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Binaural Topography of Primary Auditory Cortex
in the Ferret (*Mustela putorius*)

by

Peter W. Judge, M.A.

A thesis submitted to the faculty of Graduate Studies
and Research in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Department of Psychology

Carleton University

Ottawa, Ontario

August 1988

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ABSTRACT

Microelectrodes were used to map binaural responses in the primary auditory cortex of barbiturate-anesthetized ferrets. Gated pure tones were delivered independently to the two ears through a sealed speaker system and sensitivity to binaural intensity was determined at various sound pressure levels. Units within AI exhibited binaural response properties which were similar in most respects to those found in the cat's primary auditory cortex. The binaural neurons tended to be grouped together on the basis of their binaural response properties. Along the length of each isofrequency contour, areas of binaural summation (EE/F) alternated with areas of binaural suppression (EO/I). A third major binaural response type, first noted by Reale and Kettner (1986), combined the properties of EE/F and EO/I units. These cells exhibited summation when the contralateral intensity was near threshold and the interaural intensity was small, but were suppressed at higher ipsilateral intensities. Eight-one percent of 'mixed' units located within narrow band isofrequency contours were positioned between groups of EE/F and EO/I cells. The mixed responses appeared to mark the transition between summative and suppressive responses both by virtue of the location, and the duality of binaural response properties. Monaural and binaural thresholds obtained from units located within narrow band isofrequency contours were plotted. No consistent evidence of systematic variation of thresholds along isofrequency contours could be demonstrated.

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Tonotopic Organization

Evoked Potential Mapping

The first modern experiments concerning the functional characteristics of auditory cortex were conducted in the early 1940's. At this time the anatomical boundaries of primary auditory cortex were known only through studies of cytoarchitecture and retrograde degeneration of the thalamus (von Bonin, 1938; Brodmann, 1909; Campbell, 1905; cited in Bremer & Dow, 1939; von Economo, 1930; cited in Rose, 1949; Pennington, 1937; Walker, 1937). In particular, primary auditory cortex was identified as being the main¹ recipient of topographically organized fibers projecting from the medial geniculate body (Rose & Woolsey, 1949).

The physiological boundaries of auditory cortex were explored by recording cortical responses evoked by click stimuli (Bremer & Dow, 1939) and by electrical stimulation of the auditory nerve fibers leaving the cochlea (Tunturi, 1944; Woolsey & Walzl, 1942). These studies revealed a precise point-to-point correspondence between specific positions on the cochlear partition², and positions on the surface of auditory cortex. Because different positions on the cochlear partition are associated with different sound frequencies this organization of auditory fibers came to be known as 'tonotopic', and has since been shown to be characteristic of virtually every major element of the primary auditory pathway, including the cochlear nucleus (Rose, Galambos & Hughes, 1959), lateral superior olive (Tsuchitani & Boudreau, 1966), medial superior olive

(Goldberg & Brown, 1968), nucleus of the lateral lemniscus (Aitkin, Anderson & Brugge, 1970), inferior colliculus (Semple & Aitkin, 1979; Rose, Greenwood, Goldberg and Hind, 1963), and medial geniculate body (Aitkin & Webster, 1971; Calford & Webster, 1981). The tonotopically ordered points on the surface of the cat's primary auditory cortex are organized such that high frequencies are represented rostrally and low frequencies caudally. As well, each frequency representation is found to extend along the dorso-ventral dimension of cortex, orthogonal to the frequency gradient (Bailey, von Bonin, Garol & McCulloch, 1943; Hind, 1953; Tunturi, 1950b, 1960; Woolsey & Walzl, 1942) forming strips of auditory cortex known as 'isofrequency contours'.

The re-representation of the frequency domain on the dorsal-ventral surface of primary auditory cortex prompted Tunturi (1950a) to speculate that the isofrequency contour contained neurons which varied in their response to some dimension of acoustic stimulation other than frequency. This hypothesis has recently been substantiated by evidence derived from the cat (Imig & Adrian, 1977; Imig & Brugge, 1978; Imig & Reale, 1981; Middlebrooks, Dykes, & Merzenich, 1980; Middlebrooks & Zook, 1983; Reale & Kettner, 1986), and rat (Kelly & Sally, 1988) which show that cells of varying binaural response type but similar characteristic frequency are found along isofrequency contours.

Single-Unit Mapping

Initial attempts to map primary auditory cortex using single-unit microelectrode techniques were characterized by vague and

inconsistent reports of tonotopicity (Erulkar, Rose & Davies, 1956; Evans, 1950; Evans and Whitfield, 1964; Goldstein, Ables, Daly and McIntosh, 1970; Hind, Rose, Davies, Woolsey, Benjamin, Welkes, and Thompson, 1960). Common to these early investigations was the method of superimposing data derived from different animals onto one 'standard' reference. Therefore, different parts of cortex were mapped in different animals, and the results combined. The major limitation of this method was that functional regions of auditory cortex were later found to vary in relation to cortical landmarks such as fissural patterns (Merzenich et al, 1975). Subsequent mapping studies, based on a greater number of penetrations within a single preparation, showed that auditory cortex of cat was more complexly organized than was previously thought. In a landmark experiment, Reale and Imig (1980) explored, for the first time, the banks of the anterior and posterior ectosylvian sulci and suprasylvian sulcus in the cat's temporal cortex. These experiments revealed that fully one-half of the auditory cortical surface, previously unexplored, lay buried within the sulci. The results of these experiments redefined the physiological boundaries of auditory cortex to include no fewer than seven physiologically different fields including: Primary (AI), Secondary (AII), Ventroposterior (VP), Posterior (P), Anterior Auditory Field (A or AAF), Dorsoposterior (DP), and Temporal (T). Most of these fields were distinguished from the others by a distinct reversal in tonotopicity.

The tonotopic organization of auditory cortex has been successfully demonstrated in a variety of mammals including: the rabbit (McMullen & Glaser, 1982), the grey squirrel (Luethke, Krubitzer & Kaas, 1988; Merzenich, Kaas & Roth, 1976), the albino rat (Sally & Kelly, 1988); the marmoset (Aitkin, Merzenich, Irvine, Clarey and Nelson, 1986), the possum (Gates & Aitkin, 1982), the bat (Asanuma, Wong & Suga, 1983; Kujirai & Suga, 1983), the cat (Hind et al., 1960; Goldstein et al., 1970; Knight, 1977; Merzenich, Knight & Roth, 1975; Phillips & Orman, 1984; Reale & Imig, 1980), the ferret (Kelly, Judge & Phillips, 1986), the owl monkey (Imig, Ruggero, Kitzes & Brugge, 1977), the macaque monkey (Brugge & Merzenich, 1973; Merzenich & Brugge, 1973), and man (Romani, Williamson & Kaufman, 1982; Romani, Williamson, Kaufman & Brenner, 1982).

Response Characteristics of Single Neurons

Under conditions of monaural stimulation, recordings made from single units located in the primary auditory cortex contralateral to the stimulated ear show a number of consistent response characteristics, including short latency to first spike, and narrow frequency tuning. Neurons in primary auditory cortex are typically identified on the basis of their 'characteristic' frequency (BF or CF). The characteristic frequency is the frequency to which the unit has the lowest threshold of excitation.

Frequency-threshold functions ('tuning curves') obtained from the cat show that most neurons in physiologically-identified primary auditory cortex are narrowly tuned; that is, they respond

only to a narrow band of frequencies (Phillips & Irvine, 1981a). Sharpness of tuning is dependent on the CF of the units (Phillips & Irvine, 1981a). For example, neurons whose CF is low respond to a wider sector of the basilar membrane. These units are said to be 'broadly tuned'. On the other hand, units with high CFs are said to be 'sharply tuned' and respond to a narrower segment of the cochlear partition.

Most neurons (80%) in primary auditory cortex (AI) exhibit dynamic ranges of 40 dB³ or less (Phillips & Irvine, 1981a). Phillips & Irvine (1981a; 1983) showed that a majority of neurons in primary auditory cortex have monotonic rate-intensity functions, in which firing rate increases as a linear function of monaural intensity. Twenty-three percent, however, exhibit non-monotonic rate-intensity functions in which firing rate increases with intensity to an asymptotic level, after which further increases in intensity cause firing rates to decline. Monotonic and non-monotonic response-types are distributed evenly across units of varying characteristic frequencies.

Typical of preparations using barbiturate anesthetized mammals, cortical laminae I to II are not responsive to auditory stimulation, while laminae III to V are most responsive (Gates & Aitkin, 1982; Middlebrooks et al., 1980; Merzenich et al., 1975; Phillips & Irvine, 1981a; Reale & Imig, 1980).

Binaural Neurons in Primary Auditory Cortex

Both ears are represented in each auditory cortex in the monkey (Brugge & Merzenich, 1973a,b,c) in the cat (Brugge, Dubrovsky, Aitkin & Anderson, 1969; Hall & Goldstein, 1968), the albino rat (Kelly & Sally, 1988) and in the chinchilla (Benson & Teas, 1976). Units within the primary auditory cortex are more likely to be influenced by stimulation of both ears together, than by stimulation of either ear alone (Benson & Teas, 1976; Brugge et al., 1969; Hall & Goldstein, 1968; Imig & Adrian, 1977; Middlebrooks et al., 1980; Phillips & Irvine, 1981a). The first investigators to stimulate each ear independently found that fully 94% of units were receptive to various types of binaural stimuli including clicks, noise bursts and tone bursts (Hall & Goldstein, 1968). In the unanesthetized chinchilla all (133) units studied were responsive to binaural stimulation (Benson & Teas, 1976). This finding has been substantiated by a number of investigations of binaural interaction in auditory cortex. For example, recent work using the cat (Phillips & Irvine, 1983) and albino rat (Kelly & Sally, 1988) has shown 93% and 96%, respectively, of units studied to be sensitive to binaural tonal stimulation.

Binaural Response Properties

Neurons exhibit a wide range of response properties to binaural stimuli (Brugge et al., 1969; Hall & Goldstein, 1968; Phillips & Irvine, 1979a). Hall & Goldstein (1968) were the first to classify units according to their response to binaural stimulation. Unit

responses were identified as belonging to three major groups: 'summation', 'inhibition', or 'occlusion'. These categories were elaborated by Imig and Adrian (1977) to include 'aural dominance'⁴. The dominant ear (contralateral or ipsilateral) is that which yields the largest unit response. As well, units responsive to binaural stimulation are often classified in terms of their monaural response characteristics. Therefore, binaural responses can be described in terms of the type of monaural input (excitatory or no effect), the ear of 'dominance' (contralateral or ipsilateral), and the type of binaural interaction (summative, suppressive or occlusive).

Summation type neurons, sometimes called 'facilitatory', are defined as responding more strongly to stimulation of both ears than to stimulation of either ear alone. Summation neurons are the most frequently encountered in the cats' AI (47%: Hall & Goldstein, 1968; 67%: Imig & Adrian, 1977; 50%: Phillips & Irvine, 1983; 56%: Reale & Kettner, 1986). In the rat, however, summation units are less prevalent (35%) than suppressive response types (42%) (Kelly & Sally, 1988).

Units classified as exhibiting characteristics of 'inhibition' or 'suppression' are less frequently encountered in cat (12%: Hall & Goldstein, 1968; 34%: Imig & Adrian, 1977; 34%: Phillips & Irvine, 1983; 25%: Reale & Kettner, 1986). This type of unit responds less to binaural stimulation than to stimulation of the contralateral ear alone. Most reports indicate that the contralateral ear is the excitatory component in this interaction, while the ipsilateral ear exerts an inhibitory influence on the combined binaural spike

count. In the cat, another group of neurons was found whose responses at different intensities or frequencies combined the characteristics of summation and inhibition, depending on the degree of interaural intensity difference (2%: Imig & Adrian, 1977; 7%: Hall & Goldstein, 1968; 17%: Reale & Kettner, 1986). The proportion of 'mixed' units encountered in the rat was 18% (Kelly & Sally, 1988).

Units were observed which responded to either ear monaurally, but whose binaural response was equal to the most effective monaural stimulus. This response characteristic was known as 'occlusion' since the least effective monaural stimulus appeared to be blocked or 'occluded' (Benson & Teas, 1976; Hall & Goldstein, 1968; Imig & Adrian, 1977; Middlebrooks, Dykes & Merzenich, 1980; Phillips & Irvine, 1983).

Other units, identified as 'predominantly binaural' (PB) by Kitzes et al. (1980), responded best to binaural stimulation in which interaural time and intensity differences were nearly equal. These units showed equally robust responses for overall intensity levels ranging over 80 dB SPL. Although monaural stimulation was highly ineffective, neurons did show a weak non-monotonic response to contralateral monaural stimulation, but no response to ipsilateral stimulation. Phillips & Irvine (1983) used a combination of monaural and binaural stimuli to identify unit response type. They reported that 'PB' cells comprised 12% of their sampled population. Most investigators, however, used contralateral stimuli to search for auditory units, a method which is biased against detecting

predominantly binaural units. It is possible that PB units exist in greater numbers than has previously been reported.

A variety of nomenclatures has been adopted to represent the binaural response properties of neurons. The 'summative' and 'suppressive' categories convey less information about the exact nature of the binaural interaction than do other schemes. A better classification scheme was proposed by Goldberg and Brown (1969), extended by Aitkin et al. (1975), and used in many studies of central auditory function (Fuzessery and Pollak, 1985; Phillips & Irvine, 1983; Semple & Aitkin, 1979; Wise & Irvine, 1984, 1985). This scheme uses a three-letter code to designate the binaural interaction, and its monaural components. The first two letters indicate the responses to monaural stimulation of the contralateral and ipsilateral ears respectively (usually excitatory: 'E', or no response: 'O'). The third letter, separated by a slash or parentheses, indicates the binaural interaction, inferred from comparison of the responses to simultaneous stimulation of the two ears with the stronger monaural response (usually facilitation: 'F', inhibition: 'I', or no difference: 'O').

Single-unit studies (Phillips & Irvine, 1983) have shown that EO units and EE units can each exhibit suppressive (EO/I or EE/I) or summative (EO/F and EE/F) binaural responses. Thus, simpler classification schemes may obscure certain response types (Imig and Adrian, 1977; Middlebrooks et al., 1980).

Sound Localization Cues

The auditory receptor (the basilar membrane) is not capable of directly encoding the spatial location of a brief sound. Tones of different frequencies displace the basilar membrane maximally at different locations along the length of the cochlea. High frequencies stimulate the basal end of the cochlea, while low frequencies stimulate the apical end. Displacement of the basilar membrane is proportional to the amplitude, or intensity, of the stimulus. The acoustic signal is thus coded with respect to intensity and frequency, but not position in space. This is unlike spatial processing in the visual system, in which an object's spatial location is mapped directly onto the receptor surface (the retina), and then conveyed via precise topographic projections by way of the lateral geniculate to visual cortex. Instead, the auditory system must form a computational model of sound locus derived from inputs to the two ears.

A sound emanating from a position on the horizontal plane other than the midline will stimulate each ear differently. The ear closest to the sound source will be stimulated first, and with greater intensity. For example, a sound emanating directly opposite one ear will arrive at the farther ear about $29 \mu s$ later for every centimeter it must travel. Similarly, because the farther ear lies in a sound shadow cast by the mass of the head, which acts as a low-pass filter, differences in sound pressure may be negligible for low frequencies, but range up to 20 dB for higher frequencies. As well as sound pressure differences, therefore, the 'sound shadow'

creates a spectral difference between the ears for stimuli with multiple frequency components (Mills, 1972). The differences in the way intensity, frequency, and time of arrival cues are encoded at each ear provide the fundamental acoustic elements from which the central auditory system is able to derive a precise estimate of sound location.

The relative contribution of different binaural cues to sound localization differs widely among mammals, and even among members of the same order (Gourevitch, 1984; Masterton, Heffner, and Ravizza, 1969). Masterton, et al. (1969) reported a high negative correlation (-0.86 , $p < .01$) between maximum interaural distance and high frequency hearing. Animals with closely set ears exhibited a more extensive upper range of high frequency hearing.

For early experiments using pure tones, different binaural cues were reported to predominate at low and high frequencies. Since the human head is acoustically 'transparent' to low frequency tones, it creates little or no sound pressure difference between the ears for frequencies below 1500 Hz (Mills, 1972). Therefore, sound localization at low frequencies was thought to depend on interaural time differences (ITDs).

Interaural Intensity Differences (IID)

Differences in binaural intensity and time at each ear are important cues for sound localization (Masterton & Diamond, 1973). Single unit discharges in the superior olivary complex, inferior colliculus and medial geniculate are known to be critically dependent on these cues (Erulkar, 1975; Kuwada & Yin, 1983;

Rose et al, 1963; Tsuchitani & Boudreau, 1966), as are neurons in primary auditory cortex (Brugge et al., 1969; Phillips & Irvine, 1981b).

Among neurons of the suppressive response type, stimulation of the ipsilateral ear alone often fails to elicit spikes. However, if the ipsilateral stimulus is paired with a highly effective contralateral stimulus, the resultant binaural spike count was significantly less than that obtained when the contralateral stimulus was sounded alone. In fact, the binaural spike count could be systematically reduced by raising the intensity of the ipsilateral (inhibitory) tone (Brugge et al., 1969; Phillips & Irvine, 1981b).

Brugge et al. (1969), examined summative neurons under conditions of equal binaural intensity. Stimulation of both ears with puretones of equal intensity caused an increase in the binaural response over the largest monaural response.

The effect of manipulating intensity differences at the two ears was further investigated by Phillips & Irvine (1981b). Inter-aural intensity differences (IIDs) were varied within the range which would occur naturally as a result of attenuation of sound pressure at the ear distal to the sound source, caused by the 'shadow' of the head and ears⁶. The relation of spike count to interaural intensity differences (IIDs) varied according to an 'S-shaped' (sigmoid) function. For example, when the IID favored the contralateral ear, the unit responded maximally. When the IID shifted to favor the ipsilateral (inhibitory) ear, the response was totally suppressed. The position of the cut-off point between the two regions of maximal

effect reflected the changing balance of contralateral excitation and ipsilateral inhibition which would occur naturally with changing azimuth. The majority of units in primary auditory cortex were found to be maximally sensitive to IIDs representative of azimuths which fell within the region from 10° on the ipsilateral side to approximately 50° on the contralateral side of the medial plane. Neurons stimulated at characteristic frequency were maximally sensitive to particular IIDs which corresponded to a range of azimuth within the contralateral sound hemifield. Phillips & Irvine (1981b) have suggested that these units may encode sound locus.

Units responsive to monaural stimulation of each ear are relatively insensitive to interaural intensity differences (Phillips & Irvine, 1981b). In one example, these authors manipulated the stimulus intensity at each ear symmetrically about 0 IID, keeping the average intensity constant at 50 dB. Under these conditions, stimulation over a 40 dB range of IID resulted in an irregular firing rate which varied only 30%.

Kitzes et al. (1980) speculated that predominantly binaural neurons, which respond only to binaural stimuli of equal intensity may be specialized to detect location at 0° azimuth.

Interaural Time Differences (ITD)

Interaural time differences are comprised of two temporal mechanisms: on-going phase disparities, and transient disparities. At frequencies less than 1500 Hz, small changes in stimulus phase at each ear are easily detectable (Benson & Teas, 1976; Brugge & Merzenich, 1973c; Brugge et al., 1969). This is because a typical

adult head is one wavelength in diameter for a sound in the vicinity of 1500 Hz (Haft, 1984); and since phase disparities become ambiguous when they exceed 180° , pure tones greater than 1500 Hz cannot be resolved using phase difference cues (Haft, 1984; Mills, 1972; Yost, 1974, 1981). Human psychophysical evidence suggests that the 'crossover' point at which the predominant binaural cue changes from interaural time differences to intensity differences is 1500 Hz. Therefore, interaural time differences of up to 700 μ sec are possible for man, and up to 400 μ sec for cats (Roth et al., 1980). Transient disparities refer to the differences in time of arrival of the first wavefront of a tone pulse at the two ears and are not limited by the period of the stimulus, or subject to the phase ambiguities of steady tones.

Brugge et al. (1969) described summative neurons in primary auditory cortex of the cat which were facilitated by monaural stimulation of either ear, and which were sensitive to differences in phase angle. These neurons all had characteristic frequencies less than 2400 Hz. By extending the interaural delay beyond the environmental operating range of the cat, these authors showed that both spike count and latency were periodic functions of interaural delay, and that the time between the peaks of the function corresponded to the period of the stimulating tone. This indicates that the units were sensitive to phase differences (Irvine & Wise, 1983). Similar findings have been shown for neurons in the inferior colliculus (Kuwada & Yin, 1983; Yin & Kuwada, 1983a,b; Kuwada, Yin, Syka, Buunen & Wickesberg, 1984).

Kitzes et al. (1980), observed suppressive neurons which responded in two ways to varying interaural time differences irrespective of intensity. The first type exhibited neuronal responses which achieved more than half of maximal suppression within a range of 0.3 to 1.5 msec. The second type was typified by a progressive reduction of the binaural response over a large interaural delay of 10 to 20 msec. The magnitude of this interaural delay exceeds any delay that could result from the physical distance between the ears. On the other hand, the interaural delays to which these units are responsive correspond to those created by interaural intensity differences.

Researchers have reported neurons in cat which, without regard to intensity, detect an absolute interaural time delay at which the spike count is either maximal or minimal (Brugge et al., 1969; Kitzes et al., 1980; Rose et al., 1966). These neurons have only been observed at frequencies less than 2400 Hz, and are said to exhibit a 'characteristic delay'. Although it has been suggested that the location of low frequency sounds may be represented by a particular place in the auditory system by neurons exhibiting characteristic delays (Brugge & Merzenich, 1973b), no evidence of such an organization has been demonstrated (Imig & Adrian, 1977; Imig & Reale, 1981; Middlebrooks, Dykes & Merzenich, 1980; Middlebrooks & Zook, 1983).

The idea that the central auditory system makes use of interaural time and intensity differences to localize the source of

low frequency and high frequency pure-tones, respectively, has come to be known as the 'duplex theory' (Roth et al., 1980).

Recently, investigators have argued that although interaural time differences are not sufficient to localize high frequency pure-tones, they are nearly as effective for localizing high frequency complex signals as they are for low frequency pure-tones (Hafter, 1974; Henning, 1974a,b; Yost, 1976). Phillips & Brugge (1985) have shown that the nervous system may detect ongoing temporal disparities in high frequency signals if those signals contain low frequency elements, such as might be found in spectrally complex signals. Threshold interaural time differences of less than 20 μ s have been reported using various types of AM signals (Hafter, 1984). Electrophysiological studies using AM signals with high frequency carriers (>3.5 kHz) showed that inferior colliculus (IC) neurons in the cat responded to the period of the modulation frequency (Yin, Kuwada & Sujaku, 1984). Henning (1974a,b) showed that the ITD necessary to localize a 300 Hz puretone, and a 3900 Hz puretone amplitude modulated at 300 Hz were similar, indicating that high frequency waveforms were successfully localized using interaural time disparity cues. Yost (1976) showed the same type of result for high-frequency filtered clicks, repeated at low rates.

The classical 'duplex theory' of sound localization was derived from studies using pure-tones. Those studies concluded that high frequency sounds were not localized using interaural time disparity

cues. More recent work indicates that this view may not apply to complex auditory signals.

Binaural Columns

The functional organization of various physiological response characteristics into columns of neurons oriented perpendicular to the surface of cortex is a well documented feature of the sensory cortex of the visual and somatosensory systems. In primary visual cortex both ocular dominance, and the orientation of receptive fields are organized in columns (Hubel & Weisel, 1977). In primary somatosensory cortex the surface of the body is represented by columns within columns (Kaas, Nelson, Sur, & Merzenich, 1981).

Evidence for the columnar organization of unit response properties in primary auditory cortex was established by Abeles and Goldstein in 1970. At that time adequate histological control over electrode placement permitted the observation that units were organized in columns oriented perpendicular to the cortical surface. These units correspond to the 'radial chains'⁷ noted by anatomist Lorente de Nó in 1938, and were responsive to the same characteristic frequency. Brugge and Merzenich (1973c) reported data suggesting that the time-delay sensitivity of some (low frequency) neurons may be organized in columns, although these findings have not been substantiated by others. No other response characteristics have been observed to vary as a function of cortical depth.

Imig and Adrian (1977) first reported columns oriented perpendicular to the surface of AI which were differentiated on the

basis of binaural response properties. Each column contained either suppressive or summative units, but not both. In these experiments an electrode entered the pial surface at an oblique angle, and lesions were made near the borders between groups of summation and suppression responses. Columns were found to extend from the white matter up to layer III, but could not be traced into the uppermost layers due to the lack of responsiveness of those regions. Layers I and II are commonly found to be unresponsive in the barbiturate-anesthetized cat (Imig & Adrian, 1977; Middlebrooks et al., 1980).

Imig and Adrian (1977) categorized the binaural interactions exhibited by most neurons as either summative or suppressive. Within a category, however, response characteristics varied with respect to characteristic frequency, aural dominance, and monotonicity of the rate-intensity function. The term 'aural dominance' refers to the ear to which monaural stimulation produces the largest unit response (Imig & Adrian, 1977). Suppression-type units were almost always found to exhibit a contralateral dominance, but the effectiveness of ipsilateral stimulation to suppress these units was variable among units. Summation columns varied with respect to aural dominance, and were found to be comprised of even smaller columns which respond preferentially to stimulation of a particular ear.

Further evidence substantiating the radial (perpendicular) organization of binaural interactions in AI has been advanced recently by Middlebrooks, Dykes and Merzenich (1980). These

authors reported that all units encountered within a radial penetration were found to have the same type of response to binaural stimulation. Of 73 radial penetrations, 59% contained units which exhibited EE responses alone, 33% contained units which showed EI responses alone, and less than 1% of units exhibited either EE or EI responses.

The use of multi-unit recording techniques employed in functional mapping studies (Imig & Adrian, 1977; Merzenich et al., 1975; Middlebrooks & Zook, 1983; Middlebrooks et al., 1980; Reale & Imig, 1980) has been criticized as possibly obscuring a more complex organization of binaural response characteristics (Phillips & Irvine, 1979). Opponents of the multi-unit method have argued that it relies heavily on the assumption that all single units within a cluster will respond in a similar manner to the stimulus parameter being examined. Phillips and Irvine (1979) argue that the descriptive power of classification schemes based on multi-unit techniques is inadequate to describe the binaural response characteristics of the ipsilateral input. For example, these authors described two cells positioned within a vertical penetration parallel to the pial surface. Both units exhibited a stronger response to contralateral stimulation than to ipsilateral (i.e., the unit is contralateral-dominant), and both units exhibited summative binaural responses as described by Imig and Adrian (1977). However, the ipsilateral input to one unit was virtually non-existent (EO/F), while the ipsilateral input to the other unit was considerable (EE/F). Phillips and Irvine argue further against the

usefulness of classifying aural dominance on the basis of monaural stimulation, since in the case of one contralateral-dominant suppressive unit the binaural response is very effectively suppressed by the so-called 'non-dominant' ipsilateral input. Regardless of the nomenclature used to describe the driven ear, both groups agree that neurons within columns are likely to derive excitatory input from the same ear.

Binaural Bands

The vertical organization of binaural columns established in the cat by Imig and Adrian (1977) was found to extend across the cortical surface, orthogonal to isofrequency contours, in 'bands' or 'patches' coursing along the rostrocaudal dimension of the primary auditory field. These authors reported that binaural interaction bands varied considerably in size. Some were quite extensive, covering several square centimeters of cortical surface, while others as small as 0.3 mm were observed. In one case a suppression band approximately 0.5 mm in width and 4.0 mm in length was mapped. The band was oriented orthogonal to isofrequency contours, and contained a tonotopic representation of frequencies between 4.9 and 22.7 kHz. Units surrounding this band of suppression columns exhibited summation type binaural responses. Of the total cortical surface area mapped in all experiments, Imig and Adrian (1977) found that 66% was occupied by summation columns, 28% by suppression columns, and 6% by neurons not organized in columns. This latter group exhibited unusual binaural interactions, such as occlusive and monaural responses.

Middlebrooks et al. (1980) mapped the topographical distribution of binaural columns in cat using multi-unit electrode techniques. The electrode was passed through cortex using a combination of radial and tangential penetrations. Tangential penetrations allowed the electrode tip to pass along the isofrequency contour at the same cortical depth. Since the response characteristics of neurons remain constant with cortical depth (Imig & Adrian, 1977; Phillips & Irvine, 1979), a representative sample of columnar response characteristics could be obtained by sampling only from the middle layers of cortex. Regions of like-responding binaural units took the form of alternating bands of EE units (200 to 3400 μ wide) and EI units (100 to 2000 μ wide) as the electrode was advanced along the isofrequency contour. Sharp transitions between sequences of EI and EE units were observed. Middlebrooks et al. (1980) indicated that each binaural band crossed all isofrequency contours, and each isofrequency contour crossed all binaural bands within the frequency range tested (i.e., 3-20 kHz). More recent reports though, failed to corroborate the observation that binaural bands extend across the entire range of high-frequency representation (Imig & Reale, 1981; Reale & Kettner, 1986).

Anatomical Connectivity of Binaural Columns

Experiments to determine the sources and terminations of units located in binaural columns have been conducted with autoradiographic tracing of cortico-cortical pathways using tritiated

amino acids, and microelectrode mapping procedures in the same preparation (Imig & Brugge, 1978; Imig & Reale, 1980, 1981).

Callosal Connections

Only one experiment has been conducted which relates callosal connections to binaural interaction bands in cortex (Imig and Brugge, 1978). In these experiments the distribution of callosal connections was determined in three ways. The retrograde axoplasmic tracer horseradish peroxidase (HRP) was used to label the source of callosal axons originating in the opposite hemisphere. In other animals, the anterograde tracer [^3H]-proline was used to determine the termination of callosal fibers in the opposite hemisphere. Finally, the corpus callosum was sectioned and the brains processed so as to stain degenerating axons and axon terminals. Following the injection of tracing compounds, binaural responses to pure-tone pips were examined. The distribution of HRP-labeled cells, tritiated proline labeled terminals, and degenerating axons was related to binaural maps by plotting the positions of labeled cells on a drawing of a tissue section containing a reconstructed electrode track. Both the sources and terminations of callosal fibers in AI were more densely aggregated in binaural summation columns than in suppression columns. Therefore, regions in AI which are the major contributors to the callosal pathway also appear to be the major recipients.

Intrahemispheric Connections

The relation of ipsilateral projections from auditory cortical fields A and P to binaural bands within AI has been investigated in experiments conducted by Imig & Reale (1984). Single injections of anterograde tracer compound ($[^3\text{H}]$ -proline and $[^3\text{H}]$ -leucine) into the anterior auditory field (A) and the posterior auditory field (P), resulted in multiple regions of dense labeling within ipsilateral AI. The results of this experiment showed that suppression columns received a denser projection from field A than did the immediately adjacent summation columns.

Thalamocortical Connections

Thalamocortical projections to binaural columns were examined by Middlebrooks and Zook (1983) who determined that neuronal populations within the ventral nucleus of the medial geniculate body (GM_v) projected to different binaural bands, and that these populations were strictly segregated from one another. The ventral nucleus of the GM is the major source of thalamic input to AI (Andersen, Knight & Merzenich, 1980; Middlebrooks & Zook, 1983; Sousa-Pinto, 1973; Winer, Diamond & Raczkowski, 1977). The ovoidal part (Vo) of the ventral nucleus of GM has been shown to project heavily to EI bands, but only sparsely to EE bands. The lateral and dorsocaudal portions of GM_v project to EE bands.

Present Study

Advantages of using Ferret

The ferret (*Mustela putorius*) is a carnivore which has been commonly accepted for use in studies of anatomy (Rockland, 1985), electrophysiology (Kelly, Judge & Phillips, 1986; Phillips, Judge & Kelly, 1988; Moore, Semple & Addison, 1983) and behavior (Kavanagh & Kelly, 1983; 1986; Kelly, Kavanagh & Dalton, 1986). Like cat and dog, the ferret's cortex is gyrencephalic, but its temporal area is without distinctive anterior and posterior ectosylvian sulci. The ferret's auditory field extends, uninterrupted by sulci, along the middle ectosylvian gyrus, bounded dorsally by the suprasylvian sulcus, and ventrally by the pseudosylvian sulcus (Kelly, Judge and Phillips, 1986).

The ferret is born a highly immature (altricial) mammal. Physiological and behavioral responses to sound are seen nearly 32 days post-partum, as compared to only a few days after birth in the cat (Moore, 1982). The ferret, therefore, is an especially suitable species for studies of mammalian central auditory development.

Location and Extent of AI In the Ferret

Primary auditory cortex in the ferret is tonotopically organized. Neurons which respond to frequencies as high as 16 kHz are found dorsally, while those responding to low frequencies are located ventrally. Strips of cortical tissue in which all neurons respond to similar pure tones form isofrequency contours which are disposed in a roughly rostral-to-caudal plane, orthogonal to the frequency

gradient. In this, and other mammals, the low frequency border of this tonotopic field blends into a region that is either unresponsive to tonal stimuli, or which occasionally reveals broadly-tuned units. Although the sulcal banks surrounding AI in the ferret have not been explored in detail, no clear reversals in tonotopic sequence have been noted in penetrations through the sulcal walls. Further studies of ferret auditory cortex may reveal additional tonotopic fields, which appear to be a common feature of other placental mammals such as the cat (Imig & Morel, 1983; Knight, 1977; Merzenich et al., 1975; Phillips & Irvine, 1982; Phillips & Orman, 1984; Reale & Imig, 1980), owl monkey (Imig et al., 1977), macaque monkey (Merzenich and Brugge, 1973) and squirrel (Merzenich, Kaas & Roth, 1976).

Response Characteristics

Kelly, Judge and Phillips (1986), and Phillips, Judge and Kelly (1988) have described the responses of neurons in primary auditory cortex of the ferret. Single neurons showed narrowly tuned frequency-threshold curves. Neural activity, examined using pure tone stimuli, was transient and time-locked to stimulus onset. Most units displayed a monotonic increase in firing rate with increased intensity, although some non-monotonic responses were noted. Latency to first spike, measured from stimulus onset ranged between 11 and 20 ms.

Spontaneous spike discharge rates were low, allowing excitatory thresholds to be easily determined. The characteristic frequencies of sampled units ranged from 200 Hz to 31.3 kHz and units were

maximally sensitive between 5 and 13 kHz. This region corresponds closely to estimates of characteristic frequency obtained from the behavioral audiogram in the same species (Kelly, Kavanagh & Dalton, 1986).

Breadth of tuning was quantified using the Q_{10} factor which expresses a neuron's CF as a ratio to the tuning curve bandwidth 10 dB above CF threshold. This measure was used first in studies of cochlear nerve fibers (Kiang, Watanabe, Thomas & Clark, 1965) and subsequently has been applied throughout the central auditory system (Aitkin & Webster, 1972; Aitkin et al., 1975; Phillips & Irvine, 1981; Phillips & Orman, 1984). Q_{10} s were very low for neurons with CFs less than 2.0 kHz indicating broad frequency tuning. Q_{10} s were higher for neurons with CFs greater than 10 kHz, indicating narrower tuning.

A variety of response properties were observed for the ferret. The majority of neurons were of the summative (EE/F) category (35%). Suppressive neurons (EO/I) constituted 29% of the total sample and 36% of units could not be driven by binaural stimulation (EO/O). All three cell types were present at most CF ranges, although all frequencies were not sampled equally. In one animal, units of the same binaural response type were observed to cluster together along an isofrequency contour.

Purpose of the Present Experiment

Data regarding the binaural topography of primary auditory cortex are presently limited to four studies of cat primary auditory cortex (Imig & Adrian, 1977; Middlebrooks et al., 1980;

Middlebrooks & Zook, 1983; Reale & Kettner, 1986) and one study of the albino rat (Kelly & Sally, 1988). In as much as the primary auditory cortex of the cat may not be representative of primary auditory cortex in all carnivores, the present study aims to provide additional data derived from a different carnivore — the ferret (*Mustela putorius*). Comparison of binaural topography between these two species will help determine whether grouping of neurons with similar binaural response properties is a common organizational feature of primary auditory cortex.

The purpose of the present investigation is first, to identify the binaural response properties of neurons within primary auditory cortex of the ferret using single-unit and unit-cluster recording techniques; second, to determine the organization of binaural units within isofrequency contours; third, to test the hypothesis that binaural bands are present in a carnivore other than the cat.

METHOD

Subjects

Twenty adult ferrets with infection-free ears were used in these studies. Nine provided useful data for mapping binaural response types in individual hemispheres. Ferrets were obtained from Marshall Research Labs of North Rose, New York, and immunized against canine distemper prior to shipping. Animals with sable coats were used to avoid sensory abnormalities that may be associated with albinism. Age of the subjects ranged between 15 and 40 weeks.

Anesthesia

Animals were induced to a surgical level of anesthesia by intraperitoneal injection of Equithesin (3 ml/kg). Subjects were maintained in a state of areflexia by regular injections of Equithesin (.5 ml/kg) every one or two hours as required. This regimen continued for the duration of the experiment which lasted 16 to 20 hours, after which time the animal was sacrificed by lethal injection of Equithesin.

After induction, the animal was administered an intramuscular (im) injection of dexamethasone sodium phosphate (0.05 mg/kg) as a prophylactic against cerebral edema. Additionally, most animals received Vitamin K₁ (0.3 ml/kg; im) as an agent to promote coagulation and thereby decrease bleeding encountered during resection of the temporal musculature overlying auditory cortex.

Surgical Procedures

The subject was anesthetized, placed on a heating pad to maintain body temperature (~37°C), and secured in position by a head holder. The head holder provided unimpeded access to the region of the lateral skull and ears. The scalp was incised and the temporal muscles were resected bilaterally. Bleeding was controlled using an electric cautery. The external meatus was transected at the level of its entrance into the skull, and the opening covered with gauze to prevent the admission of fluids. Next, the bone overlying the left temporal cortex was trephined, and the hole enlarged by rongeur. A hand drill was used to avoid the conduction of heat, associated with electric drills, to the underlying cortex.

The subject was then carefully transported from the surgery to the electrophysiology laboratory. A small portion of the dura mater was reflected over the pial surface overlying the middle ectosylvian gyrus. The exposed cortex and remaining dura were bathed in warmed (37°C), highly viscous dimethylpolysiloxane oil (DMPS-SIGMA). To reduce brain pulsation, the foramen magnum was pierced with a scalpel blade, and cerebrospinal fluid was allowed to drain from the opening.

The ferret was then transferred to an electrically shielded sound attenuated chamber (Eckel). Auditory cortex was viewed through an operating microscope (Zeiss — 40X magnification) and a drawing made of the vasculature and sulcal patterns of the cortical surface (Figure 1). This drawing was used to mark the location of electrode penetrations and copies of it were used to identify the location of characteristic frequencies (frequency maps) and binaural response types (binaural maps). The electrode was positioned in cortex under visual control using a micromanipulator and an operating microscope.

Preparation

In order to avoid electrical artifacts associated with 60 Hz AC interference, the sound attenuated chamber was not fitted with electrical devices operated by alternating current. The operating microscope drew its power from a DC power supply located outside of the chamber, and a flashlight was used to aid the experimenter in marking electrode penetrations on the drawing. The subject's body temperature was maintained by a recirculating hot water pad,

the water heater and pump for which were located outside the sound attenuated chamber.

The ferret's head was placed in a horizontal position, and the sound delivery system was attached to the stub of the external meatus by acoustic couplers fitted to flexible arms (Starrett), which facilitated the insertion of the couplers into the skull. The anatomical disposition of the ferret's external meatus was unlike that encountered in cat or rat. In those species, the tympanic membrane is situated just inside the temporal bone and oriented concentric with the interaural plane. However, the external meatus of the ferret meets the skull at an oblique angle ($\sim 45^\circ$) and then proceeds caudally through the temporal bone for 5-6mm before reaching the tympanic membrane, which is oriented mediolaterally. The long passage precludes direct observation of the tympanic membrane except during histological examination. Since the probe microphone rested at the junction of the external meatus and the skull, it was not possible to precisely specify the sound pressure level at the tympanic membrane.

Sound Delivery System

The subjects' ears were stimulated independently with pure-tones of variable intensity and equal phase. Tones were produced by a function generator (HP 3310A) and their frequency verified using a digital frequency counter (General Radio; Model 1192-B). To reduce high frequency noise transients associated with switching a signal on and off, an electronic shaping gate (Coulbourn S84-04) was used to attach a 10 ms rise/fall envelope

to the signals. The gate was activated by an electronic switch (Coulbourn S22-02) for 100 ms once every second by a solid state clock (Carleton University⁸). The output of the shaping gate was split and led to two passive decade attenuators (HP 350D) which, in turn, were directed to separate channels of a stereo amplifier (Aiwa P30). The headphone output of the amplifier was led to a switch (Carleton University) which determined the active channel (left, right or both).

Acoustic Couplers

'Y-shaped' acoustic couplers were fabricated from stainless steel in such a manner as to admit a probe microphone and allow the direct attachment of a small loudspeaker (Figure 2). A calibrated probe tube-microphone assembly was used to measure the sound pressure near the entrance to the bony passageway leading to the tympanic membrane. The probe tube fit concentrically within the speculum portion of the acoustic coupler and extended to its end. Small acoustic drivers were mounted directly to the other opening in the coupler and did not interfere with the insertion of the probe tubes *in situ*.

Driver Specification and Calibration

The acoustic drivers (Pioneer SE-50D) passed a useful bandwidth of 50 Hz to 40 kHz. A frequency-response curve was calculated for the drivers coupled to a closed cavity of 0.5cc (Appendix A). It shows their output to be moderately flat across frequencies from 1 Hz to 1 kHz where it climbed to a maximum

sound pressure of 132 dB SPL (re: 20 μ Pa) at 1.7 kHz. After this point the sound pressure rolled off to 90 dB until 7 kHz, and then fluctuated between 70 and 97 dB until 17 kHz. At frequencies between 17 and 50 kHz, sound pressure varied between 60 and 70 dB. The loudspeakers remained operational up to 50 kHz, at which point their efficiency was reduced to 62 dB SPL.

During the course of an experiment sound pressure levels were recorded in dB attenuation. These values were converted to dB SPL immediately after each experiment using a calibrated probe tube-microphone assembly (2mm, Brüel & Kjær). The probe tube was used to make *in situ* measurements of stimulus sound pressure level for the frequencies used in that study. The end of the probe tube was inserted into the acoustic coupler, which was itself securely positioned at the entrance to the remaining portion of the external meatus. The output of the probe microphone was preamplified and led to a measuring amplifier (Brüel & Kjær 2608). The voltage output of the measuring amplifier was monitored on an oscilloscope to detect distortion of the acoustic signal, and the resultant sound pressure levels were corrected for the presence of the probe tube⁹. In these preparations sound delivered to one ear could not be measured at the other (i.e., crosstalk) unless sound pressure levels at each ear differed by more than 70 dB.

Extracellular Recording Methods

The responses of single-units or unit-clusters were recorded extracellularly, using insulated tungsten microelectrodes with impedances ranging between 1.2 and 1.8 M Ω (@1.0 kHz). The

electrode signal was preamplified, band-pass filtered (0.5 to 10.0 kHz), amplified 1000X (BAK Instruments; Model MDA-3), and displayed on an oscilloscope (Tektronix; Model 502A). The oscilloscope was triggered by the stimulus onset and monitored continuously through an audio amplifier (Heath; Model AA18) and loudspeaker.

Unit clusters usually consisted of up to three neurons firing together. Single units were distinguished on the basis of amplitude and waveform. Since the distance between the electrode and each neuron in the cluster was likely to be different, and since the amplitude of a recorded spike varies as an inverse function of the distance between the electrode tip and the neuron, the amplitudes of neurons within a cluster were likely to be sufficiently different that they could be distinguished visually. It was not impossible, however, that members of a cluster could be equally distant from the electrode tip. In this case, the individual units could not be separated using amplitude alone. Therefore, a window discriminator (BAK; Model DIS-1), analog delay line (BAK; Model AD-3) and storage oscilloscope were used when searching for single units. These instruments allowed spikes to be uniquely identified on the basis of their waveform. The monaural and binaural response characteristics of some single units were quantified using a signal averager (Tracor Northern; Model TN-1550). The number of spikes elicited by the stimulus was summed over 50 trials and the results used to construct Rate-intensity functions.

Data collection procedures

The data presented in this report were obtained from neurons in the primary auditory field (AI) of the ferret. This field has been identified electrophysiologically (Kelly, Judge & Phillips, 1986; Phillips, Judge & Kelly, 1988), anatomically and behaviorally (Kavanagh & Kelly, 1986). Characteristic frequencies (CF) for all units ranged between 3 and 25.5kHz. Recordings were made from neurons located in cortical layers located 500 to 1800 μ from the pial surface.

The frequency and intensity of search tones were systematically varied to maximize the probability of finding excitable neurons. Two animals (F163 and F165) were mapped throughout a broad area, using widely spaced electrode penetrations. Two others were mapped within a more circumscribed area using more closely spaced electrode penetrations (F201 and F203). The remaining five ferrets (F168, F185, F186, F187, F193) were mapped within narrow band isofrequency contours using electrode penetrations made perpendicular to the pial surface and positioned as little as 100 μ apart.

Single-units or unit-clusters were found by sweeping a wide range of frequencies at the ear contralateral to the electrode. When neurons with stimulus-locked activity were isolated, their characteristic frequency (CF) was obtained audiovisually by finding the tone frequency which evoked excitatory responses at the least intense contralateral stimulus. Each ear was then stimulated independently at characteristic frequency to determine the

monaural response properties of the cell (excitatory or no effect).

The binaural interaction was identified by manipulating the sound pressure level at both ears. Initially, the intensity level at the contralateral ear was set to within 20 dB of threshold, while the intensity at the ipsilateral ear was attenuated by about 80 dB. The intensity at the ipsilateral ear was then gradually increased in steps of 5 to 10 dB, and the threshold at which the ipsilateral ear began to increase or decrease the spike rate (threshold of binaural interaction) was noted. This interaural intensity difference (IID) was expressed in dB as ipsilateral intensity referred to contralateral intensity (Ipsi - Contra).

Evaluation of Binaural Responses

The classification procedure employed in the present study uses a three letter code to designate binaural influences. The first two letters indicate the responses to monaural stimulation of the contralateral and ipsilateral ears respectively (usually excitatory, "E", or no response, "O"). The third letter, separated by a slash, indicates the binaural interaction pattern, inferred from comparison of the responses to binaural stimulation to the stronger monaural response (usually facilitation, "F", inhibition, "I", or no difference "O"). For example, a unit for which monaural stimulation of either ear produced an excitatory response and for which binaural stimulation produced a response greater than the strongest monaural response would be termed an EE/F unit.

Construction of Binaural Maps

Binaural maps were constructed by marking the penetration number at the point on the original drawing corresponding to the position of the electrode in the exposed cortex. Placement was made in relation to the cerebral vasculature, sulci and other cortical landmarks. Drawings were made in which units were marked with characteristic frequencies and/or binaural response type.

RESULTS

Maps were obtained from primary auditory cortex (AI) in the left hemisphere of nine ferrets. Microelectrode recordings were made from a total of 514 neurons or neuron clusters, 142 of these were located within narrow band isofrequency contours. For each subject, characteristic frequencies (CF), binaural response characteristics, monaural thresholds and threshold of binaural interaction (HD) were observed for between 34 and 90 units (Appendix B).

Mapping Strategies

To reveal the topographic distribution of binaural neurons in primary auditory cortex, three mapping strategies were employed. First, responses for subjects F163 and F165 were obtained from widely spaced electrode penetrations, distributed across a broad topographic area. These maps showed how auditory cortex was tonotopically organized, and served as guides to the further study of binaural response types. A second strategy was employed for

subjects F201 and F203 in which mapping occurred over a more circumscribed area of cortex, using less widely spaced electrode penetrations. This allowed a more precise characterization of unit response types across the dorsal-ventral dimension of isofrequency contours. Finally, a third mapping strategy was employed for ferrets F168, F185, F186, F187 and F193, in which many penetrations were made in close succession (about 100 μ apart) to maximize the resolution of the map along the length of a narrow-band isofrequency contour.

Binaural Response Types

EE/F Response Type

One hundred and seventy six (176) binaural units were classified as exhibiting EE/F responses. These cells accounted for 34% of the total population of units mapped (Figure 3). EE/F neurons were characterized by excitatory responses to monaural contralateral and ipsilateral input. The binaural component of these units was excitatory, and greater in magnitude than the strongest monaural component. Figure 4 describes the EE/F response type for unit F201 (#18). When the contralateral stimulus intensity was held at threshold levels, spike rate increased linearly with ipsilateral intensity until at an IID of 43 dB the spike rate peaked at 50. Increasing the ipsilateral sound pressure by a further 10 dB caused the spike rate to plateau at 49 spikes.

EO/I Response Type

Two hundred and thirty (230) units, or 45% of the total population of units, were classified as having EO/I response types (see Figure 3). These units exhibited an excitatory monaural response to contralateral stimulation, and no response to an ipsilateral stimulus. The effect of increasing ipsilateral stimulus while holding the contralateral stimulus near threshold was to suppress the binaural response to levels below that of contralateral monaural stimulation alone. Figure 5 describes the IID function for EO/I unit F186 (#28). Stimulus intensity was held at this unit's contralateral monaural threshold of 49 dB SPL and a signal of nearly equal intensity (46 dB SPL) applied to ipsilateral ear causing the spike rate to fall from its monaural contralateral count of 62 to 59. Increasing the ipsilateral sound pressure caused the spike rate to fall monotonically until, at an IID of 47 dB, the unit's firing rate was reduced by more than half to 29 spikes.

Mixed Response Type

Of 514 units mapped, 53, or 10% of the total population, were assigned to the 'mixed' category (see Figure 3). Mixed units exhibited response characteristics that combined the major features of both EE/F and EO/I units. These cells exhibited summation when the contralateral intensity was near threshold and the inter-aural intensity was small, but were suppressed at higher ipsilateral intensities. To be sure that recordings from mixed cells did not represent a merging of responses from neighboring

EE/F and EO/I neurons, these cells were isolated from unit clusters.

The response characteristics of mixed units were explored by delivering a near threshold stimulus to the contralateral ear and then increasing the intensity of the ipsilateral signal in steps of 5 dB. The difference between the ipsilateral and the contralateral stimulus intensities, known as the interaural intensity difference (IID) was then plotted as a function of spike rate. Figure 6 shows the IID curve for F201, unit #4. This unit's contralateral monaural threshold was 45 dB SPL, and its firing rate at that sound pressure was 38 spikes. Increasing the ipsilateral intensity to a level equal to that of the contralateral ear caused the neuron to increase its firing rate to a maximum of 63 spikes. Further increases in ipsilateral sound pressure caused the neuron to reduce its rate of firing to 16 spikes, a level well below the monaural contralateral threshold. Thus, mixed neurons exhibited response characteristics of both EE/F and EO/I units.

Within narrow-band isofrequency contours, most mixed units (13 of 16 [81%]) occupied positions between binaural response segments of opposing type.

'Other' Response Type

Although most units could be classified as EE/F, EO/I or Mixed, some neurons exhibited other response properties. The majority of neurons having these 'Other' response properties failed to respond to binaural stimuli. Forty seven EO/O cells were encountered in the course of these experiments. Three other

response classifications were noted, these include two EE/O units which responded to either ipsilateral or contralateral monaural stimulation, but for whom binaural stimulation elicited a response no greater than the strongest monaural response. This type of response has also been categorized as 'occlusive' (Imig & Adrian, 1977). Three EO/F units were observed for which contralateral monaural stimulation was effective in eliciting a response, but ipsilateral monaural stimulation was not. These neurons nevertheless responded with a facilitatory response when both ears were stimulated simultaneously. Lastly three units were classified as EE/I. These neurons were responsive to monaural stimulation of either ear alone. Stimulation of both ears together, however resulted in a suppressive response.

Figure 7 shows the distribution of binaural response types across characteristic frequency plotted in third-octave bands for the two most broadly mapped animals (F163 & F165). The proportions of different binaural response types are nearly equivalent for each frequency band. More units were sampled from high frequency areas of AI than from low frequency regions.

Tonotopy

Figures 8 and 9 show the results of two mapping experiments in which the crown of the gyrus was explored across a broad area. CFs ranged from 3.0 to 25.5 kHz with the most units responding to 10-13 kHz. These data confirmed previous findings from this laboratory which showed that primary auditory cortex in the ferret is tonotopically organized (Kelly, Judge & Phillips, 1986). Figure 8

shows that, for ferret F163, neurons with characteristic frequencies higher than 17 kHz were found in the dorsal region of primary auditory cortex, and progressively lower CFs ranging to 7 kHz were found ventrally. Isofrequency contours containing neurons responsive to the same characteristic frequencies were oriented orthogonal to the frequency gradient. For example, two distinct lines of neurons, each with similar CFs can be seen crossing the entire width of the primary auditory field of ferret F163. The first isofrequency contour contained neurons with characteristic frequencies ranging between 5-6 kHz, and the second contained neurons ranging between 10-14 kHz.

The frequency map for ferret F165 clearly shows the presence of three isofrequency contours (Figure 9). The first contour was populated with neurons having CFs ranging between 6 and 8 kHz, and was located near the ventral portion of AI. The second isofrequency contour contained neurons between 11 and 13 kHz. This contour was quite broad since neurons within this band of characteristic frequencies occupy a substantially greater portion of cortex than do neurons with other CFs. A third isofrequency contour was seen near the dorsal portion of AI. This contour was comprised of neurons which ranged in CF between 13 and 17 kHz.

Topography of Binaural Response Types

The data from broadly mapped ferrets F163 and F165 show that at each third octave interval, all binaural response types were found in about the same quantity (Figure 3). No one binaural response type dominated any particular frequency. Within the

frequency range sampled in this study, as can be seen, more units were sampled from the 10-12.5 kHz range than other region of cortex.

Figures 8 and 9 show that neurons having the same binaural response properties were more likely to be adjacent to one another than not. Furthermore, these groups of like-responding neurons could be seen to alternate along the length of an isofrequency contour. For example, examination of the 6-10 kHz isofrequency contour, located in the ventral portion of AI of ferret F165, shows that it was comprised almost solely of EO/I units caudally. Moving rostral along the isofrequency contour, however, the binaural response type changes to EE/F, and then back to EO/I. Notice that the transition from one response type to the other was marked by the presence of a mixed unit.

A similar distribution of binaural response types was found for the 12-13 kHz isofrequency contour. Units at the caudal portion of the contour were of EO/I type, but further rostral on the contour units changed to EE/F. A mixed unit was again encountered between the two dominant response types. Rostral to these units were a string of EE/F units, followed by another mixed unit. This last mixed unit may have indicated a transition between EE/F and EO/I types, although the map did not extend far enough rostrally to reveal the presence of more EO/I types.

The data for ferrets F201 and F203, shown in Figure 10 and 11 provided additional evidence that like-responding neurons form aggregates. Both these subjects were mapped within a rectangular

matrix of cortical tissue in which electrode penetrations were more closely spaced than were those of F163 and F165. Ferret F201 exhibited neurons ranging in characteristic frequency between 10 and 16.6 kHz. The caudal portion of AI shows a group of EO/I units near the ventral limit of the mapped area which extended rostrally about two-thirds of the width of the mapped area. A similar grouping of EE/F units was seen near the dorsal bounds of AI. Neurons in both these groups had CFs in the range between 11.6 and 13.3 kHz. Further rostral, five mixed cells formed a diagonal line, all of which exhibited characteristic frequencies of between 12 and 12.4 kHz. Neurons of similar binaural response type were seen to group together in this map, and these groups alternated along the length of an isofrequency contour with others of different response type. A similar distribution of binaural response types was seen for ferret F203, for which 12 of 19 EE/F units were gathered together in the caudal portion of primary auditory cortex. The rostral portion of the map showed a non-random distribution of binaural response types in which groups of EE/F units were separated from groups of EO/I units.

Alternation of Response Groups

Maps for the remaining subjects (F168, F185, F186, F187 and F193) were created using closely spaced electrode penetrations (100 μ apart), oriented parallel to isofrequency contours. The higher resolution offered by maps obtained using this method allowed a more detailed analysis of the distribution of binaural response types along the length of narrow band isofrequency contours. Like-

responding binaural units tended to aggregate in 'groups', and these groups were found to alternate along the length of a contour. The transition between response types was usually sharp, and often marked by the presence of units of mixed-response type.

For each of these narrow-band subjects, the physical location within primary auditory cortex selected for mapping always included neurons whose characteristic frequencies ranged between 11.3 and 13.9 kHz. This occurred for two reasons: First, a large proportion of cortical tissue is devoted to processing frequencies between 10 and 13 kHz in the ferret (see Figure 9). Second, neurons in this frequency range were, for the most part, located on the central portion of the crown of the temporal gyrus. This tissue represented ideal ground for microelectrode mapping since it was less vascular, and well removed from the banks of the surrounding suprasylvian sulcus.

Figure 12 shows an example of an isofrequency contour taken from ferret F168. Characteristic frequencies of neurons within this contour occupied a narrow frequency band ranging from 12.8 kHz to 13.2 kHz. The caudal portion of the contour showed seven EO/I units in a row. Further rostral, unit response properties changed to EE/F for one neuron, back to EO/I for one cell and then back to EE/F for 10 units. Continuing rostrally, two mixed units were encountered between the EO/I units and the more rostral EE/F units. These were followed by four EO/I neurons and then another mixed unit. The point of transition between groups of different binaural response types, while generally sharp, was sometimes

marked by the presence of one or two members of neighboring response groups (Figures 12 & 13).

Figure 13 describes the binaural topography of an isofrequency contour ranging from 12.7 to 13.9 kHz, which contained three alternating binaural response groups. Six EO/I units mark the caudal limit of the contour. More rostrally, an EE/F unit was followed almost immediately by eight EE/F neurons. These two large groups of opposing response types were separated by three mixed units. The rostral segment of the contour was represented by a group of mainly EO/I units (6), interspersed with one mixed unit and one EE/F cell.

The frequency map for ferret F186 (Figure 14) showed four distinct binaural response groups alternating along a narrow band isofrequency contour (11.6-12.4 kHz). Proceeding from the caudal portion of the isofrequency contour rostrally, the binaural response types change from EE/F (2) to EO/I (3) to EE/F again (7), and then back to EO/I (6). At each transition between binaural type, mixed units were observed to be present.

The binaural map derived from ferret F187 shows that like-responding binaural units are clearly segregated (Figure 15). This map shows a large number of EO/I units bounded on either side by EE/F units. There was no overlap of binaural types within this isofrequency contour. Similarly, the isofrequency contour for F193, depicted in Figure 16, shows that binaural neurons were clearly segregated along the length of the narrow bandwidth contour (12.1-12.6 kHz). Four distinct transitions among clearly segregated

groups could be seen along this contour. Within each of the narrow-band isofrequency contour subjects, neurons having the same binaural response type not only grouped together but were systematically organized into segments which alternated along the length of an isofrequency contour.

Binaural Bands

The data gathered from the two most broadly mapped ferrets provided evidence that units of similar binaural response type were grouped together along the length of an isofrequency contour, and also formed 'bands' which extended across isofrequency contours. Examination of ferret F165 revealed two distinct groups of neurons which crossed isofrequency contours (Figure 9). The first group contained only EE/F units ranging in CF between 6.0 and 16.5 kHz. This band of neurons extended from the most ventral portion of the mapped area to the most dorsal. The second group contained EO/I units ranging in frequency between 6.3 and 17.1 kHz. These EO/I units also extended from the most ventral aspect of the map to the most dorsal. Ferret F163 also showed a 'band' of EE/F units stretching between the dorsal and ventral borders of the map. These units spanned frequencies ranging between 4.6 and 18.6 kHz (Figure 8).

Three predominant features of binaural topography emerge from the data obtained from broad and narrow maps of AI. They are that:

- i) units of the same response type are strongly grouped together;

- ii) groups of one response type tend to alternate with others along the length of an isofrequency contour;
- iii) groups of like-responding units tend to form 'bands' oriented parallel to the frequency gradient.

Threshold Variation along Isofrequency Contours

Isofrequency contours are so named because their constituent neurons all respond to the same characteristic frequency. The present data show that the binaural response properties of these neurons vary systematically along this re-representation of frequency. In many cases binaural response types themselves have multiple representations along the length of response segments, raising the possibility that other aspects of auditory processing also vary systematically within a binaural response group. Candidates for such a relationship include the encoding of stimulus intensity, represented by the contralateral monaural threshold, ipsilateral threshold and interaural intensity difference (IID). The possibility that either stimulus intensity or IID are represented along binaural response segments was examined by plotting contralateral and ipsilateral monaural thresholds and threshold of binaural interaction (IID) as a function distance along an isofrequency contour. The location of each neuron within a narrow-band isofrequency contour was measured across the cortical surface. However, because the endpoints of the maps were not fixed at the same location for every subject, these distances were relative among subjects. Five ferrets (F168, F185, F186, F187, F193) were mapped along narrow-band isofrequency contours with sufficient

detail to plot contralateral and IID thresholds as a function of contour distance for both EE/F and EO/I response types (Appendix C). Mixed units were too few in number to be included in these analyses.

Monaural (Contralateral) Thresholds

Figure 17 shows that virtually all EE/F units for ferret F168 exhibited similar contralateral thresholds (53-58 dB SPL) regardless of their position along the isofrequency contour. EO/I units however, were of somewhat lower threshold near the caudal portion of the contour (41-48 dB) than they were towards the rostral boundary, where they tended to cluster together at threshold values of 58 dB.

This slight difference was not replicated for ferret F185. The data for this animal showed a somewhat curvilinear trend in which contralateral thresholds for EO/I units were very high (75 dB) near the caudal limit of the isofrequency contour, dipped to a low of about 47 dB at the beginning of the second EO/I segment, and then increased to 65 dB again towards the rostral portion of the contour (Figure 18). EE/F thresholds varied over a thirteen dB range without regard to position on the isofrequency contour.

A completely different pattern of monaural thresholds was seen for ferret F186 (Figure 19). In this animal EO/I units varied only very slightly and without regard for location. EE/F thresholds, on the other hand, were moderate (47 dB) near the caudal portion of the contour except for the most caudal neuron (68 dB), low near

the middle (37 dB) and higher (57 dB) toward the rostral portion of the contour.

Recordings were made from only three EE/F units in ferret F187. Examination of Figure 20 shows that the first EE/F neuron, located near the caudal portion of the contour, has a threshold of 55 dB, while the last two neurons, located at the rostral end of the contour exhibited lower thresholds of 35 dB. EO/I units range from about 35 to 46 dB without regard to location on the contour.

Figure 21 describes the contralateral threshold for ferret F193. EO/I units exhibited thresholds varying from 40 to 54 dB. No discernable trend in these data was observed. Although EE/F neurons had thresholds which also ranged between 40 and 54 dB, there was no sign of variation with distance along the isofrequency contour.

Ipsilateral Thresholds

Stimulation of the contralateral ear usually results in an excitatory event which can be easily identified as an increase in a neuron's firing rate. Stimulation of the ipsilateral ear however, often results in an inhibitory event which cannot be detected against the background of low spontaneous activity common in barbiturate-anesthetized preparations. One way to identify the ipsilateral threshold for both EE/F and EO/I units is by implicit examination of the binaural response. Therefore, the ipsilateral component of the IID threshold was plotted against distance along the isofrequency contour.

Although ipsilateral thresholds for EO/I units occasionally could be interpreted to vary as a function of distance along an isofrequency contour, in no case were these replicated for any other animal. Ipsilateral thresholds for EE/F units appeared to vary without regard to location along an isofrequency contour. No consistent evidence of systematic variation of ipsilateral threshold along isofrequency contours was observed.

Binaural (IID) Thresholds

There was little indication of systematic variation of binaural thresholds with distance along an isofrequency contour. Figure 17 shows that binaural EO/I thresholds for F168, with the exception of the most caudal unit (-20 dB) ranged about 40 dB (5 to 45 dB). Binaural EO/I thresholds increased with distance from 5 dB at the beginning of the first segment to 45 dB and then back to 25 dB at its end. The more rostral EO/I segment contained neurons which varied in a disorderly fashion, from 5 to 25 dB. Binaural EE/F thresholds varied between 5 and 38 dB. The caudal portion of the EE/F segment contained three neurons whose thresholds increased from 5 to 38 dB. However, thresholds of the twelve neurons following these did not vary systematically with contour distance.

Ferret F185 exhibited EO/I neurons whose binaural thresholds were lower at the caudal portion of the isofrequency contour (2 dB) than they were at the rostral limit (37 dB). Unit thresholds between these two endpoints however, fluctuated between -9 dB and 44 dB.

The first four units located at the caudal portion of the EE/F response segment exhibited binaural thresholds of about 21 dB, the next five units had thresholds which ranged from 12 to 52 dB without regard to contour location.

Like F185, data from ferret F186 show binaural EE/F thresholds which tended to rise with increased distance along the isofrequency contour. Thresholds near the caudal limits of the response segment were 14 dB but increased steadily to a high of 29 dB near the rostral boundary of the response segment, where they fell to 19 dB for the last neuron. EO/I thresholds, however, varied from 14 to 47 dB without regard to their location along the isofrequency contour.

Only three EE/F units were mapped within a narrow band isofrequency contour for ferret F187. The first of these units, located almost at the caudal border of the contour, had a binaural threshold of 35 dB. The last two EE/F units were located at the rostral boundary of the isofrequency contour and had binaural thresholds of 50 and 58 dB. Binaural thresholds of EO/I units varied from 20 dB to 61 dB without regard to their location along the isofrequency contour. No discernable trend was observed for either EE/F or EO/I units for this animal.

Similar findings were noted for ferret F193 for whom both EE/F and EO/I units exhibited a wide range of thresholds which failed to vary systematically with distance along the isofrequency contour. Most EE/F units exhibited binaural thresholds of -3 to 7 dB and occupied positions from one end of the contour to the other.

Interspersed among these units were those with thresholds ranging from 16 to 27 dB. Similarly, half (11 of 22) of the EO/I units, occupying nearly the full length of the isofrequency contour, had binaural thresholds of 17 dB. The lack of variance encountered in this cluster of equal thresholds severely reduced the likelihood of finding a trend in the data. The remaining units displayed thresholds ranging from -3 to 37 dB without regard to their location within the isofrequency contour.

DISCUSSION

Microelectrode recordings were made from unit clusters and single units across the surface of the ectosylvian gyrus in the ferret. The resultant maps illustrated the distribution of characteristic frequency and binaural response type. Monaural and binaural thresholds were recorded for each unit studied. The experimental protocol was optimized for the rapid classification of binaural response type in order to reveal the binaural topography of AI in as much detail possible.

Most neurons were sensitive to binaural intensity differences and were classified as EE/F, EO/I, Mixed or 'Other'. Recordings were made from 514 neurons. Thirty-four percent (34%) of these units exhibited EE/F response types, somewhat less than the proportion seen in the cat, which ranges between 47% and 67% (Hall & Goldstein, 1968 [47%]; Imig & Adrian, 1977 [67%]; Phillips & Irvine, 1983 [50%]; Reale & Kettner, 1986 [56%]). EO/I units represented 45% of the total population of neurons sampled.

Previous studies of the cat observed that between 12% and 34% of neurons sampled were of the EO/I response type (Hall & Goldstein, 1968 [12%]; Imig & Adrian, 1977 [34%]; Phillips & Irvine, 1983 [34%]; Reale & Kettner, 1986 [25%]). Neurons whose responses combined the characteristics of summation and inhibition (mixed units) comprised 10% of the total neural population in the ferret, a proportion which corresponds to that found for the cat (Imig & Adrian, 1977 [2%]; Hall & Goldstein, 1968 [7%]; Reale & Kettner, 1986 [17%]). Ten percent (10%) of neurons sampled in the ferret did not respond to binaural stimulation. A similar percentage of neurons fail to respond to binaural stimulation in other species (Benson & Teas, 1976 [0%]; Hall & Goldstein, 1968 [6%]; Phillips & Irvine, 1983 [7%]). The 'predominantly binaural' (PB) response type (Kitzes et al., 1980) has been reported to account for up to 12% of binaural neurons in cat (Phillips & Irvine, 1983). Our method of searching for responsive neurons, based on the presentation of contralateral stimulation, precluded the possibility of finding PB units.

The difference in the proportions of summative and suppressive binaural response types between the cat and the ferret might be accounted for by the mapping strategies used in this study. Five of the nine animals were mapped along narrow isofrequency contours, positioned on similar portions of AI (the 10-13 kHz range). In many cases these contours were characterized by the presence of two groups of EO/I units which marked the beginning and endpoints of the cortical strip, in between which one group of EE/F units was

interposed. Furthermore, the rostral and caudal limits of each isofrequency contour were not mapped. Since binaural response types alternate along the length of isofrequency contours, an extension of the alternating sequence would require the presence of an EE/F group. It is therefore likely that a number of EE/F units occupying the unexplored limits of the isofrequency contour remained unmapped, contributing to the large proportion of EO/I units. If, however, the data from those ferrets which were mapped along narrow band isofrequency contours are removed, the proportion of binaural response types for the remaining ferrets (F163, F165, F201 and F203) correspond more closely to those obtained from the cat. The proportions in this case are, 39% EE/F, 35% EO/I, 11% mixed and 14% other.

Tonotopy

Data presented in this report confirm earlier findings that primary auditory cortex in the ferret occupies the crown of the ectosylvian gyrus, is tonotopically organized, and has frequency response characteristics similar to those found in the cat (Phillips, Judge & Kelly, 1988). Neurons with high characteristic frequencies (CF) are found in the dorsal regions of AI, and low CFs in the ventral portion (Kelly, Judge & Phillips, 1986). This dorsal-ventral frequency gradient is similar to that found for the marsupial possum (Gates & Aitkin, 1982), the rabbit (Galli, et al., 1971; McMullen & Glaser, 1982) or the grey squirrel (Luethke et al., 1988; Merzenich et al., 1976). The orientation of frequency gradients in primary auditory cortex differs widely among species.

For example, the tonotopic organization in AI for cat (Hind et al., 1960; Goldstein et al., 1970; Merzenich, Knight & Roth, 1975; Reale & Imig, 1980), dog (Tunturi, 1944) and albino rat (Sally & Kelly, 1988) is such that high frequencies are represented rostrally and low frequencies caudally. In the marmoset, however, low CFs were encountered in the rostroventral portion of AI, and high CFs dorsocaudally (Aitkin et al., 1986). The frequency organization of AI for Old and New World monkeys consists of a high to low frequency gradient oriented along the caudomedial-rostrolateral axis (Merzenich & Brugge, 1973; Brugge & Merzenich, 1973; Imig, Ruggero, Kitzes, Javel and Brugge, 1977).

It is well known that the development of the temporal lobe in primates introduces a rotation in the temporal plane of approximately 80 to 90°, as compared to the cat (Hines, 1922; Pollak, 1932). Some researchers have interpreted this to mean that tonotopic orientation can be taken as a sign the organism's level of 'primitiveness' (Merzenich et al., 1976). However, the significance that differing orientations of the primary field have for the interpretation of phylogenetic 'primitiveness' remains obscure. Gates and Aitkin (1982) suggest that the various orientations of primary auditory field in different species may be seen as reflecting "... the structural demands of an evolving brain rather than its state of primitiveness" (p. 9). Indeed, a similarity of tonotopic orientations may be observed for a variety of species of widely separated taxonomy. For example, the ferret (carnivore), the

possum (marsupial), the grey squirrel (rodent) and the rabbit (lagomorph) all share a similar tonotopic organization.

A relatively large area of ferret primary auditory cortex is devoted to processing frequencies in the range 10-13 kHz. The disproportionate representation of frequency is a common feature of primary auditory cortex. For example, in the marmoset, neurons with characteristic frequencies between 2 and 16 kHz occupied a greater cortical area than did other frequencies (Aitkin et al., 1986). This was also true of the rabbit, for which neurons with characteristic frequencies between 1 and 18 kHz were best represented (McMullen & Glaser, 1982). A greater proportion of primary auditory cortex is devoted to high frequencies than to low for the albino rat (Sally & Kelly, 1988); grey squirrel (Merzenich et al., 1976), cat (Merzenich et al., 1975), and rhesus monkey (Brugge and Merzenich, 1973). It has been suggested that disproportionate cortical representation of frequency may be correlated with an organism's pattern of vocalization (Aitkin et al., 1986), which in turn corresponds to the band of greatest sensitivity in the behavioral audiogram. The best represented frequencies in ferret primary auditory cortex correspond with the area of maximum sensitivity in the ferret's behavioral audiogram and its unit characteristic frequency thresholds (Phillips, Judge & Kelly, 1988).

Binaural Topography

The present data show that neurons of similar binaural response type are grouped together, and that these groups alternate along the length of an isofrequency contour. Grouping of

binaural response types has also been observed in the rat (Kelly & Sally, 1988), and alternation of these groups has been observed in the cat (Imig & Brugge, 1978; Imig and Reale, 1981; Middlebrooks and Pettigrew, 1981; Middlebrooks & Zook, 1983). These observations were extended by Middlebrooks et al. (1980) to include the notion that like-responding binaural units form elongated bands oriented orthogonal to isofrequency contours (Middlebrooks et al., 1980).

While the juxtaposition of different binaural response groups has been observed previously, it has been difficult to establish binaural topography along the length of an isofrequency contour since, with some exceptions (Middlebrooks and Pettigrew, 1981; Middlebrooks and Zook, 1981), maps have been of coarse resolution and not oriented along narrow bandwidth isofrequency contours. Imig and Adrian (1978) noted that the neurons surrounding a group of suppression units were all excitatory. More recently, groups of like-responding neurons were seen to alternate during tangential electrode penetrations of cat AI (Middlebrooks et al., 1980; Middlebrooks & Zook, 1983). The present data, obtained from closely spaced electrode penetrations directed along the length of isofrequency contours, show that like-responding units not only group together, but that there is an alternation of response type along the length of an isofrequency contour with each group having multiple representations.

The function served by groups of differing binaural response types alternating along the length of isofrequency contours is not

well understood. The sources and terminations of excitatory and suppressive neurons differ in the cat. Imig and Reale (1980, 1981) reported that contralaterally dominant suppression columns are innervated by fibers originating in ipsilateral anterior auditory field (A), while summation columns receive a denser projection from callosal fibers originating in corresponding regions of contralateral AI. Thalamocortical projections also appear to be segregated on the basis of binaural response type. Middlebrooks and Zook (1981) observed that cortical EI bands derived their input from the lateral and ovoidal parts of the ventral aspect of the medial geniculate nucleus (GMv). Cortical EE bands, on the other hand, derive their input from the dorsal and lateral parts of the GMv.

Mixed Units — Elements of Transition

Binaural responses which combined both excitatory and suppressive properties were observed during the earliest binaural mapping studies (Hall & Goldstein, 1968; Imig & Adrian, 1977). However, because these data were derived from unit clusters, it was not clear whether individual neurons possessed disparate response properties or whether the data represented the merged output of a cluster of units containing both excitatory and suppressive neurons. Moreover, data from early studies were usually not acquired using interaural intensity differences in excess of 20 dB (Brugge et al., 1969; Imig & Adrian, 1977). These excitatory-suppressive neurons were formally classified in the cat as 'mixed' by Reale and Kettner (1986). These authors found that 31% of neurons which they previously classified as summative using

smaller IIDs were later revealed as mixed when IID was increased (up to 70 dB). The present data show that mixed cells constitute a similar proportion of the total population of neurons (10%) as is found for the cat (17%). Reale and Kettner (1986) found that a significant proportion of mixed cells were encountered near the ventral border of isofrequency contours. In the ferret, 81% (13 of 16) of mixed response types mapped within narrow band isofrequency contours were encountered at the junction of EE/F and EO/I groups. These mixed response types do not represent the merged outputs of EE/F and EO/I cells since they were identified as originating from single units.

Relation of Thresholds to Location

Since the early work of Rose and Woolsey (1949) and Tunturi (1950a) investigators have speculated that the extension of frequency representation along isofrequency contours may provide a substrate for encoding some other aspect of auditory function. Indeed, recent work in the cat has shown that binaural response types vary as a function of distance along an isofrequency contour (Imig & Adrian, 1977; Imig & Brugge, 1978; Imig & Reate, 1981; Middlebrooks et al, 1980; Middlebrooks & Zook, 1983; Reale & Kettner, 1986). The present data also show this to be true for the ferret. Moreover, since similar binaural response types are found to group together, the possibility arises that stimulus intensity and/or IID may be encoded within a binaural response group, superimposed on the multiple representations of binaural response type.

Contralateral Monaural Thresholds

Examination of the present data shows no clear evidence that monaural thresholds vary systematically as a function of distance along an isofrequency contour. Although occasionally data could be interpreted as showing differences, these were not consistent across animals either with regard to binaural response type or to the nature of the differences. For example, the fact that, for ferret F168, monaural thresholds of EO/I units were lower caudally than rostrally on the isofrequency contour might be taken to indicate a positive linear correlation. However, no other animal shows a similar trend for monaural EO/I thresholds. A second example is found in the data from ferret F185. In this case, EO/I units showed a somewhat curvilinear trend in which monaural thresholds were high near the caudal limit of the isofrequency contour, were reduced in the center and increased again towards the rostral its end. However, no similar trend was observed for EO/I units in any other animal. Finally, data from ferret F187 shows a large difference between monaural thresholds measured at the caudal and rostral limits of the isofrequency contour. Neither this difference is not substantiated by data obtained from any other animal. With the exception of the inconsistent threshold differences mentioned above, monaural thresholds fail to show any systematic variation with distance along an isofrequency contour.

Ipsilateral Thresholds

Generally, ipsilateral thresholds varied without regard to location along an isofrequency contour. Although thresholds

occasionally could be interpreted to vary as a function of distance along an isofrequency contour, in no case were these replicated in other animals.

Binaural (IID) Thresholds

Binaural thresholds also failed to show consistent variation with contour distance. Binaural EE/F thresholds of ferrets F168, F185 and F193 varied without regard for location on the isofrequency contour. A slightly positive trend was seen for EE/F units in ferret F186, but not for other animals. Binaural EO/I thresholds for ferret F185 differed between the caudal and rostral extremes of the contour at 2 and 49 dB, respectively. However, for no other case did binaural EO/I thresholds exhibit such a difference. Binaural thresholds obtained from the remaining animals could not be shown to vary systematically with distance along an isofrequency contour.

No consistent systematic variation in binaural thresholds were observed for either the EE/F or EO/I response type across animals.

Relation to Behavioral Studies

Behavioral studies in the cat, dog and monkey have shown that auditory cortex is essential for sound localization (Heffner, 1978; Heffner & Masterton, 1975; Neff, Fisher, Diamond & Yela, 1956; Strominger, 1969a,b; Wegener, 1964b). Complete destruction of auditory cortex results in a total inability to localize a brief sound presented from a loudspeaker located in the horizontal plane. Unilateral lesions of auditory cortex in the cat and the ferret

produce severe sound localization deficits confined to the auditory hemifield contralateral to the lesion (Jenkins & Masterton, 1982; Kavanagh & Kelly, 1987). Lesions within the primary auditory cortex (AI), in both the cat and ferret produce severe contralateral deficits. In the cat, a lesion of an isofrequency contour in one hemisphere results in a frequency specific deficit in sound localization in the opposite spatial field. For example, after lesion of a band of frequencies between 5 and 13 kHz in right primary auditory cortex of a cat, a pronounced sound localization deficit results in the left auditory hemifield for stimulus frequencies of 5.6, 8 and 11.2 kHz, but not for frequencies of 1, 2, 4, 12.5 or 16 kHz (Jenkins & Merzenich, 1984).

In the ferret, it has been shown that deficits resulting from AI lesions have a preferential effect on lateral field localization. Bilateral ablation of AI results in a total incapacity to localize sounds within both lateral fields, but leaves intact the ability to distinguish left and right sound sources in a midline localization task (Kavanagh & Kelly, 1987; 1988). One possible explanation for the differential behavioural effect of lesions on lateral field sound localization is that the binaural cues involved are highly dependent on sound frequency (Merzenich, Jenkins & Middlebrooks, 1984). For example, a particular position within a hemifield cannot be unambiguously represented by a set of absolute interaural differences. Instead, the specific binaural differences associated with a given position vary as a function of frequency. A much larger interaural intensity difference would be expected for a high

frequency stimulus than for a low one emanating from the same position in space. This is because the 'sound shadow' created by the presence of the head is larger for high frequencies than low (Mills, 1972). As well, interaural phase differences change as a function of frequency (Durlach & Colburn, 1978). Therefore, an analysis of binaural cues and sound frequency is essential for the accurate localization of sound sources at different positions within a hemifield. On the other hand, the cues needed to distinguish sounds emanating from one or another side of midline (i.e., left vs. right) are unambiguous, and are not frequency dependent. In the case of midline localization, the direction of the stimulus will always be located on the side receiving the first wavefront, and no confusion arises if frequency is not taken into account.

The underlying neural architecture which serves cortically dependent sound localization might be found in the intersection of isofrequency contours and binaural response areas within AI (Merzenich, et al., 1984). The alternation of binaural response types along isofrequency contours observed for both the cat and the ferret could provide an opportunity for the combined processing of sound frequency and binaural cues necessary to support sound localization within the contralateral auditory hemifield. On the other hand, a similar cortical architecture has been described for AI in the albino rat even though the capacity for lateral field sound localization of brief stimuli is largely lacking in this species (Kavanagh & Kelly, 1986). It is possible that the alternation of binaural response types across isofrequency contours is a general

feature of primary auditory cortex in mammals unrelated to the capacity for lateral field sound localization.

Reference Notes

¹ Using the fiber-tracing method of retrograde degeneration, Rose and Woolsey (1949) were able to identify regions of auditory cortex which received thalamic projections. These authors made the distinction between projections which were essential and those which were sustaining. The projections from the principal division of the medial geniculate were termed essential, since even small lesions of primary auditory cortex would cause them to degenerate. Discrete lesions of non-primary auditory cortex, however, did not cause degeneration, leading Rose to hypothesize that these unharmed cell bodies projected to multiple regions of cortex, and were therefore sustained by collaterals.

² The term 'cochlear partition' refers to the auditory sensory epithelium. Also known as the basilar membrane, this structure is coiled throughout the length of the cochlea. Sound waves, amplified by the mechanics of the middle ear, cause the basilar membrane to vibrate. High frequency sounds maximally stimulate the basal end of the cochlear partition, and low frequencies stimulate the apical end.

³ Sound pressure, also known as stimulus intensity, varies over a large range (100,000 fold) and is measured using a logarithmic scale. The decibel (dB) notation is used to express sound pressure. Since it is a relative scale, decibels can only be compared if they are referenced to the same fixed sound pressure. Modern studies refer the decibel to $0.0002 \text{ dynes/cm}^2$ ($20 \mu\text{Pa}$). Decibels expressed relative to this reference are referred to as dB SPL (Sound Pressure Level).

⁴ The term 'dominance' as it has been used in this literature is actually a misnomer. In fact, 'dominance' is a term of convenience which serves to identify the ear that provides excitatory stimulation to cortex. The 'dominant' (excitatory) ear is, of course, no more or less important in its contribution to the binaural response than is the inhibitory ear. However, because inhibition is more difficult (sometimes impossible) to measure against low rates of spontaneous neural activity, the term "dominant ear" has come to be synonymous with the "excitatory ear".

⁵ This interaural time difference assumes a speed of sound in air of 343 m/s (Mills, 1972).

6 The maximum interaural intensity difference (IID) for humans may be about 20 dB SPL (Mills, 1972). This difference is even larger for mammals that are able to move their ears independently. Generally speaking, for these animals, sound is amplified along the pinna axis aimed at the sound source, while it is attenuated at the distal ear by the sound shadow of the pinna (Phillips, Calford, Pettigrew, Atkin & Semple, 1982).

7 'Radial' electrode penetrations are those made perpendicular to the pial surface, and may be distinguished from 'tangential' penetrations which course through the middle layers of cortex, parallel to the pial surface.

8 All devices marked Carleton University were designed and manufactured by the Science and Technology Centre, Carleton University, Ottawa, Ontario.

9 Correction of observed sound pressure was necessary to compensate for the non-linearity of the sound system at different frequencies, and to convert from attenuator settings to SPL. This calculation was made in the following way: The observed sound pressure was subtracted from the calibration data for that particular frequency measured at -10 dB attenuation, and corrected for the presence of the probe-tube. This figure was then adjusted to reflect the difference between the attenuator setting and

-10 dB. The resulting sound pressure was expressed as dB referred to 20 μ Pa (dB SPL).

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Figure 1. Photograph of primary auditory cortex of the ferret, in vivo. Maps of electrode penetrations were made in reference to vasculature and sulcal pattern.

Figure 2. Photograph of acoustic coupler used to deliver
♦ auditory signals to the ferret.

Figure 3. Proportional representation of binaural
response types in the total population of units.

Proportion of Response Types

Figure 4. Rate-IID Function for unit #18 from ferret F201. Binaural response is typical of the EE/F response type. Spike rate represents a cumulative sum of action potentials from stimulus onset to 40 ms.

F201 Unit 4 (Mixed)

Spike Rate (50 Trials)

Figure 5. Rate-IID Function for unit #28 from ferret

F186. Binaural response is typical of the EO/I response type.
Spike rate represents a cumulative sum of action potentials
from stimulus onset to 40 ms.

F201 Unit 18 (EE/F)

Figure 6. Rate-IID Function for unit #4 from ferret F201. Binaural response is typical of the 'Mixed' response type. The cross indicates the spike rate resulting from contralateral stimulation at threshold intensity. Spike rate represents a cumulative sum of action potentials from stimulus onset to 40 ms.

F186 Unit 28 (EO/I)

Spike Rate (50 Trials)

Figure 7. Frequency histogram showing the proportion of the three major binaural response types across frequency. Frequency is measured in eight third-octave bins ranging from 3.15 kHz to 20 kHz. These data are drawn from broadly mapped animals F163 and F165.

Distribution of Response Types

Figure 8. Lateral view of mapped area within AI and frequency and binaural maps for ferret F163. Note that frequencies are measured in kHz and rounded to the nearest whole number for the sake of clarity. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outlines on the frequency map (right) indicate isofrequency contours. The outlines on the binaural map (left) indicate binaural bands.

1

Figure 9. Lateral view of mapped area within AI and frequency and binaural maps for ferret F165. Note that frequencies are measured in kHz and rounded to the nearest whole number for the sake of clarity. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outlines on the frequency map (right) indicate isofrequency contours. The outlines on the binaural map (left) indicate binaural bands.

Figure 10. Lateral view of mapped area within AI and frequency and binaural maps for ferret F201. Note that frequencies are measured in kHz and rounded to the nearest whole number for the sake of clarity. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outlines on the binaural map (left) indicate binaural bands.

F201

17 17 17 17 17
 16 16 13 13 12 12 12
 16 15 12 12 12 12 12
 15 14 12 12 12 12 12
 14 14 12 12 12 12 12
 14 12 12 12 12 12 12
 13 12 12 12 12 12 12
 10 10 11

1 mm

Figure 11. Lateral view of mapped area within AI and frequency and binaural maps for ferret F203. Note that frequencies are measured in kHz and rounded to the nearest whole number for the sake of clarity. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outlines on the frequency map (right) indicate isofrequency contours. The outlines on the binaural map (left) indicate binaural bands.

Figure 12: Lateral view of mapped area within AI and frequency and binaural maps for ferret F168. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outline indicates the binaural topography present within a narrow band isofrequency contour. The bandwidth of the contour is marked to the right of the outline.

F168

12.8-13.2

KHz

1 mm

Figure 13. Lateral view of mapped area within AI and frequency and binaural maps for ferret F185. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outline indicates the binaural topography present within a narrow band isofrequency contour. The bandwidth of the contour is marked to the right of the outline.

F185

12.7-13.9

KHz

1 mm

Figure 14. Lateral view of mapped area within AI and frequency and binaural maps for ferret F186. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outline indicates the binaural topography present within a narrow band isofrequency contour. The bandwidth of the contour is marked to the right of the outline.

F186

11.6-12.4

KHz

1 mm

Figure 15. Lateral view of mapped area within AI and frequency and binaural maps for ferret F187. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outline indicates the binaural topography present within a narrow band isofrequency contour. The bandwidth of the contour is marked to the right of the outline.

F187

11.3-12.0

KHz

1 mm

Figure 16. Lateral view of mapped area within AI and frequency and binaural maps for ferret F193. The symbols indicate the binaural response type of the unit located at that position. Closed circles indicate EE/F responses, open circles indicate EO/I responses, open triangles indicate 'Mixed' responses and open squares indicate 'Other' response. The top drawing shows a lateral view of left temporal cortex of the ferret. The shaded portion indicates the area within AI which was mapped in this experiment. The outline indicates the binaural topography present within a narrow band isofrequency contour. The bandwidth of the contour is marked to the right of the outline.

F193

12.1-12.6
KHz

1 mm

Figure 17. Scatterplots showing monaural contralateral (top) and binaural (IID) thresholds (bottom) as a function of position along an isofrequency contour for ferret F168. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses.

F168 (12.8-13.2 kHz)

F168 (12.8-13.2 kHz)

Figure 18. Scatterplots showing monaural contralateral (top) and binaural (IID) thresholds (bottom) as a function of position along an isofrequency contour for ferret F185. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses.

F185 (12.7-13.9 kHz)

F185 (12.7-13.9 kHz)

Figure 19. Scatterplots showing monaural contralateral (top) and binaural (IID) thresholds (bottom) as a function of position along an isofrequency contour for ferret F186. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses.

F186 (11.6-12.4 kHz)

F186 (11.6-12.4 kHz)

Figure 20. Scatterplots showing monaural contralateral (top) and binaural (IID) thresholds (bottom) as a function of position along an isofrequency contour for ferret F187. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses.

F187 (11.3-12.0 kHz)

F187 (11.3-12.0 kHz)

Figure 21. Scatterplots showing monaural contralateral (top) and binaural (IID) thresholds (bottom) as a function of position along an isofrequency contour for ferret F193.

Closed circles represent units having EE/F responses, open circles represent units having EO/I responses.

F193 (12.1-12.6 kHz)

F193 (12.1-12.6 kHz)

Figure 22. Scatterplot showing monaural ipsilateral threshold as a function of position along an isofrequency contour for ferret F168. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses. Ipsilateral thresholds were derived from the ipsilateral component of the IID threshold.

F100 (12.0-13.2)

Ipsilateral Threshold (dB SPL)

0 1 2 3 4

→ Caudal → Rostral (mm)

Legend: ○ EO/I, ● EE/F

Figure 23. Scatterplot showing monaural ipsilateral threshold as a function of position along an isofrequency contour for ferret F185. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses. Ipsilateral thresholds were derived from the ipsilateral component of the IID threshold.

F185 (12.7-13.9 kHz)

Figure 24. Scatterplot showing monaural ipsilateral threshold as a function of position along an isofrequency contour for ferret F186. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses. Ipsilateral thresholds were derived from the ipsilateral component of the IID threshold.

Figure 25. Scatterplot showing monaural ipsilateral threshold as a function of position along an isofrequency contour for ferret F187. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses. Ipsilateral thresholds were derived from the ipsilateral component of the IID threshold.

F187 (11.3-12.0 kHz)

Figure 26. Scatterplot showing monaural ipsilateral threshold as a function of position along an isofrequency contour for ferret F193. Closed circles represent units having EE/F responses, open circles represent units having EO/I responses. Ipsilateral thresholds were derived from the ipsilateral component of the IID threshold.

F193 (12.1-12.6 kHz)

APPENDIX A

ACOUSTIC DRIVER DATA

Pioneer SE-50D Calibration Curve

Probe Tube Table

Frequency (kHz)	Probe Tube	Reference	Correction Factor
0.10	114	99	-5
0.20	117	105	-2
0.30	118	106	-2
0.40	116	106	0
0.50	112	106	4
0.60	110	107	7
0.70	108	108	10
0.80	107	109	12
0.90	106	111	15
1.00	106	112	16
1.10	112	114	12
1.20	107	116	19
1.30	108	117	19
1.40	110	122	22
1.50	112	125	23
1.60	115	129	24
1.70	118	132	24
1.80	117	131	24
1.90	115	130	25
2.00	114	128	24
2.10	114	128	24
2.20	112	127	25
2.30	111	121	20
2.40	106	121	25
2.50	105	119	24
2.60	105	117	22
2.70	104	116	22
2.80	105	116	21
2.90	104	114	20
3.00	102	110	18
3.10	98	105	17
3.15	94	101	17
3.30	89	95	16
3.40	88	93	15
3.50	88	94	16
3.70	90	96	16
3.80	90	98	18
3.90	90	99	19
4.00	89	99	20
4.20	83	95	22
4.40	81	95	24
4.60	78	95	27
4.70	77	96	29
5.00	70	94	34
5.50	68	94	36
6.00	72	99	37

Probetube Table

6.40	77	102	35
7.00	48	90	32
7.50	56	75	29
8.00	59	79	30
8.50	62	84	32
9.00	57	79	32
9.50	59	78	29
10.00	63	81	28
10.50	70	84	24
11.00	77	89	22
11.40	83	97	24
12.00	80	96	26
12.50	78	96	28
13.00	75	92	27
13.40	67	84	27
14.10	59	76	27
14.50	57	74	27
15.00	54	72	28
15.60	54	74	30
16.00	56	77	31
16.30	64	85	31
16.70	59	80	31
17.10	56	74	28
18.00	51	61	20
19.00	52	61	19
20.00	50	61	21
21.00	54	67	23
22.00	57	76	29
23.00	55	74	29
24.00	56	66	20
25.00	57	64	17
26.00	55	61	16
27.00	51	60	19
28.00	50	60	20
29.00	50	60	20
30.00	51	60	19
31.00	52	60	18
32.00	57	61	14
33.00	63	62	9
34.00	69	66	7
35.00	72	68	6
36.00	69	67	8
37.00	65	63	8
38.00	76	72	6
39.00	65	63	8
40.00	54	61	17
41.00	55	61	16
42.00	59	62	13
43.00	64	70	16

Probetube Table

44.00	64	70	16
45.00	66	63	7
46.00	51	60	19
47	52	61	19
48	52	61	19

APPENDIX B

ORIGINAL DATA

UNIT#	Best Prog (KHz)	Measured Thresholds				Measured Components of IID				Interactions	
		Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Ipsilateral (dB Attenu)	Contralateral (dB SPL)	Contralateral (dB SPL)	IID (dB SPL)	Type	Response
1	12.5	-85	34	-60	44	-80	44	28	15	EE/F	EE/F
2	13.9	-70	42	-20	70	-30	60	32	28	EE/F	EE/F
3	15.5	-60	44	-20	71	-10	81	34	47	EE/F	EE/F
4	18.6	-30	74	00	83	-15	83	64	04	EE/F	EE/F
5	16.7	-65	43	-10	92	-10	92	38	54	EE/F	EE/F
6	17.0	-30	85	00	94	-05	89	75	14	EE/F	EE/F
7	23.6	-20	91	00	80	-	-	-	-	EE/F	EE/F
8	12.4	-80	37	-60	42	-60	42	27	15	EE/F	EE/F
9	14.0	-70	37	-	-	-30	60	47	13	EE/F	EE/F
10	13.9	-70	42	-	-	-60	40	42	02	EE/F	EE/F
11	13.5	-70	42	-	-	-40	50	42	08	EE/F	EE/F
12	12.1	-85	26	-20	88	-20	88	28	62	EE/F	EE/F
13	11.7	-80	29	-10	96	-60	46	28	17	EE/F	EE/F
14	17.0	-70	45	-	-	-	-	-	-	EE/F	EE/F
15	14.3	-70	37	-	-	-30	60	37	23	EE/F	EE/F
16	17.0	-70	45	-	-	-	-	-	-	EE/F	EE/F
17	13.6	-70	42	-30	60	-	60	42	18	EE/F	EE/F
18	12.7	-80	39	-	-	-80	54	48	05	EE/F	EE/F
19	12.9	-80	38	-	-	-	-	-	-	EE/F	EE/F
20	13.0	-75	42	-	-	-80	46	47	01	EE/F	EE/F
21	23.5	-40	71	-	-	-	-	-	-	EE/F	EE/F
22	22.1	-42	65	-	-	-	-	-	-	EE/F	EE/F
23	12.6	-70	49	-	-	-	-	-	-	EE/F	EE/F
24	12.3	-80	31	-	-	-40	68	41	27	EE/F	EE/F
25	15.5	-65	39	-	-	-20	71	44	27	EE/F	EE/F
26	12.0	-80	65	-	-	-	-	-	-	EE/F	EE/F
27	17.0	-60	55	-	-	-	-	-	-	EE/F	EE/F
28	23.1	-45	71	-	-	-	91	118	25	EE/F	EE/F
29	16.8	-60	48	-	-	-10	82	48	44	EE/F	EE/F
30	17.0	-60	55	-10	84	-10	84	55	29	EE/F	EE/F
31	16.9	-60	65	-10	84	-10	84	63	18	EE/F	EE/F
32	16.5	-20	88	-	-	-	-	-	-	EE/F	EE/F
33	18.7	-40	44	-	-	-	-	-	-	EE/F	EE/F

UNIT#	Dist Presq (KHz)	Measured Thresholds				Measured Components of MD				Interactions	
		Constructural (dB Attenu)	Constructural (dB SPL)	Isolation (dB Attenu)	Isolation (dB SPL)	Ipul (dB Attenu)	Contru (dB Attenu)	Ipul (dB SPL)	Contru (dB SPL)	IID (dB SPL)	Responses Type
34	N/R	-60	49	-	-	-	-	-	-	-	BO/O
35	26.5	-40	67	-	-	-	-	-	-	-	BO/O
36	22.0	-40	28	-30	67	-30	-40	67	28	39	EE/F
37	12.8	-40	28	-	-	40	-70	68	41	27	BO/I
38	12.2	-85	28	-	-	-	-	-	-	-	BO/O
39	N/R	-60	52	-	-	-	-	-	-	-	BO/O
40	17.1	-70	46	-20	74	-30	-80	64	36	28	EE/F
41	16.9	-80	36	-	-	-	-	-	-	-	BO/O
42	16.9	-80	28	-	-	-10	-70	92	38	54	BO/I
43	16.5	-80	48	-20	82	-20	-75	82	38	44	mixed
44	16.6	-80	34	-20	71	-30	-70	61	29	32	EE/F
45	15.0	-70	35	-30	62	-40	-70	52	36	17	EE/F
46	14.7	-70	42	-40	50	-40	-70	50	42	08	EE/F
47	13.3	-70	42	-40	50	-40	-70	50	42	08	EE/F
48	13.3	-70	37	-	-	-40	-40	30	47	-17	BO/I
49	14.0	-70	37	-	-	-30	-40	80	47	13	BO/I
50	14.0	-70	45	-	-	-30	-50	62	55	07	BO/I
51	14.7	-60	42	-	-	-20	-40	70	42	28	BO/I
52	14.9	-60	55	00	94	-20	-65	74	50	24	EE/F
53	N/R	-40	68	-	-	-	-	-	-	-	BO/O
54	17.0	-40	31	-60	58	-60	-40	58	31	27	EE/F
55	12.1	-80	31	-60	34	-80	-49	34	31	03	EE/F
56	10.6	-80	33	-60	44	-	-	-	-	-	BO/O
57	10.8	-80	31	-60	34	-80	-70	34	41	-07	EE/F
58	10.5	-80	41	-40	54	-40	-70	54	41	-13	EE/F
59	10.5	-75	42	-	-	-40	-70	62	47	15	BO/I
60	12.4	-75	37	-	-	-	-	-	-	-	BO/O
61	11.1	-70	25	-	-	-70	-70	27	25	02	BO/I
62	08.4	-40	44	-	-	-80	-40	35	44	-08	BO/I
63	08.5	-	-	-	-	-	-	-	-	-	BO/I
64	N/R	-	-	-	-	-	-	-	-	-	BO/I
65	N/R	-	-	-	-	-	-	-	-	-	BO/I
66	N/R	-	-	-	-	-	-	-	-	-	BO/I
67	N/R	-70	27	-70	29	-70	-70	29	27	02	EE/F
68	08.0	-70	-	-	-	-	-	-	-	-	EE/F

		Measured Thresholds				Measured Components of IID				Isolation	
UNIT#	Best Freq (kHz)	Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Ipsilateral (dB Attenu)	Contralateral (dB Attenu)	Ipsilateral (dB SPL)	Contralateral (dB SPL)	IID (dB SPL)	Isolation Type
69	10.0	-70	38	-40	37	-80	-70	37	38	21	EE/F
70	09.1	-70	27	-40	58	—	—	—	—	—	EE/F
71	10.5	-40	51	—	—	-30	-40	64	51	13	EO/I
72	11.6	-40	49	-50	56	-40	-40	56	49	07	EE/F
73	08.6	-40	37	-70	28	-70	-40	28	37	09	EE/F
74	N/R	—	—	—	—	—	—	—	—	—	—
75	08.3	-40	45	—	—	-50	-40	53	45	08	EO/I
76	04.4	-40	31	—	—	-40	-40	31	31	00	EO/I
77	06.5	-70	40	-70	36	-40	-70	46	40	09	EE/F
78	08.3	-40	36	-40	43	-40	-40	43	36	08	EE/F
79	04.8	-70	24	-70	24	-70	-70	24	24	00	EE/F
80	N/R	—	—	—	—	—	—	—	—	—	—
81	N/R	—	—	—	—	—	—	—	—	—	—
82	N/R	—	—	—	—	—	—	—	—	—	—
83	08.0	-40	34	—	—	-40	-40	57	24	33	EO/I
84	06.0	-40	34	—	—	-40	-40	68	34	32	EO/I
85	03.0	-70	39	-40	41	-40	-40	41	49	08	EE/F
86	N/R	—	#N/A	—	—	—	—	—	—	—	—
87	06.0	-100	14	—	—	-30	-40	77	24	83	EO/I
88	06.0	-100	14	-40	47	-40	-100	47	14	33	EE/F
89	08.2	-100	14	—	—	-40	-40	57	24	33	EO/I
90	06.2	-100	14	—	—	-40	-40	57	24	33	EO/I
91	06.1	-40	24	—	—	-40	-40	47	24	23	EO/I
92	06.9	-40	70	—	—	-40	-40	108	110	04	aborted
93	N/R	—	—	—	—	—	—	—	—	—	—
94	10.3	-40	18	—	—	-40	-40	37	18	19	EO/I
95	12.0	-40	31	—	—	—	—	—	—	—	EO/I
96	N/R	—	—	—	—	—	—	—	—	—	—
97	N/R	—	—	—	—	—	—	—	—	—	—
98	21.6	-40	23	—	—	—	—	—	—	—	—
TOTAL EO/I		28	33.73%	—	—	—	—	—	—	—	EO/O
TOTAL EE/F		30	36.14%	—	—	—	—	—	—	—	—
TOTAL other		23	27.71%	—	—	—	—	—	—	—	—
TOTAL MIXED		02	2.41%	—	—	—	—	—	—	—	—
TOTAL UNITS		83	—	—	—	—	—	—	—	—	—

F163 CALIBRATION DATA		
Frequency (kHz)	Construal Ear (dB SPL)	Ipsilateral Ear (dB SPL)
03.0	91	83
04.4	67	67
06.0	60	72
08.5	74	70
08.0	77	70
08.3	88	66
08.5	82	63
08.4	65	67
09.1	65	66
09.5	75	66
10.0	80	69
10.5	87	70
10.8	89	70
11.1	80	74
11.6	85	82
12.4	91	76
12.8	90	69
13.3	85	63
14.0	80	63
14.7	78	65
14.9	76	63
16.0	76	63
16.3	77	71
16.9	85	63
17.0	84	63
18.7	64	62
21.0	50	60
22.0	77	77
22.0	78	76
23.1	87	62
23.5	82	61

UNIT#	Best Freq (kHz)	Monaural Thresholds			Monaural Components of IID			Interaction	
		Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Ipsilateral (dB Attenu)	Contralateral (dB SPL)	IID (dB SPL)	Response Type
1	16.4	-60	41	-10	95	-70	105	74	EE/F
2	17.0	-60	53		00	-60	98	53	BO/O
3	17.0	-60	43		-60	-60	46	43	MIXED
4	17.1	-60	40		-10	-60	83	40	BO/I
5	17.0	-60	43			-60			BO/O
6	16.3	-60	44		-30	-60	72	44	BO/I
7	12.5	-60	35	-60	-60	-60	68	35	EE/F
8	16.5	-60	41	00	-20	-60	85	41	EE/F
9	16.8	-60	51						BO/O
10	16.1	-60	41						BO/O
11	17.0	-40	63						BO/O
12	12.6	-60	37						BO/O
13	16.9	-60	41						BO/O
14	N/R								
15	16.5	-60	51		-10	-60	95	51	BO/I
16	17.1	-60	50		-20	-60	73	50	BO/I
17	16.5	-60	41		-10	-60	95	41	BO/I
18	16.5	-60	41		-10	-60	95	41	BO/I
19	16.5	-60	41	-20	-20	-60	85	41	EE/F
20	16.5	-60	51	-20	-10	-60	95	51	EE/F
21	17.0	-60	53						BO/O
22	11.3	-60	47	-10					EE/O
23	11.4	-70	39	-20		-70	89	39	EE/F
24	N/R								
25	10.7	-70	38		-60	-70	54	38	BO/I
26	12.2	-60	25	-60	-60	-60	58	35	MIXED
27	12.4	-60	35	-60	-60	-70	58	45	EE/F
28	12.4	-60	35	-70	-60	-80	68	35	EE/F
29	12.5	-60	37	-60	-60	-70	60	47	EE/F
30	12.2	-60	25	-60	-60	-60	38	25	EE/F
31	11.6	-65	14	-60	-60	-60	29	19	MIXED
32	12.4	-60	25		-60	-60	58	25	BO/I

UNIT#	Best Freq (Hz)	Measured Thresholds				Measured Components of IID				Response	
		Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Ipsilateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB SPL)	Contralateral (dB SPL)	IID (dB SPL)	Type
33	12.4	-60	25	-60	25	-60	25	58	25	33	BO/I
34	12.4	-60	25	-60	25	-60	25	38	25	13	BO/I
35	12.5	-60	27	-70	50	-60	26	40	26	14	MIXED
36	12.5	-60	27	-70	50	-60	27	30	27	03	MIXED
37	11.3	-60	27	-70	37	-70	27	37	27	10	EE/F
38	11.6	-60	29	-60	49	-60	29	49	29	20	EE/F
39	11.1	-60	26	-60	42	-60	26	42	26	16	EE/F
40	11.5	-60	29	-60	29	-60	29	29	29	00	EE/F
41	12.6	-60	27	-70	50	-60	27	50	27	23	EE/F
42	12.5	-60	27	-60	40	-60	27	40	27	13	EE/F
43	12.5	-60	27	-60	40	-60	27	50	27	23	BO/I
44	12.4	-60	25	-60	48	-60	25	48	25	23	BO/I
45	12.5	-60	27	-60	40	-60	27	40	27	13	BO/I
46	12.5	-60	37	-70	50	-60	37	50	37	13	EE/F
47	12.0	-60	31	-60	58	-60	31	51	31	20	BO/I
48	12.3	-60	25	-60	58	-60	25	58	25	33	EE/F
49	12.4	-60	35	-60	38	-60	35	38	35	03	MIXED
50	13.1	-70	40	-60	46	-70	40	46	40	08	MIXED
51	12.5	-70	47	-40	80	-70	47	80	47	33	BO/I
52	16.8	-60	51	-10	95	-60	51	95	51	44	BO/I
53	N/R										
54	10.2	-70	23	-60	49	-70	23	49	23	26	BO/I
55	11.7	-70	39	-60	49	-70	39	49	39	10	BO/I
56	09.1	-60	37	-60	53	-60	37	53	37	16	BO/I
57	10.0	-70	23	-60	39	-70	23	39	23	16	BO/I
58	11.0	-60	26	-60	52	-60	26	52	26	28	BO/I
59	10.0	-70	23	-60	39	-70	23	39	23	16	BO/I
60	08.2	-70	25	-60	44	-70	25	44	25	19	BO/I
61	08.1	-70	27	-60	39	-60	27	39	17	22	MIXED
62	N/R										
63	07.5	-70	26	-70	28	-70	26	28	26	02	EE/F
64	08.5	-60	29	-70	39	-60	29	39	29	10	EE/F
65	06.4	-60	29	-70	39	-60	29	39	29	10	EE/F

Target	Best Prog (KHz)	Measured Thresholds				Measured Components of ID				Interaction	
		Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Ipsilateral (dB Attenu)	Contralateral (dB Attenu)	Ipsilateral (dB SPL)	Contralateral (dB SPL)	ID (dB SPL)	Response Type
65	06.2	-80	31			-80	-80	51	31	20	BO/I
67	06.0	-80	20			-80	-80	40	20	20	BO/I
68	08.0	-80	37			-80	-80	69	37	32	BO/I
69	08.3	-80	21	-70	41	-70	-80	41	21	20	MIXED
70	N/R										
71	08.1	-80	20			-70	-80	30	20	10	MIXED
72	06.8	-70	29			-30	-70	69	29	40	BO/I
73	06.2	-80	21	-80	51	-80	-80	51	21	80	MIXED
74	08.2	-80	21	-80	31	-80	-80	31	21	10	EE/F
75	08.2	-80	31	-70	41	-70	-80	41	21	20	EE/F
76	08.0	-80	20	-80	20	-80	-80	20	20	00	EE/F
77	N/R										
78	08.1	-80	10			-80	-80	20	10	10	BO/I
79	06.2	-70	41			-40	-70	71	41	30	BO/I
80	06.7	-80	39	-80	19	-80	-80	19	39	20	MIXED
81	06.3	-80	31	-80	61					NIL	BO/O
82	06.3	-80	31			-80	-80	51	31	20	BO/I
83	08.0	-80	37	-40		-40	-80	59	37	22	BO/I
84	08.5	-70	39	-70		-70	-70	39	39	00	BO/I
85	N/R										
86	07.2	-70	36	-70	36	-70	-70	36	36	00	MIXED
87	08.2	-80	17	-70	36	-70	-80	36	17	19	MIXED
88	08.2	-70	25	-70	34	-70	-70	34	25	09	MIXED
89	09.8	-70	24			-80	-70	50	24	26	BO/I
90	10.6	-70	38	-80	26	-80	-70	54	38	16	BO/I
91	08.5	-80	17	-80	26	-80	-70	43	17	09	EE/F
92	08.0	-70	27	-80	43	-80	-70	39	27	26	EE/F
93	10.0	-80	13	-80	39	-80	-80	39	13	46	BO/I
94	10.0	-80	13			-40	-80	89	13	66	BO/I
95	10.4	-70	23			-10	-70	78	23	43	BO/I
96	12	-80	35			-40	-80	108	35	60	BO/I
97	12	-70	45			-10	-70	89	45	63	BO/I
98	12	-70	39			-30	-80	75	39	24	EE/F
99	17	-80	51	-30	75	-80	-80	75	51	24	EE/F

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UNIT#	Beak Freq (kHz)	Measured			Thresholds			Measured Components of IID					Interaction	
		(dB Attenu)	(dB SPL)	(dB Attenu)	(dB SPL)	(dB Attenu)	(dB SPL)	Ipl	Contr	Ipl	Contr	IID	Response	Type
1	10.5	30	88											
2	12.8	-70	53					-40	-70	66	53	13	BO/O	
3	13.5	-50	73											
4	N/R													
5	N/R													
6	13.2	-60	68											
7	12.8	-70	53					-20	-60	86	63	23	EE/F	
8	13.0	-70	58					-10	-70	93	58	35	EE/F	
9	13.1	-70	58					-30	-70	73	58	15	EE/F	
10	13.1	-70	58					-40	-70	63	58	5	EE/F	
11	13.1	-70	58					-30	-70	73	58	15	EE/F	
12	13.0	-70	58					-40	-70	63	58	5	EE/F	
13	13.1	-70	58					-30	-70	73	58	15	EE/F	
14	13.1	-70	58					-10	-73	93	58	38	EE/F	
15	13.1	-70	58											
16	13.1	-70	58					-30	-70	73	58	15	EE/F	
17	13.2	-73	55					-20	-70	83	58	25	BO/O	
18	13.0	-70	58					-40	-70	63	58	5	EE/F	
19	13.1	-70	58											
20	13.1	-60	48											
21	13.1	-70	58					-10	-70	93	58	35	BO/O	
22	13.0	-70	58					0	-70	103	58	45	BO/O	
23	13.1	-60	48					-30	-60	73	48	25	BO/O	
24	13.1	-60	48					-30	-60	73	48	25	BO/O	
25	13.1	-60	48					-40	-60	63	48	15	BO/O	
26	13.0	-60	48					-60	-60	53	48	5	BO/O	
27	11.1	-75	41					-70	-70	28	46	-20	EE/F	
28	13.1	-70	58					-20	-70	83	58	25	EE/F	
29	13.1	-60	48					-60	-60	53	48	5	mixed	
30	13.1	-70	58					-40	-70	63	58	5	BO/O	
31	13.1	-70	58					-20	-70	83	58	25	BO/O	
32	13.1	-70	58					-30	-70	73	58	15	BO/O	
33	13.1	-70	58					-40	-70	63	58	5	BO/O	

UNIT#	Best Freq (kHz)	Contralateral (dB Attenu)	Measure Thresholds		Measure Components of IID		Interaction	
			(dB SPL)	(dB Attenu)	(dB SPL)	(dB Attenu)	(dB SPL)	Type
34	13.0	-70	58		58	-70	58	-5 mixed
36	13.1	-70	58		58	-70	58	-5 mixed
36	13.1	-70	58		58	-70	58	15 BO/I
37	13.1	-70	58		58	-70	58	5 BO/I
38	13.1	-70	58	40	63	-70	58	5 EE/F
38	13.1	-70	58	40	63	-70	58	5 EE/F
40	10.5	-40	58		43	-40	58	-15 mixed
41	11.5	-66	52		64	-66	82	12 BO/I
42	10.8	-40	61		63	-60	61	2 BO/I
43	10.6	-70	46		53	-60	58	-5 BO/I
44	10.6	-40	58		43	-60	58	-15 mixed
45	10.6	-70	48	-50	43	-70	48	-5 EE/F
46	10.8	-70	51	-50	43	-70	51	-8 EE/F
47	10.7	-70	51	-50	43	-70	51	-8 mixed
48	10.7	-70	51		53	-70	51	2 BO/I
49	10.7	-70	51		53	-70	51	2 BO/I
50	10.7	-70	51		43	-70	51	-8 BO/I
51	10.7	-70	51		43	-70	51	-8 BO/I
52	10.6	-70	39		46	-70	39	7 BO/I
53	10.7	-40	61		53	-60	61	-8 BO/I
54	10.7	-40	61		53	-60	61	-8 BO/I
55	10.7	-40	61		53	-60	61	-8 BO/I
TOTAL BO/I		27	0.51923					
TOTAL EE/F		16	0.30769					
TOTAL other		3	0.05769					
TOTAL MIXED		6	0.11538					
TOTAL UNITS		52						

F168 CALIBRATION DATA		
Frequency (kHz)	Contralateral Ear (dB SPL)	Ipsilateral Ear (dB SPL)
0.5	80	87
1.0	84	89
1.5	94	89
2.0	97	89
3.0	94	74
4.0	83	80
5.0	96	78
6.0	101	76
7.0	101	76
8.0	96	74
9.0		
10.0		
11.0		
12.0		
13.0		
14.0		
15.0		
16.0		
17.0		
18.0		
19.0		
20.0		
21.0		
22.0		
23.0		
24.0		
25.0		
26.0		
27.0		
28.0		
29.0		
30.0		
31.0		
32.0		
33.0		
34.0		
35.0		
36.0		
37.0		
38.0		
39.0		
40.0		
41.0		
42.0		
43.0		
44.0		
45.0		
46.0		
47.0		
48.0		
49.0		
50.0		
51.0		
52.0		
53.0		
54.0		
55.0		
56.0		
57.0		
58.0		
59.0		
60.0		
61.0		
62.0		
63.0		
64.0		
65.0		
66.0		
67.0		
68.0		
69.0		
70.0		
71.0		
72.0		
73.0		
74.0		
75.0		
76.0		
77.0		
78.0		
79.0		
80.0		
81.0		
82.0		
83.0		
84.0		
85.0		
86.0		
87.0		
88.0		
89.0		
90.0		
91.0		
92.0		
93.0		
94.0		
95.0		
96.0		
97.0		
98.0		
99.0		
100.0		

UNIT#	Best Freq (kHz)	Contributed (dB Attenu)	Measured Thresholds		Isolated (dB SPL)	Ipel (dB Attenu)	Measured Components of IID		Interactions		Response Type
			(dB SPL)	(dB Attenu)			Coatra (dB Attenu)	Ipel (dB SPL)	Coatra (dB SPL)	IID (dB SPL)	
1	12.3	-80	39	-20	108						BO/O
2	N/R										BO/O
3	13.0	-80	47			-30	-83	88	44		BO/O
4	13.0	-70	57	-30	88	-30	-70	88	57		EE/F
5	13.0	-70	57			-70	-70	48	57	9	BO/O
6	12.8	-80	49	-30	91	-30	-80	101	49	52	EE/F
7	13.2	-70	55			-80	-70	67	55	12	EE/F
8	13.6	-70	52	-40	72	-40	-70	72	52	20	EE/F
9	13.4	-70	55	-40	77	-40	-60	77	55	12	EE/F
10	13.2	-70	55	-40	77	-30	-60	87	65	20	EE/F
11	13.9	-80	62	-30	82	-70	-60	82	62	22	EE/F
12	13.3	-70	55	-40	77	-40	-70	77	55	22	EE/F
13	13.4	-85	60	-40	77	-40	-65	77	60	17	MIXED
14	13.5	-80	65	-40	77	-40	-65	77	60	17	MIXED
15	13.7	-80	62	-30	82	-30	-60	82	62	20	MIXED
16	13.1	-70	57	-30	88	-40	-70	78	57	21	EE/F
17	13.1	-70	57			-40	-70	78	57	21	BO/O
18	13.1	-70	57			-40	-70	68	57	11	BO/O
19	13.1	-70	57			-40	-70	78	67	11	BO/O
20	13.1	-80	67			-40	-60	88	67	21	BO/O
21	13.1	-80	67			-30	-40	87	65	2	BO/O
22	13.3	-80	75			-80	-60	68	67	1	MIXED
23	13.1	-80	67	-30	101	-20	-70	91	51	40	EE/F
24	12.7	-85	64			-85	-65	91	64	27	BO/O
25	12.7	-85	64			-20	-65	101	64	37	BO/O
26	12.7	-85	64			-30	-67	107	58	49	BO/O
27	13.3	-80	65								

UNIT#	Dist Type	Measured Thresholds				Measured Components of IED				Interdiction	
		(dB Attenu)	(dB SPL)	(dB Attenu)	(dB SPL)	(dB Attenu)	(dB SPL)	(dB SPL)	(dB SPL)	IED	Response
1	12.1	-70	47	-10	104	-30	84	47	37	37	BOI
2	11.8	-70	45			-70	89	45	45	14	BOI
3	12.1	-70	47			-70	81	47	47	34	BOI
4	12.2	-70	47			-70	74	47	47	27	BOI
5	12.1	-70	47			-70	84	47	47	32	BOI
6	12.0	-70	47			-70	81	47	47	34	BOI
7	12.2	-70	47			-70	14	47	47	33	MIXED
8	12.4	-60	57			-10	104	57	57	47	BOI
9	12.1					-65	34	32	32	2	MIXED
10	12.1	-65	52			-65	51	52	52	-1	MIXED
11	12.1	-60	57	-40	71	-40	71	52	52	19	EE/F
12	12.1	-60	57	-30	81	-65	81	52	52	28	EE/F
13	12.0	-60	57	-30	81	-60	81	57	57	24	EE/F
14	11.8	-70	45	-40	89	-70	89	45	45	24	EE/F
15	12.2	-70	47	-60	64	-70	64	47	47	17	EE/F
16	12.3	-70	47	-40	64	-70	74	47	47	27	EE/F
17	12.0	-70	47	-30	81	-70	81	47	47	34	MIXED
18	11.6	-70	40	-60	48	-70	38	40	40	-2	MIXED
19	12.0	-60	37	-60	51	-60	61	37	37	24	EE/F
20	12.0	-60	37	-40	71	-60	61	37	37	24	MIXED
21	12.0	-70	47			-70	81	47	47	34	BOI
22	12.0	-70	47			-70	81	47	47	34	BOI
23	12.1	-70	47	-60	64	-70	64	47	47	17	EE/F
24	12.0	-70	47	-60	61	-70	61	47	47	14	MIXED
25	12.0	-60	87	-60	81	-60	81	67	67	14	EE/F
26	12.4	-75	42	-60	64	-60	64	42	42	22	EE/F
27	12.5	-70	49	-30	98	-70	78	49	49	27	EE/F
28	12.5	-70	49			-70	78	49	49	3	BOI
29	12.2	-70	47			-70	84	47	47	37	BOI
30	12.2	-75	42			-70	74	47	47	27	BOI
31	12.4	-75	42			-75	84	42	42	42	BOI
32	12.6	-65	49	-60	63	-65	63	49	49	14	EE/F

UNIT#	Back Freq (Hz)	Measured Thresholds				Measured Components of IID				Measured	
		Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Ipsilateral (dB Attenu)	Contralateral (dB Attenu)	Ipsilateral (dB SPL)	Contralateral (dB SPL)	IID (dB SPL)	Response Type
33	12.0	-70	47	-50	61	-50	-70	61	47	14	EE/F
34	12.2	-55	62	-40	74	-50	-40	64	57	7	EE/F
35	12.2	-55	62	-50	64	-70	-50	44	67	23	MIXED
36	15.9	-70	45								BO/O
37	15.7	-60	55			-50	-40	65	56	9	BO/T
38	12.8	-70	44	-50	63	-40	-70	73	44	29	EE/F
39	12.8	-70	44			-30	-70	83	44	39	BO/I
40	12.2	-70	47			-20	-70	94	47	47	BO/I
41	12.4	-60	57			-30	-60	84	57	27	BO/I
42	N/R										
43	N/R										
44	10.8	-60	50			-40	-60	58	50	8	BO/I
45	10.6	-70	40			-40	-70	58	40	18	BO/I
46	13.5	-60	53			-20	-60	82	63	29	BO/I
47	N/R										
48	15.8	-70	45								BO/O
49	16.4	-60	58			-10	-50	104	58	46	BO/I
TOTAL BO/I		21	046652								

[illegible]

UNIT#	Best Prog (dB)	Measured Thresholds				Measured Components of ID				Interactions	
		Constr. (dB)	Constr. (dB SPT)	Ipel. (dB)	Ipel. (dB SPT)	Constr. (dB)	Ipel. (dB SPT)	Constr. (dB SPT)	ID (dB SPT)	Type	Response
1	11.7	-70	43	-10	88	-70	88	43	55	BO/O	BO/O
2	11.8	-70	43							BO/O	BO/O
3	11.7	-70	43							BO/O	BO/O
4	12.0	-70	40	-10	100	-60	70	50	20	BO/O	BO/O
5	11.9	-65	45	-20		-65	80	45	45	BO/O	BO/O
6	11.8	-65	45	-10		-65	100	45	55	BO/O	BO/O
7	12.6	-65	46	-20		-65	88	46	52	BO/O	BO/O
8	12.1	-65	46	-20		-65	84	46	48	BO/O	BO/O
9	11.9	-65	45	-20		-65	80	45	45	BO/O	BO/O
10	11.8	-70	40	-30		-70	80	40	40	BO/O	BO/O
11	11.8	-70	40	-30		-70	80	40	40	BO/O	BO/O
12	11.8	-70	40	-10		-70	100	40	60	BO/O	BO/O
13	11.8	-70	40	-10		-70	80	40	60	BO/O	BO/O
14	11.8	-70	40	-20		-70	80	40	50	BO/O	BO/O
15	12.8	-65	39	-10		-65	101	39	62	BO/O	BO/O
16	12.8	-65	40	-10		-65	101	40	61	BO/O	BO/O
17	12.8	-65	40	-10		-65	101	40	61	BO/O	BO/O
18	11.8	-65	45	-10		-65	80	45	55	BO/O	BO/O
19	11.8	-75	35	-30		-75	80	35	45	BO/O	BO/O
20	11.8	-70	40	-30		-70	80	40	40	BO/O	BO/O
21	12.8	-75	30	-10		-75	101	30	71	BO/O	BO/O
22	12.9	-65	40	-20		-65	91	40	51	BO/O	BO/O
23	11.8	-70	40	-10		-70	100	40	60	BO/O	BO/O
24	11.8	-75	35	-30		-75	80	35	45	BO/O	BO/O
25	11.8	-75	35	-30		-75	80	35	45	BO/O	BO/O
26	11.8	-65	55	-20		-65	90	55	35	EE/F	EE/F
27	12.2	-65	44	-40		-65	78	44	32	BO/O	BO/O
28	N/R										
29	N/R										
30	11.5	-75	38	-10		-75	86	38	57	BO/O	BO/O
31	11.1	-65	45	-10		-65	83	45	48	BO/O	BO/O

UNIT#	Best Freq (KHz)	Measured Thresholds			Measured Components of IID			Interaction	
		Contralateral (dB Attenu)	Contralateral (dB SPL)	Ipsilateral (dB Attenu)	Ipsilateral (dB SPL)	Contralateral (dB Attenu)	Contralateral (dB SPL)	IID (dB SPL)	Response Type
32	11.5	-75	38	-20	94	-70	90	40	EO/O
33	11.9	-70	40	-20	90	-70	90	40	EE/F
34	11.8	-75	35	-20	90	-75	93	35	EE/F
35	11.3	-75	35	-10	93	-60	99	53	EO/I
36	11.8	-75	38	-20	98	-70	98	41	EE/F
37	12.7	-70	41	-20	98	-70	98	41	EE/F
38	12.5	-60	51	-10	108	-60	108	51	EO/I
39	12.4	-60	49	-20	98	-60	98	49	EO/I
40	12.7	-70	41	-30	88	-70	88	41	EO/I
41	12.5	-60	51	-20	98	-60	98	51	EE/F
42	12.5	-60	51	-20	98	-60	98	51	EE/F
43	12.7	-60	51	-10	108	-60	108	51	EO/O
44	12.3	-70	41	-10	108	-60	108	51	EO/I
45	N/R								
46	N/R								
47	09.6	-65	52	-30	80	-65	80	52	EO/I
48	11.0	-60	50	-30	73	-70	73	40	EO/I
49	11.1	-70	40	-30	73	-70	73	40	EE/F
50	11.2	-70	40	-10	83	-70	83	40	EE/F
51	11.2	-70	40	-20	83	-70	83	40	EE/F
52	11.7	-70	43	-10	90	-70	90	43	EO/I
53	11.9	-70	40	-20	90	-70	90	40	EO/I
54	11.3	-70	40	-10	93	-70	93	40	EE/F
55	12.4	-70	39	-20	98	-70	98	39	EO/I
56	10.6	-70	42	-20	85	-70	85	42	EE/F
57	11.4	-70	43					43	EO/O
TOTAL EO/I	36	67.92%							
TOTAL EE/F	11	20.75%							
TOTAL EO/O	6	11.32%							
TOTAL UNITS	53								

UNIT#	Best Freq (kHz)	Contratlonal (dB Atten)	Measured Thresholds		Measured Components of ID		Interaction	
			(dB SPL)	(dB Atten)	Ipel (dB SPL)	Contra (dB Atten)	ID (dB SPL)	Response Type
1	12.3	-60	62		-60	58	62	BO/1
2	12.4	-70	42		-60	59	62	BO/1
3	12.5	-60	54		-60	91	64	BO/1
4	12.2	-60	50		-60	77	50	BO/1
5	12.6	-60	52	-20	-60	49	52	MIXED
6	12.2	-70	40		-70	47	40	BO/1
7	12.3	-70	42		-70	48	42	BO/1
8	12.5	-60	54		-60	71	54	BO/1
9	12.6	-60	52		-60	79	52	BO/1
10	12.5	-60	54		-60	51	54	BO/1
11	12.5	-60	54		-60	61	54	BO/1
12	12.5	-70	44		-60	61	44	BO/1
13	12.4	-70	42		-70	59	42	BO/1
14	12.5	-60	54		-60	71	54	BO/1
15	12.4	-70	42		-70	59	42	BO/1
16	12.5	-70	44		-70	61	44	BO/1
17	12.2	-60	50		-60	77	50	BO/1
18	12.4	-60	52		-60	79	52	BO/1
19	12.6	-70	42		-70	60	42	BO/1
20	12.4	-70	42		-70	59	42	BO/1
21	12.4	-70	42	-60	-60	59	42	EE/F
22	12.4	-70	42	-50	-60	59	42	EE/F
23	12.4	-70	42	-70	-70	49	42	EE/F
24	12.4	-70	42	-70	-70	39	42	EE/F
25	12.4	-70	42	-60	-70	49	42	EE/F
26	12.3	-70	42	-70	-70	38	42	EE/F
27	12.4	-70	42	-70	-70	39	42	EE/F
28	12.4	-70	42	-70	-70	39	42	EE/F
29	12.3	-70	42	-60	-70	48	42	EE/F
30	12.4	-70	42	-60	-70	48	42	EE/F
31	12.3	-70	40	-40	-70	67	40	EE/F
32	12.2	-70	40	-40	-70	77	40	EE/1

UNIT#	Back Prog (Hrs)	Measured Thresholds				Measured Components of IID				Interaction	
		Contraband (dB Attenu)	Contraband (dB SPL)	Isolation (dB Attenu)	Isolation (dB SPL)	Isol (dB Attenu)	Contra (dB Attenu)	Isol (dB SPL)	Contra (dB SPL)	IID (dB SPL)	Response Type
33	12.2	-70	40	-70	37	-70	-70	37	40	3	EE/F
34	12.4	-60	52			-40	-60	69	52	17	BO/I
35	12.4	-60	52			-40	-60	69	52	17	BO/I
36	12.2	-60	50			NIL	NIL	NIL	NIL	NIL	ABORTED
37	12.1	-60	46	-30	73	-30	-60	73	46	27	EE/I
38	12.3	-70	42	-50	58	-60	-70	58	42	16	EE/F
39	12.5	-60	54			-40	-60	71	54	17	BO/I
40	12.4	-60	52	-50	59	-60	-60	59	52	7	EE/F
41	12.5	-60	54	-50	61	-60	-60	61	54	7	EE/F
42	12.4	-60	52	-60	49	-60	-60	49	52	3	EE/F
43	12.3	-60	52	-60	58	-60	-60	58	52	6	EE/F
44	12.5	-70	42	-60	49	-60	-70	49	42	7	EE/F
45	12.2	-70	40	-60	47	-60	-70	47	40	7	EE/F
46	12.2	-70	40			-60	-70	47	40	7	BO/I
47	12.2	-60	52	60	168	-70	-60	38	52	14	MIXED
48	12.2	-70	40			-60	-70	57	40	17	BO/I
49	12.3	-70	42			-40	-70	58	42	26	BO/I
50	12.2	-70	40			-60	-70	57	40	17	BO/I
51	12.2	-70	40	-70	37	-60	-70	17	40	23	MIXED
52	12.3	-70	42			-40	-70	68	42	26	BO/I
53	12.3	-60	52	-60	48	-60	-60	48	52	4	EE/F

UNIT#	Beet Freq (Hz)	Measured Thresholds			Measured Components of IID				Estimation		
		Conductance (dB Attenu)	(dB SPL)	(dB Attenu)	Isolation (dB SPL)	Ipsi (dB Attenu)	Contra (dB Attenu)	Ipsi (dB SPL)	Contra (dB SPL)	IID (dB SPL)	Response Type
54	12.3	-60	52	-60	55	-40	-60	68	62	6	EE/F
55	N/R										
56	12.2	-60	50			-20	-60	87	50	37	BO/I
57	12.1	-70	36	-40	63	-40	-70	63	36	27	EE/F
58	12.2	-70	40	-80	27	-80	-70	27	40	-13	MIXED
59	12.2	-60	50	-60	47	-60	-60	57	50	7	MIXED
60	12.3	-60	52			-40	-60	68	52	16	MIXED
61	11.7	-70	34			-60	-70	41	34	7	BO/I
62	11.7	-60	44			-40	-60	61	44	17	BO/I
63	12.3	-70	40			-40	-70	67	40	37	BO/I
64	12.3	-60	52			-60	-60	48	52	4	BO/I
65	12.3	-60	52			-60	-60	58	52	6	BO/I
66	N/R										
67	N/R										
68	N/R										
69	N/R										
70	N/R										
71	10.6	-70	25			-60	-70	49	25	24	BO/I
72	11.5	-80	23	-60	51	-40	-60	61	23	38	EE/F
73	11.5	-70	33	-60	51	-40	-70	61	33	28	EE/F
74	12.2	-60	50			-60	-60	47	50	-3	EE/F
75	11.4	-60	35			-40	-60	59	35	24	BO/I
76	12.2	-80	30			-80	-80	27	30	-3	BO/I
TOTAL BO/I 34 55.74%											
TOTAL EE/F 22 36.07%											
TOTAL other 0 0.00%											
TOTAL MIXED 5 8.20%											
TOTAL UNITS 61											

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UNIT#	Desct Freq		Contribution		Thresholds		Measured Components of ID				Interaction	
	(Hz)	(dB Attenu)	(dB SPL)	(dB Attenu)	Isolated	(dB SPL)	Ipel	Contra	Ipel	Contra	ID	Response Type
1	14.0	-70	32	-40	65	65	-40	-70	65	32	34	BO/O
2	14.0	-70	32	-40	65	65	-40	-70	65	32	34	BO/O
3	12.0	-60	35				-30	-60	84	35	49	BO/O
4	12.0	-70	45				-70	-60	44	65	-11	MIXED
5	12.4	-65	45				-70	-65	47	45	2	MIXED
6	12.0	-70	45				-70	-70	44	45	-1	MIXED
7	12.1	-70	45				-40	-70	74	45	29	BO/O
8	12.2	-70	45				-70	-70	44	45	-1	BO/O
9	12.0	-75	40				-60	-60	64	35	29	BO/O
10	12.0	-80	35	-60	24	24	-100	-80	14	35	-21	MIXED
11	12.4	-75	35	-60	27	27	-80	-75	27	35	-8	MIXED
12	13.1	-75	29	-60	34	34	-80	-75	34	32	5	EE/F
13	14.1	-70	32	-60	41	41	-60	-70	51	29	22	EE/F
14	14.5	-70	29	-60	49	49	-60	-75	39	27	12	EE/F
15	16.4	-75	27	-60			-60	-75	9	27	-18	MIXED
16	16.4	-70	32				-80	-70	19	32	-13	MIXED
17	16.4	-70	25	-60	48	48	-40	-70	68	25	43	EE/F
18	15.0	-75	27	-70	35	35	-70	-75	73	27	8	EE/F
19	14.4	-65	37	-60	24	24	-30	-65	47	29	18	EE/F
20	14.0	-65	39	-60	47	47	-60	-65	39	37	7	BO/O
21	13.2	-65	29	-60			-60	-65	29	37	-8	BO/O
22	16.6	-65	37	-60			-40	-60	49	47	2	BO/O
23	16.6	-60	47	-60			-60	-60	39	27	2	BO/O
24	16.6	-60		-60			-70	-70			2	EE/F
25	16.6	-60		-60			-70	-70			2	EE/F
26	16.6	-60		-60			-70	-70			2	EE/F
27	16.6	-70		-60			-70	-70			2	EE/F

UNIT #	Best Prog (KIB)	Measured Thresholds				Measured Components of MD				Estimation	
		Contributed (KIB Actual)	Contributed (KIB SP1)	Isolated (KIB Actual)	Isolated (KIB SP1)	Isol (KIB Actual)	Coactive (KIB Actual)	Isol (KIB SP1)	Coactive (KIB SP1)	MD (KIB SP1)	Response Type
28	16.6	-65	32	-60	29	-60	-65	29	32	3	EE/F
29	16.6	-65	32	-60	29	-60	-65	29	32	3	EE/F
30	13.3	-70	34	-70	42	-70	-70	42	34	8	EE/F
31	13.3	-65	39	-60	52	-60	-65	52	39	13	EE/F
32	11.8	-70	40	-60	51	-60	-70	51	40	11	EE/F
33	11.8	-70	40			-40	-70	71	40	31	BO/I
34	11.8	-60	50			-20	-60	95	50	41	BO/I
35	11.8	-70	40			-60	-70	51	40	11	BO/I
36	11.8	-60	50			-60	-60	61	50	11	BO/I
37	11.7	-70	28			-60	-70	52	28	24	BO/I
38	12.3	-70	45			-60	-60	64	55	9	BO/I
39	12.3	-60	65			-30	-60	84	65	19	BO/I
40	11.8	-60	60	-70	41	-60	-60	61	60	1	EE/F
41	11.8	-70	40			-60	-70	51	40	11	BO/I
42	N/R										
43	11.8	-70	40	-60	61	-40	-70	71	40	31	EE/F
44	11.8	-60	50	-60	51	-60	-60	51	50	1	EE/F
45	11.8	-70	40	-60	51	-60	-70	51	40	11	EE/F
46	11.8	-70	40	-60	61	-30	-70	81	40	41	EE/F
47	11.8	-70	40	-60	51	-60	-70	51	40	11	EE/F
48	10.9	-65	33	-70	42	-70	-65	42	33	9	EE/F
49	10.0	-60	38	-70	32	-60	-60	42	38	4	EE/F
50	10.0	-60	48			-40	-60	62	48	14	MIXED
TOTAL BO/I		17	35.42%								
TOTAL EE/F		21	43.75%								
TOTAL other		2	4.17%								
TOTAL MIXED		8	16.67%								
TOTAL UNITS		48									

UNIT#	Beet Freq (Hz)	Measured Thresholds			Measured Components of ID					Interactions	
		Contraband (dB Attenu)	Contraband (dB SPL)	Isolated (dB Attenu)	Isolated (dB SPL)	Ipel (dB Attenu)	Costrn (dB Attenu)	Ipel (dB SPL)	Costrn (dB SPL)	ID (dB SPL)	Response Type
1	12.3	-40	77	-40	71	-40	-40	74	77	3	BO/F
2	12.0	-30	67	-40	71						BO/O
3	11.1	-30	62	-40	67						BO/O
4	13.5	-30	78							8	ABORTED
5	11.7	-40	73	-40	69	-40	-40	69	73	4	BO/F
6	11.7	-40	73			-40	-40	69	73	4	BO/F
7	12.2	-60	57			-60	-60	64	67	3	MIXED
8	11.8	-60	53			-60	-60	69	53	18	BO/I
9	12.3	-60	67			-60	-60	94	67	37	BO/I
10	12.3	-62	66			-60	-62	64	66	-1	BO/I
11	12.3	-63	64			-60	-63	64	64	0	BO/O
12	12.2	-60	67	-40	74	-60	-60	64	67	-13	MIXED
13	12.0	-40	77	-30	81	-30	-40	81	77	4	BO/F
14	12.0	-60	67	-40	71	-40	-60	71	67	4	BO/F
15	N/R										
16	12.2	-40	77	-40	74	-40	-40	74	77	3	BO/F
17	12.3	-40	77	-40	74	-40	-40	74	77	3	BO/F
18	12.2	-40	77	-60	64	-40	-40	74	77	3	BO/F
19	12.2	-40	77	-30	84	-30	-40	84	77	7	BO/F
20	12.0	-60	67	-30	81	-30	-60	81	67	14	BO/F
21	12.5	-60	62	-60	69	-60	-60	69	62	7	BO/F
22	12.2	-60	67	-60	64	-60	-60	64	67	3	BO/F
23	12.7	-40	69	-60	67	-60	-40	67	69	2	BO/F
24	12.2	-40	77	-40	74	-40	-40	74	77	3	BO/F
25	12.0	-60	67			-60	-60	61	67	6	BO/I

[illegible]

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APPENDIX C

ISOFREQUENCY CONTOUR DATA

Contour -- Distance (mm)	EE/F (Mon)	EE/F (IID)	EO/I (Mon)	EO/I (IID)
0.492			41	-20
0.554			48	5
0.585			48	15
0.615			48	25
0.677			48	25
0.738			58	45
0.800			58	35
0.954	58	05		
1.015			55	25
1.077	58	15		
1.231	58	38		
1.323	58	15		
1.385	58	05		
1.415	58	15		
1.446	58	05		
1.508	58	15		
1.538	58	35		
1.569	53	23		
1.600	58	25		
1.600	58	05		
1.692	58	05		
1.692			58	5
1.785			58	15
1.785				
1.815			58	5
1.846				
1.877			58	15
1.938			58	25
2.000			58	5
2.062			53	13
2.092				

3

of/de

3

MICRO

Contour Distance (mm)	EE/F (Mon)	EE/F (IID)	EO/I (Mon)	EO/I (IID)
0.941			75	2
1.035			67	21
1.129			67	11
1.200			57	11
1.294			57	21
1.388			57	21
1.459	57	21		
1.529				
1.647				
1.741				
1.812	55	22		
1.859	62	20		
1.906	55	22		
1.953	55	12		
2.047	52	20		
2.141	55	12		
2.212	49	52		
2.306	57	31		
2.376			57	-9
2.494			47	44
2.588				
2.729			64	27
2.800			64	37
2.918			65	49
3.035			65	37

Contour Distance (mm)	EE/F (Mon)	EE/F (HD)	EO/I (Mon)	EO/I (HD)
0.541	67	14		
0.659	47	14		
0.776	47	17		
0.894			47	34
1.012			47	34
1.129				
1.247	37	24		
1.318				
1.365				
1.435	47	27		
1.553	47	17		
1.671	45	24		
1.765	57	24		
1.859	57	29		
1.953	57	19		
2.047				
2.071				
2.141			57	47
2.188				
2.235			47	34
2.259			47	37
2.282			47	27
2.353			47	34
2.400			45	14
2.471			47	37

Contour Distance (mm)	EE/F (Mon)	EE/F (IID)	EO/I (Mon)	EO/I (IID)
0.918			35	45
0.918	55	35		
0.988			35	45
1.012			40	60
1.082			40	40
1.082			35	45
1.176			45	55
1.200			40	61
1.271			40	60
1.294			40	50
1.388			40	60
1.412			40	40
1.459			46	52
1.459			46	48
1.600			45	55
1.788			40	20
1.953			38	47
1.976			45	48
1.976			38	57
2.188	35	58		
2.212	35	50		

Contour				
Distance				
(mm)	EE/F (Mon)	EE/F (IID)	EO/P (Mon)	EO/I (IID)
0.918			42	26
0.941			40	17
0.988				
1.012	40	7		
1.082	42	7		
1.082			40	7
1.129	52	6		
1.153	54	7		
1.200	52	7		
1.200			54	17
1.224	42	16		
1.318			50	37
1.365			52	17
1.365			52	17
1.388	40	-3		
1.412	42	7		
1.435	40	27		
1.459	42	6		
1.482	42	-3		
1.506	42	-3		
1.600	42	7		
1.647	42	-3		
1.647	42	-4		
1.694	42	17		
1.718	42	7		
1.788	42	17		
1.788			42	17
1.859			52	27
1.882			42	27
1.953			44	17
1.953			50	27
2.000			42	17
2.024			54	17
2.094			44	17
2.118			42	17
2.165			54	7
2.188			54	-3
2.259			54	17
2.282			52	27
2.376			42	6
2.424			40	7
2.471				
2.565			50	27
2.588			54	27
2.659			42	7
2.753			52	6

END

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FIN