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Neurophysiological mechanisms of sound localization[1]

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Sound localization depends on the detection of signal differences at the two ears of times of arrival (Δt), of phase ($\Delta \phi$), and of intensity (ΔI). (See Erulkar (4) for a thorough review of the field.) The relative significance of each of these parameters is affected by the spectral content of the signal and the spatial separation of the two ears, or head size. For instance, in man, the maximum interaural time difference encountered is about 900 μsec whereas, in the rat, with its smaller head, maximum interaural time differences are no more than 150 μsec. Interaural intensity differences of up to 20 dB occur when the head can act to shadow the acoustic signal. In man this should appear with spectral components greater than 1.5 kHz whereas, in the rat, because of its small head size interaural intensity differences appear above 3 kHz.

The neural basis for sound localization depends on convergence of inputs from each of the ears onto binaural centers which then process the relevant interaural acoustic cues. While the superior olive is clearly the first site along the central auditory pathway for binaural interaction (7), there is evidence of binaural processing more centrally at inferior colliculus (2), medial geniculate (17), and auditory cortex (3), as well. At all of these sites investigators have recorded single units sensitive to sounds whose rates of firing were modified by changes in binaural parameters of the acoustic signal. An example of one such unit sensitive to interaural time difference is shown in Fig. 1. This unit was recorded from the medial geniculate body of squirrel monkey in response to binaural clicks presented with various interaural delays. The unit almost always responded to monaural clicks presented to the contralateral ear and almost never to ipsilateral signals

ABSTRACT

Some of the neurophysiological data for understanding the neural basis of sound localization are reviewed. There are single units at many levels of the auditory pathway that are sensitive to acoustic cues of interaural differences in time of arrival (Δt) and of intensity (ΔI). The unit sensitivities take the form of a gradual change in response probability over a limited portion of the Δt or ΔI continuum. The possibility that the response change supports a receptive field organization of auditory space similar to the neural analysis of the visual and somatosensory dimensions is rejected because of the gross character of the sensitivity. Most auditory units are "tuned" to between 50 and 180° of auditory space, measures that are more than 10-fold greater than the usual psychoacoustic threshold. It is suggested that information about auditory space is contained in the difference of activity between populations of units sensitive to right-sided and to left-sided inputs which are segregated into the paired auditory nuclei. The comparators of the relative levels of activity of these paired nuclei are through segmental connections to various kinds of motor mechanisms tending to direct the animal to move in a lateralized manner.—STARR, A. Neurophysiological mechanisms of sound localization. *Federation Proc.* 33: 1911–1914, 1974.

and, in fact, ipsilateral stimulation was followed by a brief period of suppression of spontaneous activity. With binaural click stimulation the response probabilities changed gradually over a portion of the Δt continuum becoming maximum when the contralateral click led by 200 μsec and minimum when the ipsilateral click led by 100 μsec. This particular pattern of binaural interaction to either interaural time or intensity disparities has been frequently observed at other binaural sites along the auditory pathway. For instance, more than 50% of the units showing binaural interaction at medial geniculate body display this type of response function (17).

Can the unit data be used to generate a neurological model of auditory spatial analysis comparable to those developed for the visual and somatosensory spheres? In both of the latter systems, units are maximally sensitive to signals arising from a restricted portion of the environment, i.e., their receptive field. The shape of the receptive fields may vary but the underlying principles are for each unit *1)* to have a particular and *limited* receptive field and *2)* to relate to one another in such a way that visual and somatosensory space become rerepresented in an orderly anatomical array (Fig. 2). For instance, consider the disposition of the visual fields on occipital cortex or the somatosensory homunculus on postcentral gyrus.

Jeffress (10) proposed just such a neural model for the analysis of auditory space including *1)* elements sensitive to signals arising from a restricted portion of auditory space, and *2)* a systematic anatomical ordering of the binaural elements to rerepresent auditory space in the central nervous system (Fig. 3). Let us examine in more detail the single unit data to see how they complement this type
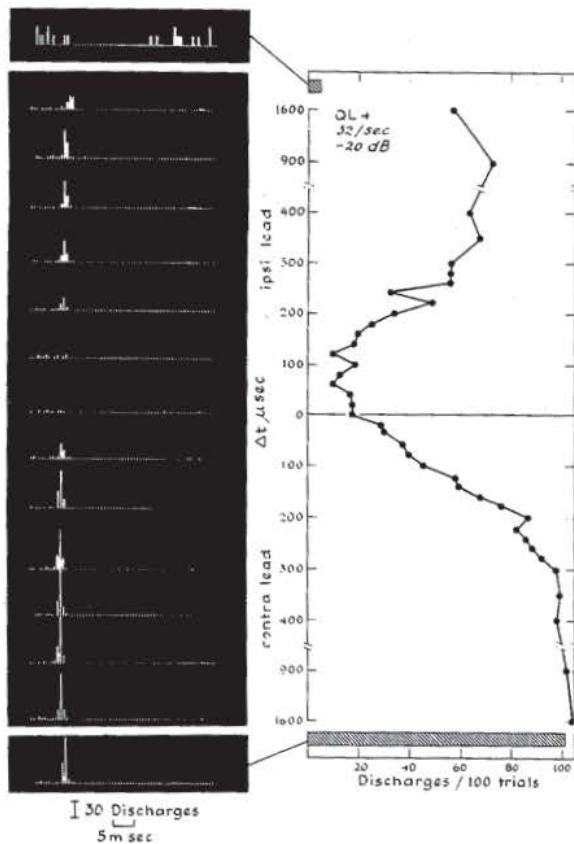
Figure 1. Poststimulus time histograms of 100 click presentations (left) and binaural response probabilities as a function of interaural time differences (Δt) (right) for unit in medial geniculate. Histograms are aligned with the appropriate portion of the Δt function. The amplitude bar represents one discharge for the top histogram. Note that the effect of varying Δt is on the number of discharges and not on the discharge pattern or latency. (From Starr and Don (17).)

of model. Investigators have found sensitivities or receptive fields of interaural time disparities extending from 100 to 3,000 μsec (2, 7, 9, 17) and to interaural intensity disparities from 6 to 20 dB (17, 19). While a microsecond measure of sensitivity is impressive at the neural level and raises a whole host of questions concerning its synaptic mechanisms, interaural dimension of 200 μsec or of 6–12 dB in the cat or monkey are really gross measures as they represent almost 180° of auditory space. Thus, it is difficult to conceive that these binaural units possess sufficiently restricted receptive fields to signal information about narrow regions of auditory space. Moreover, in some units, changes in the average intensity of the acoustic signal can significantly shift the region of binaural sensitivity (17, 19). Thus knowledge of the firing rate of these kinds of binaural can provide little detailed information about the *finite* locus of the sound source.

Rose and his colleagues (15) have described another type of response function using binaural low-frequency acous-

tic signals (<3 kHz, see Fig. 4). The firing rates of these units are sensitive to interaural phase or time differences resulting in sinusoidal response functions with the maximum discharge occurring at one binaural time difference and minimum discharge at adjacent times. Rose's data suggest that the point of maximum discharge is *relatively independent* of both signal frequency and intensity. The point of maximum sensitivity has been called the "characteristic delay" of the unit. The definition of binaural units with a restricted sensitivity independent of signal parameters could certainly provide a neural basis for discrete sound localization. However, inspection of the data indicates that the "characteristic delay" is probably not sufficiently critical for fine localization. First, the point of maximum discharge is really not punctate but extends as a plateau over 100 μsec, or for the cat 80° of auditory space. Second, as Stillman (18) has indicated in the kangaroo rat, the region of "characteristic delay" may occur at a binaural time difference to which the animal could

never be exposed in natural life. For instance, 400 μsec contralateral ear leading, in an animal with a maximum interaural disparity of 100 μsec.

Single unit sensitivities to interaural intensity differences are also not sufficiently precise to allow the individual elements to function as detectors of discrete localization using intensity cues. Stillman (19) classified three types of interactions to binaural intensity disparities in inferior colliculus of kangaroo rat. In the first two types, binaural interaction took the form of a gradual change in firing rate over a 10–30 dB interaural intensity range, similar to the response functions seen with interaural time disparities. In one of the intensity types, the portion of the ΔI continuum over which the unit was sensitive shifted with overall stimulus strength while in the other type, ΔI sensitivity was independent of overall intensity. The third response type discharged maximally at certain interaural values producing a peaking function similar to that described by Rose for "characteristic delay" units. The peak is, in fact,

Figure 2. Relation of environment to nervous system showing point in stimulus field connected to neuron in central nervous system. The neurons are organized to rerepresent the stimulus environment.
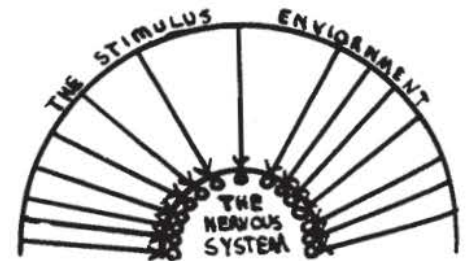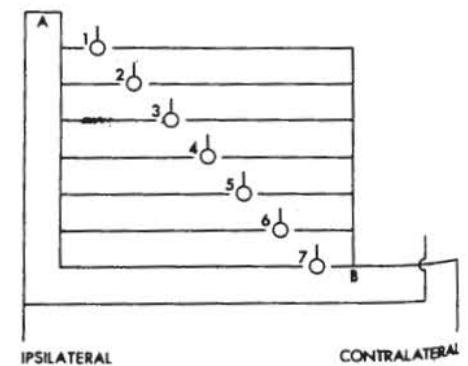

Figure 3. Jeffress proposal for coding of binaural time differences using convergence of inputs on individual neurons. Units 1 through 7 are activated when the time of arrival at the two ears has the appropriate relationship (From Erulkar (4).)

IPSILATERAL   CONTRALATERAL

a plateau extending over 5–10 dB making it unlikely that the discharge rates of these units could be used for discrete localization.

Would the response functions of binaural units be any more precise if both time and intensity cues could be combined as occurs in natural free field stimulation in distinction to the laboratory methods of using insert earphones? Leiman and Hafter (11) recently explored this problem using multiple speakers displayed around an animal's head in an anechoic chamber. Their results again showed gradual changes in discharge as a function of speaker position with the most abrupt slopes occurring across the midline or 90° position. Thus, combining intensity and time cues does not significantly increase the resolving power of units to detect signals in a restricted locus of auditory space.

An alternative hypothesis, first formulated by von Bekesy (22) and then enlarged on by van Bergeijk (21), assumes that information about a sound's locus is contained in the difference in discharges between cells sensitive to "right-sided" inputs and cells sensitive to "left-sided" inputs. Van Bergeijk specified that these two cell types were segregated into two anatomical groupings, the right and left superior olivary nuclei, and comparison of the relative activities of the two nuclei would be made at some higher

auditory station (Fig. 5). (An image that comes to mind is of the goddess Minerva assessing the relative balance of the pans on her balance.) Thus, an individual cell can provide information only about the laterality of acoustic input while the ensemble provides details for the finite locus of the signal. For instance, units in the right superior olive are more active then those in the left nucleus to signals originating from the left of midline and the magnitude of the difference increases as the signal becomes more lateralized. The situation is reversed when signals originate from the right midline with the left superior olivary units being more active than those in the right nucleus.

Hall (9) examined details of this model by mathematically lumping all of the single unit responses derived from experiments on medial superior olive in cat to interaural time disparities. The population analysis provided suprisingly precise predictions of auditory localization allowing for the detection of changes in interaural time disparities of 5–10 μsec and of time/intensity trading ratios of 2dB/20 μsec. Both of these figures are remarkably close to psychophysical data derived from human subjects. It must be emphasized that the population model of von Bekesy and van Bergeijk requires a neural mechanism to compare the relative levels of activity in the paired olivary nuclei. Van Bergeijk thought the comparison would
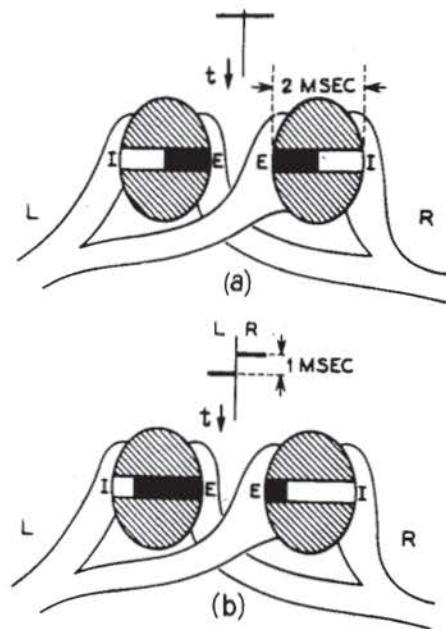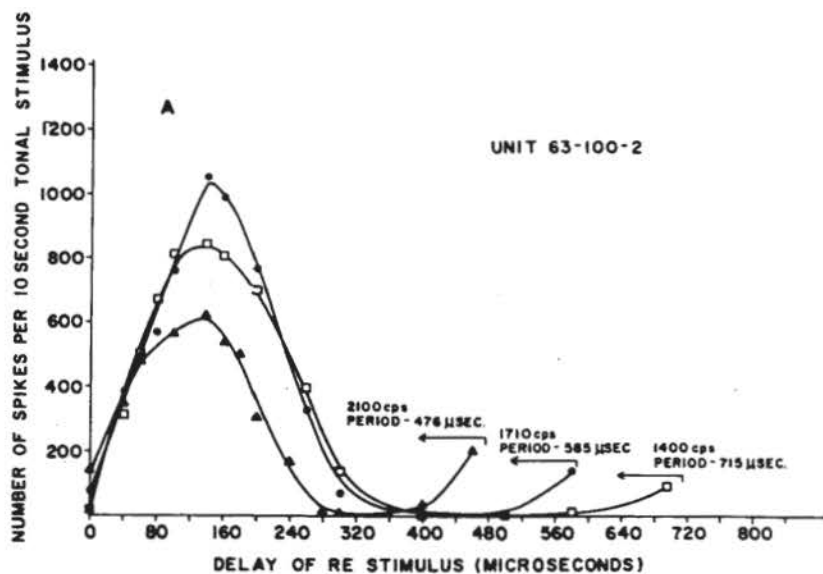

Figure 5. *a*: Simultaneous, equal-intensity clicks excite equal areas (black) in the two nuclei, resulting in a center image. *b*: When one click leads, it causes a larger excited area on the contralateral side, resulting in an off-center image. Inhibited area white, unaffected area hatched.

occur at some higher level of the auditory pathway where the inputs from the two olivary nuclei would interact. The response characteristics of these comparator units were not stipulated but certainly should be different and preferably more selective to limited parameters of binaural stimulation than occurs at superior olive.

Dr. Don and I examined binaural interaction at two higher levels of the auditory pathway, the inferior colliculus and medial geniculate body (17), and found essentially the same kinds of sensitivities to binaural stimulation as described by Hall for superior olive. Furthermore, when we mathematically lumped our medial geniculate unit data, the response function of the population was remarkably similar to the population data obtained at the superior olive by Hall (Figs. 6, 7). Thus, the same information which is initially encoded at superior olive is preserved in a relatively unaltered form through the inferior colliculus and medial geniculate.

Perhaps comparator neurons are at auditory cortex and rely on the corpus callosum to provide the neural pathways for intergrating activity from the paired medial geniculate nuclei. My own expectation is that auditory cortical neurons are no more selective for spatial sensitiv-

Figure 4. Periodic discharge curves generated by unit to binaural stimulation at three frequencies when the right ear tone was successively delayed with respect to that delivered to the left ear. Intensity of the stimuli: 48 dB SPL for 1,400 and 1,710 cycles/sec; 50 dB SPL for 2,100 cycles/sec; duration: 10 sec. Note that the period of each curve equals that of the stimulating frequency but a maximum response for each occurs at the same delay of 140 μsec. *Abscissa*: delay of the right ear stimulus in microseconds. (From Rose et al. (15).)
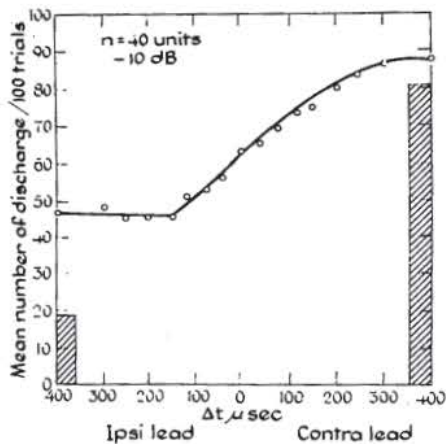
Figure 6. Mean discharge frequency of 40 medial geniculate units from 12 animals as a function of interaural time differences (Δt) tested at the same intensity level. The variance was approximately 40 discharges/100 trials at each of the Δt values tested. Points have been fitted by a smooth curve. (From Starr and Don (17).)
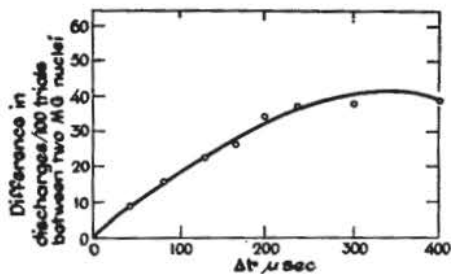

Figure 7. Difference in discharge rates between the two medial geniculate nuclei as a function of the interaural time differences. Each plotted point is obtained by subtracting equivalent points along the average discharge function of the 40 units plotted in Fig. 6 (i.e., discharges/100 trials, 40 μsec, etc.). (From Starr and Don (17).)

ity than are subcortical units and alternative mechanisms for comparing the levels of activity in the paired auditory nuclei must be explored.

There is both anatomical and physiological (6, 13, 14) evidence of lateralized sensorimotor interactions at multiple sites along the auditory pathway affecting middle ear muscle activity (brainstem), pinna, and eye movements (midbrain), and orienting and arousal responses (thalamus). These motor behaviors are sensitive to binaural features of the acoustic input and can occur independent of the presence of cortical or even thalamic structures (1, 5). For instance, middle ear muscles respond more to ipsilateral than to contralateral inputs (12), whereas pinna, head, neck, and eye movements directed to one side occur with stimulation of the contralateral inferior colliculus nucleus (18) or medial geniculate nucleus (20). It would appear, therefore, that the motor systems active in binaural behavior are organized to effect lateralizing movements. We would suggest that the comparator of activity in the paired sensory nuclei, postulated by von Bekesy and van Bergeijk, may not be another sensory structure at all but, rather, is the balance between the outputs of the motor systems which direct the animal to move to the right or left. The similarity of the population's activity in medial geniculate defined in the present experiments to that obtained by Hall in superior olive and hinted at by Benevento et al. (2) in inferior colliculus indicates that the same information about sound position is present at several nuclei of the auditory pathway. This information may be utilized for the different levels of sensorimotor integration relevant to specific kinds of binaural behavior. Thus, superior olivary activity influences middle ear muscle responses; inferior colliculus activity influences eye and pinna movements, and medial geniculate activity influences orienting movements of the head and body. Conscious awareness of sound localization might merely be a secondary consequence of the differential activation of these lateralizing motor systems (16). We view binaural behavior as a serial system beginning perhaps with lateralized middle ear muscle contractions and culminating with the concept of "to the right."▣

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