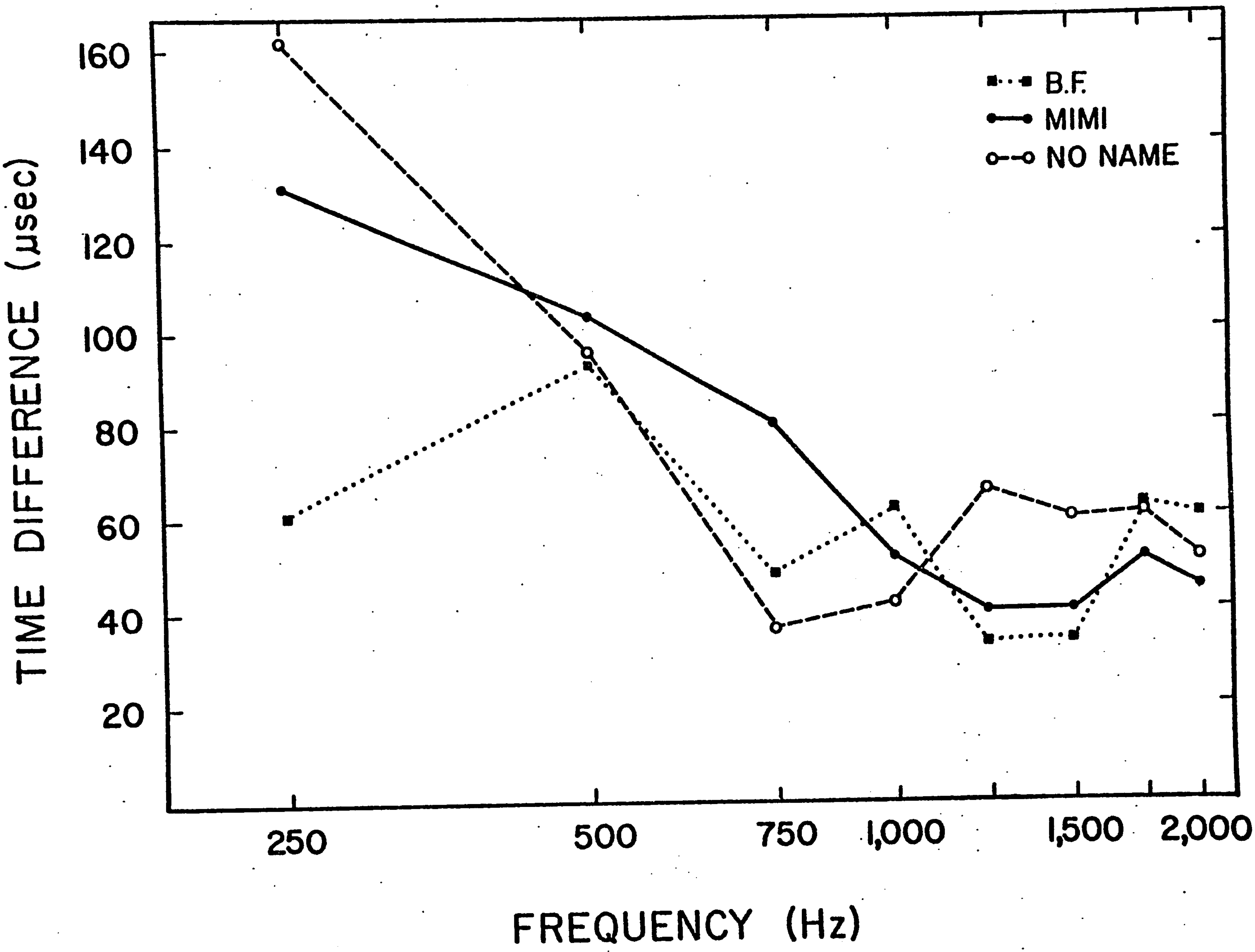
The results of a chi-square test to evaluate the discrepancies between obtained z scores and corresponding points on the best-fitting straight line also appear in Table 4. Large disparities between thresholds estimated by linear interpolation and by the z transformation procedure are in almost all cases associated with a significant chi-square ($p \leq 0.05$). This indicates that the underlying psychometric functions departed from normality. For this reason the thresholds estimated by linear interpolation were chosen for presentation in subsequent figures.

Figure 25 shows the individual interaural time difference thresholds as a function of frequency. The agreement among the thresholds of the three monkeys is good at all frequencies except at 250 Hz. The thresholds cluster most at 500 Hz and least at 750 Hz, falling within ±6 μsec and within ±23 μsec of each other. At 250 Hz the scatter of the thresholds is larger, extending over 100 μsec; it is primarily due to the divergence of B.F.'s function. The individual time difference functions, with the exception noted above for B.F., decrease with increasing frequency before beginning to level off around 750 Hz.

Mean interaural time difference thresholds for three

Figure 25

Interaural time difference thresholds for tonal stimuli in three monkeys.



B.F.
MIMI
NO NAME
TIME DIFFERENCE (µsec)
160
140
120
100
80
60
40
20
250
500
750
1,000
1,500
2,000
FREQUENCY (Hz)

monkeys are plotted in Figure 26. The function declines rapidly from 250 Hz to 750 Hz. Above this frequency the time difference thresholds remain pretty much constant at about 50 µsec up to 2,000 Hz, which is the upper limit for lateralization of pure tones in monkeys.

The only other time difference threshold for pure tones reported for monkeys (Wegener, 1974) is also depicted in Figure 26 and agrees very closely with the present results.

Human time difference thresholds obtained by Zwislocki and Feldman (1956) are also included in Figure 26. The function declines slightly from 250 Hz to 1,000 Hz, and rises at 1,250 Hz. This frequency is the upper limit, in man, for lateralization of pure tones.

The greatest difference between the human and monkey functions occur at 250 Hz, and the smallest at 1,250 Hz.

Examination of the probability of correct responding as a function of lever indicates that bias was not a serious problem in this experiment (Figure 27). If there had been a preference for one lever over the other, the probability correct on the preferred lever would have been consistently lower, independent of frequency, which was not the case.

Figure 26

Mean interaural time difference thresholds for three *M. nemestrina*. ▨ , Time difference thresholds for *M. mulatta* (Wegener, 1974); ▲ , Human time difference thresholds (Zwislocki & Feldman (1956).

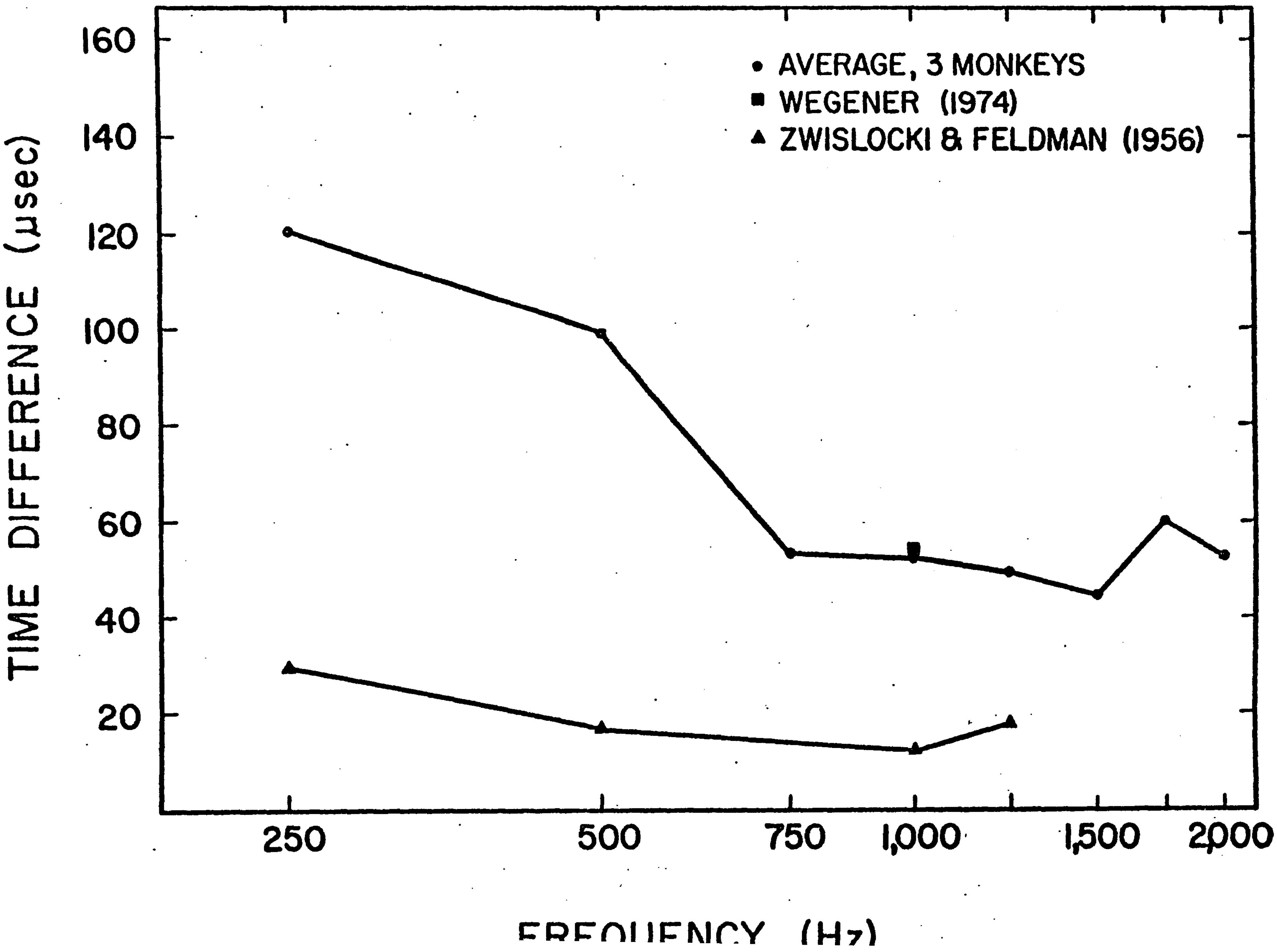
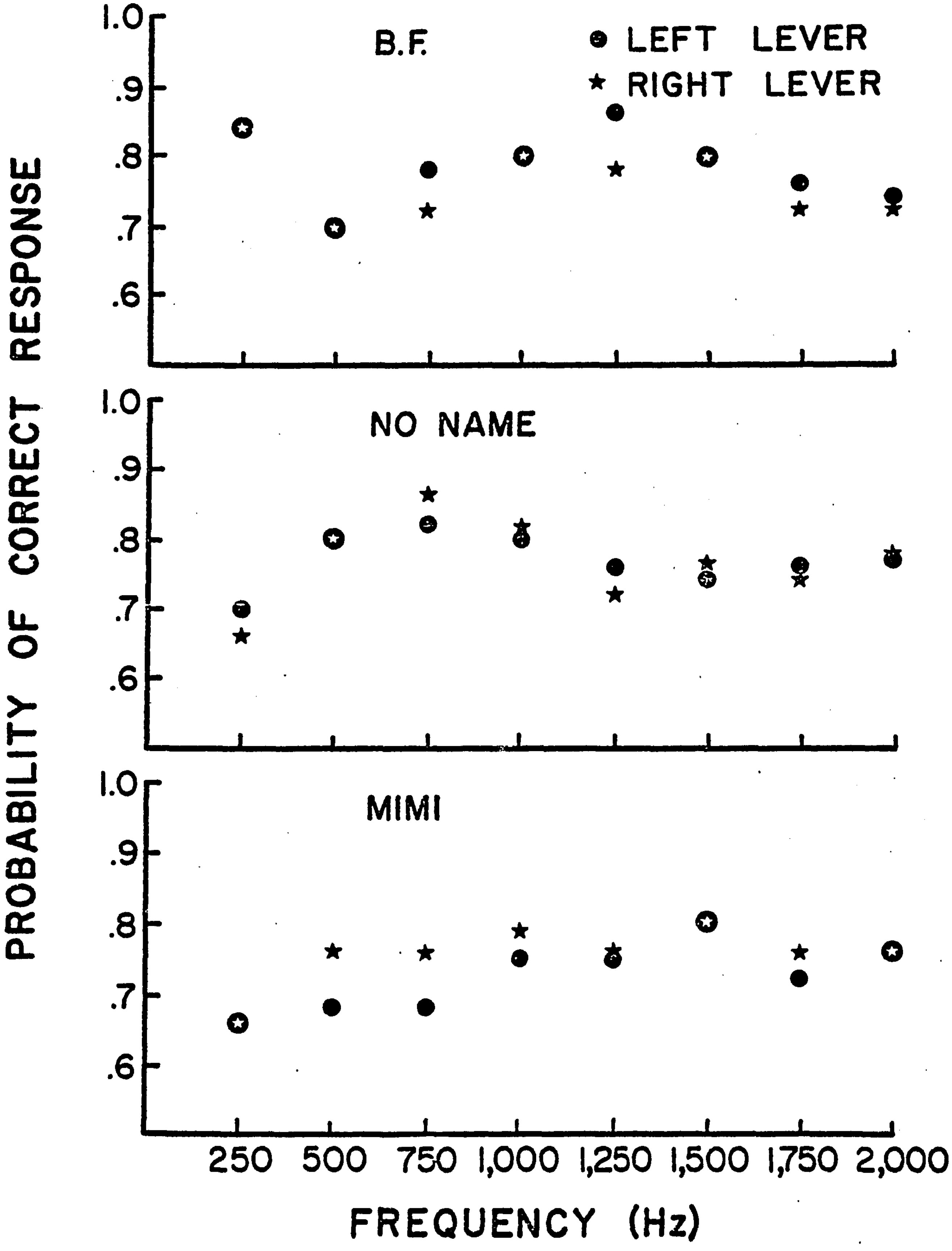

• AVERAGE, 3 MONKEYS
■ WEGENER (1974)
▲ ZWISLOCKI & FELDMAN (1956)
TIME DIFFERENCE (µsec)
160
140
120
100
80
60
40
20
250
500
750
1,000
1,500
2,000
FREQUENCY (Hz)

Figure 27

Probability correct for left and right choices for each frequency. The points represent the data reported in Experiment II. The circles indicate the proportion of left lever responses that were correct; the stars represent the proportion of right lever responses that were correct. Any large disparity between plotted points at a frequency indicates a bias for the choice associated with the lower probability.


B.F.
● LEFT LEVER
★ RIGHT LEVER
NO NAME
MIMI
1.0
.9
.8
.7
.6
PROBABILITY OF CORRECT RESPONSE
250
500
750
1,000
1,250
1,500
1,750
2,000
FREQUENCY (Hz)

Experiment III

Lateralization of combined interaural time and intensity cues at 1,000 Hz

The subjects, apparatus, and psychophysical method used in this part of the study have already been described in Experiments I and II

Only a 1,000 Hz dichotic tone was used in this experiment. It was first presented to the monkey at an interaural intensity difference selected from Table 2 which corresponded to the animal's threshold. As expected, in 100 trials all three animals lateralized correctly on 73% to 77% of the trials. After this verification of the intensity difference thresholds was completed the signal was modified. Threshold interaural time differences were selected from Table 4 and imposed on the signal. Now, the signal consisted of a joint interaural intensity and time difference, with both components favoring lateralization in the same ear. The performance of the animals dropped to near 50% correct. This finding was unexpected since it was assumed that discrimination of the compound stimulus would improve or, at least, be no worse than with either component alone.

While maintaining the intensity difference at threshold, other time disparities were investigated. When the time difference was reduced to zero the performance based on the intensity cue alone again reached about 75% correct. Introduction of time differences in 10 μsec steps caused the performance to deteriorate progressively until it reached the 50% level, which corresponded to a 40 μsec time difference for No Name and a 60 μsec time difference for both B.F. and Mimi. Each of the above determinations was based on 100 trials.

In a further attempt to clarify the nature of the phase-intensity interaction, intensity differences that had been lateralized correctly 90% or better in Experiment I were combined with time differences. The addition of time differences ranging from 20 μsec to 100 μsec (see procedure in Experiment II) did not alter in any way the performance; it remained in the vicinity of 90% correct.

These results were consistent with observations made during training of the time difference discrimination. In attempting to facilitate acquisition of the discrimination, a compound stimulus consisting of both time and intensity cues was presented. As long as the interaural intensity difference was maintained at above threshold levels, performance to the compound stimulus was good. However, when the intensity difference was reduced as part of the fading out procedure, performance dropped to chance level.

Further training with interaural time differences alone was succesful and was reported in Experiment II.

Discussion

Interaural intensity difference

The intensity difference threshold function shown in Figure 14, as was mentioned earlier, indicates that monkeys are quite a bit less sensitive than humans at all frequencies between 125 Hz and 8,000 Hz. Below 1,000 Hz the thresholds range from 3.5 dB to 4.5 dB whereas man's hovers just below 1 dB. Above 1,000 Hz the two functions diverge, the sharpest rise occurring between 1,000 Hz and 2,000 Hz. Since over the same frequencies the human function decreases somewhat, it is surprising to find that the monkey function increases substantially. This rise in the function cannot be attributed to lower sensation levels at these frequencies, since the lowest sensation levels occurred at the lowest frequencies (250 Hz and 500 Hz) and at these frequencies the intensity difference thresholds were at their minimum.

Support for the shape of the intensity difference function comes from the localization studies by Brown et al. (1975, 1976). They found that monkeys localize pure tone sources less accurately at frequencies above 1,000 Hz even though interaural intensity difference cues are presumably increasing with frequency.

The poorer performance of monkeys reported here and observed by others (Don & Starr, 1972; Wegener, 1974) raises the question whether this smaller sensitivity is a characteristic of monkeys or of other non-human species. The only other animal that has been tested in a lateralization study is the cat (Wakeford & Robinson, 1974). As reported, the cat thresholds range from a high of 2 dB at 500 Hz to a low of 0.5 dB at 3,000 Hz and are lower than any reported for the monkey, regardless of the waveform of the stimulus. This would suggest that the cat's sensitivity to intensity differences is similar to man's. There are, however, methodological differences between the cat study and the monkey studies reported in the literature. The cats were required to detect a reversal in trains of tone pulses having an initial interaural disparity, while the monkeys were required to identify the direction of a single dichotic pulse.[1] The lower detection thresholds were due in part to the difference in task rather than to a difference in sensitivity.

Another, possibly more important, difference between the cat and monkey studies concerns the definition of the magnitude of interaural difference. Implicit in the

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[1] This difference in task was pointed out by Wegener (1974).

experiments of Don & Starr (1972) and Wegener (1974) is the assumption that on every trial the subjects were making a judgment about whether the stimulus appeared to be to the left or right of the midline. In the present study a standard tone burst was presented that served as a reference against which the test tone could be compared. It is clear that in these cases the magnitude of the stimulus is equal to the interaural intensity difference presented on a particular trial. In the study of Wakeford & Robinson (1974) the stimulus consisted of tone pulses with an initial intensity difference which was shifted symmetrically to the other ear. Thus, if the initial tone pulses were 1 dB more intense in the left ear, then the warning signal pulses were 1 dB more intense in the right ear. The interaural intensity difference is 1 dB, but the magnitude of the shift is 2 dB. It appears that the authors reported the steady state intensity difference, and not the magnitude of the shift. If that is the case, the thresholds reported for the cat should be doubled to make the stimulus conditions comparable to those used in the monkey studies. This would cause the cat thresholds to range from 1 dB to 4 dB, and possibly higher if the methodological differences pointed out by Wegener (1974) are considered. The elevated cat thresholds would then support the suggestion that animals are less sensitive to interaural intensity differences than is man.

Interaural time difference

The time difference threshold function shown in Figure 26 indicates that for this cue the monkeys are also less sensitive than are humans. The monkeys were unable to lateralize tones of 125 Hz or 2,250 Hz, regardless of the interaural time difference. Human sensitivity to interaural phase differences extends below 250 Hz; threshold determinations at 125 Hz and 90 Hz indicate that sensitivity decreases rapidly to 56 µsec and 75 µsec, respectively (Klumpp & Eady, 1956).

Also plotted in Figure 26 is the one pure tone interaural time difference threshold determined by Wegener (1974). The mean threshold for the nine monkeys used in Wegener's study is 1 µsec greater than the one determined in this study. These thresholds, high compared to the human data, are also supported by the 60 µsec click-train time difference threshold in squirrel monkeys (Don & Starr, 1972). The thresholds reported for the cat (Wakeford & Robinson, 1974) have been interpreted by these authors as being similar to those of man, although they do point out that the cat thresholds at 500 Hz and 1,000 Hz (24 µsec in both cases) are about 10 µsec greater than the human thresholds.

The arguments raised in the last section with respect to the study by Wakeford & Robinson (1974), apply equally here. An on-going time difference with one ear leading was shifted to the opposite side, the total shift in time difference being twice the initial difference. Unless this doubling was taken into account, the thresholds should be increased two-fold; the resulting 48 µsec threshold at both 500 Hz and 1,000 Hz would then place the cat closer to the monkey in sensitivity.

In their conclusion Wakeford & Robinson (1974) state that their data offer no evidence of significant differences between cat and man in their ability to resolve binaural time differences. This conclusion ignores the fact that, like the monkey, their cats were able to utilize time cues to lateralize 2,000 Hz pure tones. In this respect both animals are clearly different from man. While recent studies (Henning, 1974; McFadden & Pasanen, 1976) have shown that human subjects can use variations in the envelopes of time delayed complex tones and noise, no study has shown that human subjects can lateralize pure tones of 1,500 Hz or greater based on time differences.

Estimates of monkey localization ability based on the Woodworth model.

Free-field sound sources produce differences in intensity at the ears of human and animal subjects that are a complex function of both frequency and azimuth of the source (Feddersen, Sandel, Teas, & Jeffress, 1957; Harrison & Downey, 1970). It is therefore difficult to make inferences about localization accuracy based on interaural intensity difference thresholds.

Time differences produced by actual sound sources are predicted by the geometric model proposed by Woodworth (1938). This model, which is described in the introduction, allows the threshold time difference obtained in this study to be converted to azimuth angles. A threshold time difference can thus be expressed as an equivalent minimum audible angle. The adequacy of the Woodworth model for predicting interaural time differences produced by clicks has been demonstrated by Feddersen et al. (1957). These investigators found almost perfect agreement between the predicted and actual functions relating interaural time differences to direction of click source.

The equation for interaural time difference introduced earlier,

$$\Delta t = 29 \text{ usec/cm} \times r \text{ cm} \times (\theta + \sin \theta)$$

can be solved for θ. For angles less than 25 degrees (0.436 radians),

$$\sin \theta \sim \theta;$$

thus,

$$2 \sin \theta = \Delta t/(29 \times r)$$

$$\sin \theta = \Delta t/(29 \times 2 \times r)$$

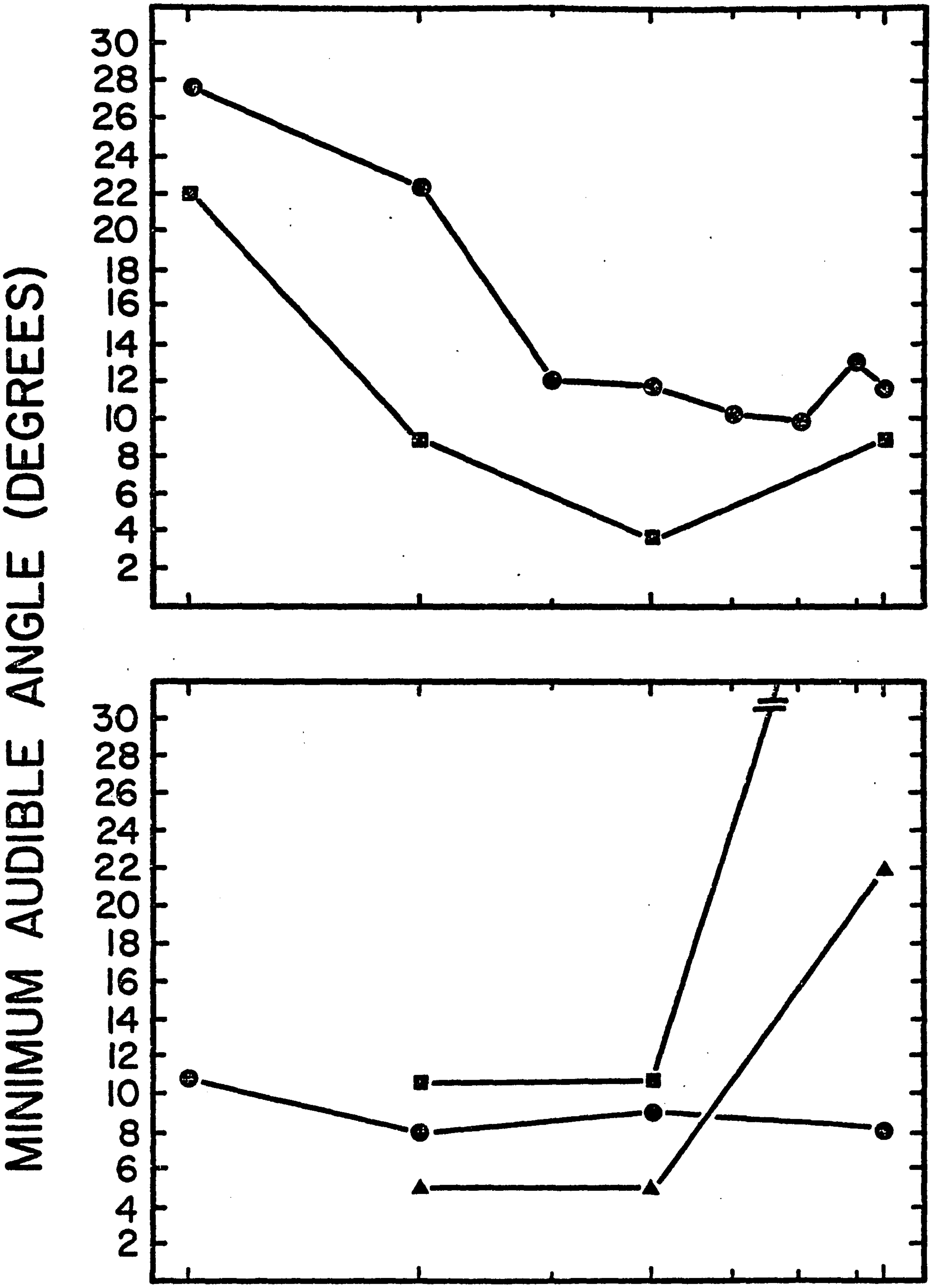
The mean diameter of the heads of the monkeys used in this study was found to be 9 cm; the value of r for the preceding equations is thus 4.5 cm. The time difference thresholds from Figure 26 were converted to angles and the resulting estimates of minimum audible angle based on on-going time cues alone are shown in Figure 28 (top panel). These estimates may be compared to the free-field localization thresholds obtained by Brown et al. (1976), also depicted in the figure. The two functions are essentially parallel, with the estimates based on time difference thresholds elevated relative to the actual localization function.

Similar estimates of minimum angles for the cat can be made, using the data of Wakeford & Robinson (1974); the geometric considerations are simpler. The cat head is as a sphere with the pinnae attached on top and facing foward in such a way that the sphere does not add to the distance travelled by a sound originating at azimuths other than 0° and 180°. Given this assumption, the extra distance is simply,

$$\Delta d = d_p \times \sin \theta$$

Figure 28

Estimated minimum audible angles for cat and monkey based on interaural time difference thresholds. Top panel: ● Estimates of minimum angles derived according to the Woodworth model from results of the present study; ■ Minimum angles for macaques (Brown et al., 1976). Bottom panel: ▲ Estimates of minimum audible angle for the cat based on interaural time differences (Wakeford & Robinson, 1974); ● The same estimates based on a twofold increase of the interaural intensity difference thresholds; ■ Minimum angles for cats (Casseday & Neff, 1973).



MINIMUM AUDIBLE ANGLE (DEGREES)
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
250
500
1,000
2,000
FREQUENCY (Hz)

where d_p is the separation between the pinnae. As in the analysis done for the monkey, (p. 124),

$$\Delta t = 29 \text{ usec/cm} \times \Delta d$$

and by substitution,

$$\Delta t = 29 \times d_p \times \sin \theta$$

solving for θ,

$$\theta = \sin^{-1} (\Delta t/29 \times d_p)$$

If we assume that the distance between the pinnae in the cat is the same as the diameter of our monkey heads, 9 cm, then the estimates shown in Figure 28 (bottom panel) can be made. One function depicts estimated minimum angles derived from the threshold reported by Wakeford & Robinson (1974). The other corrects for their interpretation of interaural intensity difference threshold and represents a two-fold increase of these thresholds (see p. 123). Finally, a portion of the localization function for cats obtained by Casseday & Neff (1973) is also plotted.

It is difficult to imagine that the time cue alone could lead to minimum audible angle estimates that are lower than thresholds measured in free-field condition, where both head movement and intensity differences can provide additional cues. It would seem more reasonable to accept the minimum angle estimates given by the upper curve as representative of the contribution of the time cue to localization of low frequencies. The correspondence of minimum angle estimates with those determined by Casseday & Neff (1973) is quite good for 500 Hz and 1,000 Hz. The poor fit at 2,000 Hz is difficult to explain since intensity differences should provide even less of a cue for cats with their high pinna placement, than for monkeys. Presumably then, the much better than predicted localization performance of the cats at 2,000 Hz is due to head and pinna movement and, possibly, the combined effects of both time and intensity cues.

Estimates of monkey localization ability based on modifications of the Woodworth model

It was noted in the previous section that the estimates of minimum audible angle derived in the present study were higher than those measured directly by Brown et al. (1976). The better than predicted localization ability of the monkeys is not likely to be due to intensity cues since the monkey head does not cast an appreciable "sound shadow" below 4,000 Hz. It is also not likely that the better performance was due to head movement cues, since Brown had restrained his subjects' heads.

Another explanation for the high estimates is that the model on which the calculations were based underestimates the interaural delay produced by off-center sound sources.

The Woodworth (1938) model is independent of frequency, and, as already mentioned, it accurately predicts the interaural delay introduced by click stimuli from speakers placed at various azimuth positions (Feddersen et al. 1957). Recent physical measurements of interaural delays produced by pure tone sources indicate that a frequency-independent model may not be appropriate. Abbagnaro, Bauer, & Torick (1975) measured interaural time and intensity differences as a function of frequency on human subjects and for a manikin. For all azimuth positions (30°, 60°, 120°, 150°) the measured phase difference between the ears was frequency dependent. The phase shift was greatest for frequencies near 250 Hz, and diminished to a constant value at frequencies greater than 2,000 Hz.

Kuhn (1976) extended these measurements and proposed a frequency dependent model for describing the interaural delay function. The observed delays for tones below 500 Hz were frequency independent for azimuth positions between 15° and 90°. Above 3,000 Hz the interaural time difference was frequency independent for azimuth positions between 15° and 60°. For frequencies between these limits, the time difference diminished with increasing frequency. The approximate ratio between the low frequency delays and those obtained at high frequencies was 3/2.

For man, the Woodworth model accurately predicts interaural delays for frequencies above 3,000 Hz; below this frequency the model underestimates the delays. Kuhn developed a model that takes into account the scattering of sound by a rigid sphere. This model, which predicts sound transmission time as a function of angle of incidence, wavelength, and radius, accurately fits the physical measurements.

The model consists of two parts. At high frequencies, above 3,000 Hz for humans, Kuhn's mathematical and physical model closely approximates the geometrical model of Woodworth. To predict the azimuth angle associated with an interaural time difference Kuhn derived the following equation:

$$\sin \theta = \Delta t / 2 \times a / C_o \qquad (1)$$

where Δt is the interaural time difference in sec, a is the radius of the sphere, and C_o is the speed of sound (34×10^3 cm/sec). This is the equivalent to the equation used in the previous section to estimate minimum audible angles for the monkey.

For low frequencies, below about 500 Hz for man, Kuhn's model states that

$$\sin \theta = \Delta t / 3 \times a / C_o \qquad (2)$$

will predict the azimuth angle associated with a particular interaural delay.

The only difference between equations (1) and (2) is in the Δt divisor; thus, for the same interaural time difference, the ratio of low frequency angles to high frequency angles is 2/3. The model also states that for frequencies between 500 Hz and 3,000 Hz the ratio changes smoothly from 2/3 to 1. Physical measurements supported these predictions.

Kuhn's model applies to spheres of any radius, so that predictions can be made for organisms with heads smaller than man. The only difference would be the frequency boundaries for using the equations. These boundaries are related to the parameters k and a, where k is the acoustic wave number ($2\pi f/c$) and a is the radius of the head. The model and the empirical results indicate that when $ka \leq 1$ equation (2) for low frequencies is appropriate; on the other hand, when $ka \geq 5$, the high frequency equation (1), is applicable.

In man, assuming a head radius of 9 cm, ka is equal to 1 at about 500 Hz, and ka is equal to 5 at about 3,000 Hz. For the monkey, with a head radius of 4.5 cm, similar calculations show that the frequency cut-offs corresponding to ka equal to 1 and ka equal to 5 are 1,250 Hz and 6,000 Hz, respectively.

To summarize, Kuhn's empirical findings and his physical-mathematical model indicate that at low frequencies the Woodworth model underestimates the interaural time difference produced by an off-midline sound source. "Low frequency" is defined in terms of the radius of the head by $ka \leq 1$. The converse is also true; at low frequencies the Woodworth model overestimates the azimuth position associated with an interaural delay.

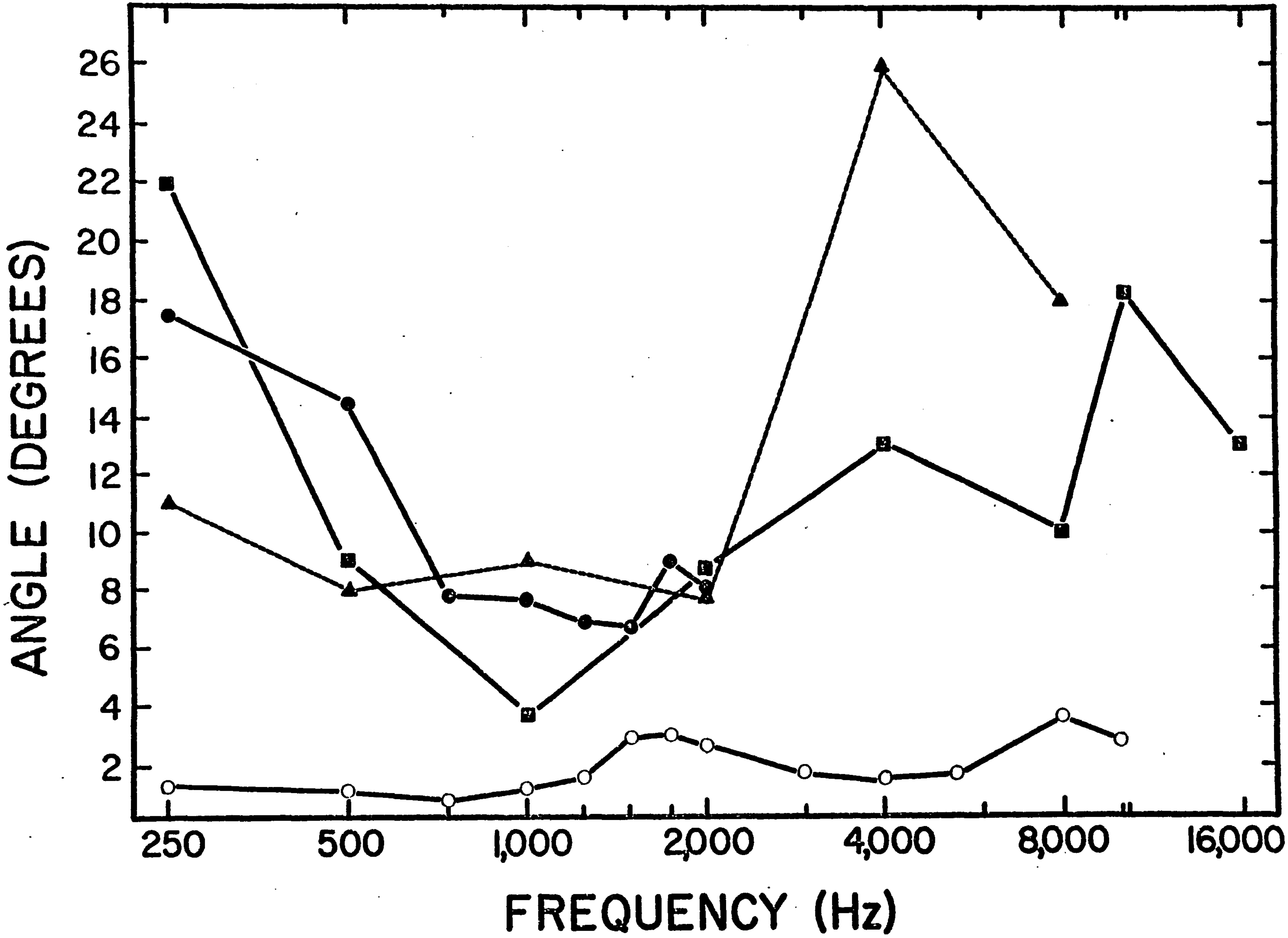
Figure 29 displays the estimated minimum audible angles derived from the time difference thresholds measured in this experiment and adjusted according to the frequency-dependent model. There is very close agreement between them and the localization thresholds obtained by Brown et al. (1976), which suggests that for the monkey the cue for localization up to 2,000 Hz is interaural phase difference.

Combined interaural time and intensity differences

The effect of combined phase and intensity cues on lateralization behavior in animals is completely unknown. We infer that an animal can deal with such combinations because they surely occur in open-field localization of actual sound sources. By definition, such combinations of phase and intensity are "natural", i.e., at a given azimuth the time difference and intensity difference at the ears will be governed by the geometry of the animal's head and

Figure 29

Estimated minimum audible angles based on a frequency dependent model for interaural delays. ● Estimates derived from thresholds of the present study. ▨ Minimum angles for macaques (Brown et al., 1976). ▲ Minimum angles for the cat (Casseday & Neff, 1973). ○ Human minimum audible angles (Mills, 1958).



ANGLE (DEGREES)
26
24
22
20
18
16
14
12
10
8
6
4
2
250
500
1,000
2,000
4,000
8,000
16,000
FREQUENCY (Hz)

the spectral content of the sound. Molino (1974) presented such "natural" combinations of phase and intensity to human subjects via earphones and verified that these combinations would indeed result in an appropriate perception of sound azimuth position. Molino also presented combinations of time and intensity not found in nature. At 500 Hz the perceived location was practically unaffected by intensity cues, and at 8,000 Hz judgments of image location were independent of time cues. These findings indicate that human subjects have no difficulty in lateralizing combinations of time and intensity, whether they occur naturally or not; the subjects simply assigned lateral position according to the dominant cue - intensity at high frequencies, phase at low frequencies.

Gilliom & Sorkin (1972) sought to determine the exact nature of such time and intensity interactions. They concluded that the sensations arising from interaural time and intensity cues correlate to a high degree (r=0.88). This would mean that the sensation from one cue adds as a scalar quantity to the sensation from the other cue. The lack of perfect correlation means that some residual sensation would remain which would prevent the time and intensity image from completely fusing into a single lateralized image.

A similar conclusion was reached by Hafter & Carrier

(1972). In a same-different signal detection paradigm various combinations of time and intensity differences, both congruent and in opposition, were presented to subjects who were also given a 500 Hz diotic reference tone. In general, congruent phase and intensity differences combined to yield higher d' measures than phase information alone. When the cues were in opposition, d' was lower than for either cue alone, but no combination of opposing time and intensity was effective in dropping d' to zero. Again, this study indicates that interaural time and intensity produce sensations in man that are at least partially independent.

Moushegian & Jeffress (1959) used a technique that required subjects to match the location of an image shifted by combined intensity and time cues by adjusting the interaural time difference in a noise "pointer". Such matches were possible for both congruent and opposing cues. The authors pointed out that the subjects had great difficulty making matching judgments involving combinations of large time and intensity differences. Sayers (1964) reported similar difficulties when subjects were asked to assign peripheral positions to lateralized images. "Experiments using pure tones with significant IAD are difficult to conduct. When the interaural amplitude difference significantly exceeded about 12 dB, all listeners reported that the image became too diffuse and ill-defined to judge its position (p. 925)."

In the light of these various human studies, how can one interpret the findings in the present study with respect to combinations of interaural phase and intensity? An intuitive prediction of the results of Experiment III would have required equal or better performance when threshold time and intensity cues are combined. Much of early psychophysics rested on the assumption that just noticeable differences produce equivalent sensations. This does not seem to be true for the monkey when a just noticeable difference in phase is added to a just noticeable difference in intensity. The combination of these supposedly equivalent sensations leads to a complete breakdown of the discrimination.

The results of Gilliom & Sorkin (1972) also would lead to a prediction of equal or better performance when congruent cues are combined. If time and intensity add as signed scalar sensations with only a small residual component, then the result should be a dominant fused image. One possible explanation for the lack of simple addition of sensation in the monkey is that time shifted and intensity shifted images are not equivalent and do not therefore sum. If this is true the monkey might be hearing an image shifted by threshold time difference in one location, and an image shifted by threshold intensity difference in another location. The combination of the two might then be a diffuse image that is difficult to lateralize.

The foregoing hypothesis assumes that for the monkey there is an intracranial image like the one reported by human subjects. Other than the fact that monkeys can learn to respond "left" and "right" to phase and intensity differences, we have no insight into their perceptual world. It is possible that one cue, phase, results in an intracranial image that varies location as a function of delay, and that intensity results in a binary perception: in the head for below threshold intensity differences, and at the ear receiving the louder stimulus for above threshold intensity differences. Such a hypothesis would explain the difficulty with which the transfer from the intensity task to the phase task was accomplished.

Finally, although Molino (1974) reported that humans had no difficulty with unnatural combinations of phase and intensity, the same may not be true for the monkey. Threshold time difference of 53 μsec at 1,000 Hz was estimated in the previous section to be associated with an azimuth position of 8°. The threshold intensity difference of 4.5 dB at 1,000 Hz is much larger than could occur naturally, regardless of azimuth position. If the monkey lateralizes and localizes based on experience with the environment and the combinations available naturally, then he might be unable to categorize unnatural combinations of threshold disparities.

Conclusion

The data and the arguments presented here suggest that non-human mammals are unable to localize pure tones as accurately as is man. Minimum audible angle as a function of frequency is poorer for both cat and monkey (Casseday & Neff, 1973; Brown et al., 1976) than it is for humans (Mills, 1958). There are two reasons for this poorer performance. At a given frequency the localization cues available to an animal with a small head are smaller, and, as reported here, the sensitivity to the cues that are presented is poorer.

Man's superiority in localizing and lateralizing complex sounds is somewhat less pronounced, but still clearly in evidence. Minimum audible angles for wide-band clicks are about 3/4° for human subjects (Banks & Green, 1973). In contrast, the cat's threshold for localizing broadband noise is about 6° (Casseday & Neff, 1973) and the monkey's threshold is no better than about 5° for broadband noise (Brown et al. 1976). Again, the results from lateralization studies point at the reason for the animal's relatively poorer ability to localize. For the monkey, thresholds for click intensity differences have been reported as 2.25 dB, and 6-10 dB (Heffner, 1973; Don & Starr, 1972). The intensity difference threshold for noise reported in this study is slightly lower than the best pure tone threshold, but still far from the human sensitivity to interaural intensity differences. Similar measures are not available for the cat.

On the basis of a negative correlation between maximum interaural time available to animals because of their head size and the upper frequency cut-off in their audiograms, it was suggested that the high frequency hearing characteristic of most mammals "... is a result of selective pressure to allow accurate and instantaneous localization of brief sounds." (Masterton, Heffner, & Ravizza, 1969, p. 983). Although the upper frequency of monkey hearing is about an octave higher than man's (Masterton et al., 1969; Stebbins, 1973), this does not find expression in the monkey's ability to localize with any greater accuracy at high frequencies. On the contrary, over the limited range of frequencies tested in this study, sensitivity to interaural intensity differences decreased with increasing frequency. As the localization function of Brown et al. (1976) shows, this decrease in sensitivity to intensity differences leads to a steadily increasing threshold for angular separation, at least up to 11,200 Hz (see Figure 29). It is only at 16 kHz that the monkey is able to localize pure tones with somewhat greater accuracy but the threshold is still high (13°).

Finally, the hearing of monkeys and other animals appears to be different from man's in one other respect. They can discriminate interaural time differences for pure tones at higher frequencies than man. As mentioned earlier, monkeys can lateralize phase shifted tones up to 2,000 Hz, and the same finding has been reported for the cat (Wakeford & Robinson (1974). Apparently the rat and the tree shrew are similar in this respect (Masterton, Thompson, Bechtold, & Robards, 1975). The accuracy of localization for both of these organisms declines at frequencies above 2,000 Hz, and increases again for frequencies above 8,000 Hz.

Thus, it appears that the selective pressures on the localization mechanisms of auditory systems in animals may not have been the same as in man. In the light of these findings, different metrics for accuracy of localization may be needed when considering localization in animals and man.

APPENDIX

Calibration of the headphones was carried out in the Industrial Acoustics test chamber. The response curve of the phones was measured by placing a 1/4" B & K condenser microphone perpendicular to each phone, just touching the cushion. Output was monitored via a Hewlett-Packard # 302A wave analyzer and # 7035B X-Y recorder. Over the range from 125 Hz to 8 kHz the response of the phones varied 6 dB; at all test frequencies the SPL of the left and right phones was within 2 dB.

Final calibration of level was done with the headphones in place on the monkey. An 1/8" B & K microphone, together with the cathode follower , was sandwiched between the monkey's head and the cushion such that the tip of the microphone was positioned at the ear canal entrance. Small changes in the position of the microphone caused less than 1 dB variation in the measured output level. The final attenuators were adjusted to match the output of the phones at 100 dB SPL. Then both channels were attenuated a further 40 dB to arrive at the 60 dB level for testing. No more than 1 dB interchannel difference was required to match the output of the phones at any of the eleven test frequencies.

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