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Responses of Squirrel Monkey (*Samiri sciureus*) Medial Geniculate Units to Binaural Click Stimuli

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THE NEURAL BASIS for sound localization has been examined with single-unit techniques at various levels of the auditory pathway (superior olive (19, 22, 23, 31, 35, 40), lateral lemniscus (11), inferior colliculus (9, 15, 20, 34, 38), medial geniculate (1, 2, 6), and auditory cortex (12, 24)). The general conclusion to be drawn from these studies is that there are neurons sensitive to features of acoustic signals relevant for localization including interaural intensity, time, and phase differences at all levels of the pathway. We have undertaken a single-unit analysis of binaural processes at the medial geniculate in the squirrel monkey, an animal for which we have also obtained psychophysical measures of binaural performance on a lateralization task (14) using dichotic clicks differing in interaural time or intensity parameters. Our aim is to relate in the same animal both behavioral and single-unit data to describe further some of the neural mechanisms underlying binaural behavior.

METHODS

Experiments were performed on 12 squirrel monkeys (*Samiri sciureus*) anesthetized with pentobarbital sodium (20 mg/kg initially and 6 mg as supplemental doses were needed). The animals were placed in a stereotaxic holder and a 3-mm-diameter trephine hole drilled at A4.0, L6.0. The dura was removed and the exposed brain covered by an agar solution. A screw was then mounted on the frontal bone with dental acrylic and clamped onto the stereotaxic frame. This allowed the ear bars and mouth piece to be removed to facilitate the presentation of acoustic signals without affecting stereotaxic relationships. The animal was moved into a sound-attenuating chamber, where body tem-

perature was maintained between 37 and 39 C.

Single-unit activity was recorded with tungsten microelectrodes (100- to 200-megohm impedance at 60 Hz) controlled by a hydraulic microdrive from outside the experimental room.

Acoustic signals were presented from 0.5-inch condenser microphones (Bruel and Kjaer) placed snugly against the opening of the external auditory canal. The microphones, biased with 200 v, were activated with square-wave pulses (150 v in amplitude and 250 μ sec) to generate clicks whose waveform, as monitored free field by a 0.25-inch Bruel and Kjaer microphone 1.45 mm away, is shown in Fig. 2 of the companion paper (14). An attenuator in series with the square-wave generator allowed intensity adjustment in 1-dB steps below the maximum of approximately 60 dB re normal human threshold. An estimate of acoustic crossover was made in one monkey by placing a bipolar recording electrode (125- μ wires separated vertically by 0.5 mm) in one cochlear nucleus and recording the responses evoked to ipsilateral and then to contralateral clicks of graded intensity. There was a shift in the intensity functions of the evoked responses by 30–35 dB between contralateral and ipsilateral stimulation.

The procedure for generating binaural click signals with varying interaural time (Δt) and intensity differences (ΔI) is shown in Fig. 1. There was independent control of click rate, number of click trials, interaural time (Δt), and interaural intensity (ΔI) differences.

Electrical activity recorded by the microelectrode was amplified (band pass 7 Hz–10 kHz) and monitored both by loudspeaker and an oscilloscope in the adjacent room. Single-unit discharges were converted to standard square-wave pulses by a Schmitt trigger. Both the electrical activity and the Schmitt trigger pulses were recorded on magnetic tape along with event markers synchronous with the earphone stimuli for subsequent analysis by computer.

The microelectrode was lowered into the medial geniculate body while presenting clicks

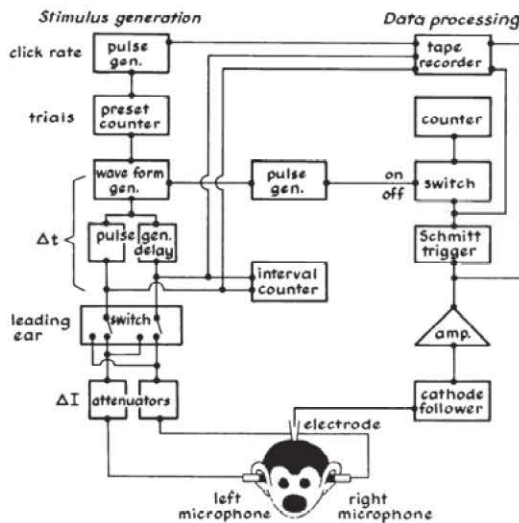


FIG. 1. Block diagram showing stimulus generation and data processing procedures.

at 1/sec. Since this structure in the squirrel monkey measures only 2.5 mm in the lateral dimension and 2.0 mm in the rostral-caudal, several penetrations (an average of four) were required to locate it. When a unit was encountered, its responsiveness to monaural and binaural signals was separately assessed by summing the number of unit discharges evoked by 100 click trials. For spontaneously active units the sample period was 5–25 msec following each click. The click rates varied from 32 to 0.5/sec. The faster rate corresponded to that employed in the behavioral experiments (14). Our standard procedure was to select Δt intervals of 0, 40, 80, 120, 160, 200, 240, 300, and 400 μ sec and to alternate the ear receiving the initial click. The intensity level selected was usually -10 dB below the reference level. If binaural sensitivity was not evident, longer Δt intervals (up to 9,000 μ sec) were scanned. This process was repeated for other intensity levels (0, -20 , -30 , -40 dB). The unit's responses to interaural intensity differences (ΔI) when Δt was 0 μ sec were then examined by keeping the intensity of one of the inputs constant while the other input was raised or lowered. Our protocol obviously biased us to study Δt interaction more thoroughly than ΔI interaction since many units were lost before the entire protocol could be completed.

The depth of each unit encountered along a pass was recorded. At the end of a successful penetration, cathodal current was passed through the microelectrode to mark the pass. The agar was removed from the exposed cortex, the wound closed with clips, and the animal

given 150,000 U of procaine penicillin intramuscularly and allowed to recover. The monkey could then be used the following week in the same manner to study the contralateral medial geniculate nucleus. At the end of the second experiment the animal was anesthetized and perfused, the ears examined for intactness of the tympanic membrane or signs of otitis media, and the brain removed for subsequent histological preparation to define the electrode penetrations.

We will also report on studies from five other squirrel monkeys whose single-unit responses in inferior colliculus to the same types of binaural signals were analyzed. The experimental procedures employed were identical to those described for medial geniculate except for changes in the stereotaxic coordinates.

The unit data recorded on tape were available for additional study such as latency measurements, poststimulus time histograms, and analysis of trial-by-trial responses.

RESULTS

Monaural response

Two hundred and five units comprised the study.¹ The units were first classified according to their monaural response characteristics (Table 1).

Ninety-three units (45%) discharged once or twice and occasionally up to five times at short latency (6–30 msec) to monaural clicks. Their responsiveness varied as a function of the ear that was stimulated; 38 discharged in response to monaural clicks presented to either ear. The requirements for this classification were that the ratio of the number of discharges evoked by contralateral stimulation over the number of discharges evoked by contralateral + ipsilateral stimulation was

¹ One unit could not be securely classified and was omitted in Table 1; thus the total shown in Table 1 is only 204 units.

TABLE 1. Medial geniculate monaural response classification

| | | Contra Ear | | | Total |
|----------|-------|------------|-----|---|-------|
| | | + | – | 0 | |
| Ipsi Ear | + | 38 | 0 | 0 | 38 |
| | – | 8 | 106 | 1 | 115 |
| | 0 | 47 | 1 | 3 | 51 |
| | Total | 93 | 107 | 4 | 204 |

+ = excitatory, – = inhibitory, 0 = no apparent effect.

between 0.1 and 0.9. Eight discharged to monaural clicks presented to the contralateral ear but were suppressed with ipsilateral input; and 47 units discharged in response to contralateral clicks while ipsilateral stimulation had no apparent effect. Both spontaneous discharge rate and click intensity were variables that influenced monaural classification. If the spontaneous discharge rate were slow, 100 trials were often inadequate for clarifying whether an ipsilateral stimulus caused a suppression of activity or was without effect. When this uncertainty existed, the unit was arbitrarily classified as being unresponsive to an ipsilateral stimulus (18 of the 47 units in this class). Click intensity was critical in five cells for revealing dichotic sensitivity. For instance, unit CR 6 was sensitive to only a contralateral stimulus at 0 and -30 dB and dichotically sensitive at -10 and -20 dB. Since monaural responses to two or more intensity levels were examined in only about one-sixth of the population studied, our estimate of units sensitive to dichotic inputs must be low.

Click repetition rate did not affect the monaural response classification. In general, the ability to discharge to each click was inversely related to click repetition rate. The maximum following observed was at 50/sec, with most units being unable to sustain following greater than 8–10/sec. There were some units, however, that were better able to follow at click rates between 8–12/sec compared to both slower (1–5/sec) and faster (12–16/sec) rates.

Monaural latencies were similar to other reports (2, 6, 18) ranging between 6 and 30 msec, with the mode falling between 8 and 11 msec. The relative latencies of ipsilateral and contralateral responses were examined in 13 units responsive to both inputs. For five of these units, latencies to ipsilateral and contralateral clicks were within 0.25 msec of one another; for the remaining eight units, latencies were from 0.5 to 1.75 msec earlier in response to ipsilateral than to contralateral clicks. During binaural stimulation ($\Delta t = 0$ μ sec), three of the units assumed the latency of the ipsilateral input while five units assumed the latency of the contralateral input. Figure 2 shows re-

sponses in the form of a dot display from one of the latter units demonstrating the latency changes.

One hundred and six units (52% of the sample) had a suppression of spontaneous activity following a monaural click to either ear. There might be occasional discharges in this period, but such discharges did not account for more than 15 of the total discharges evoked in the course of the 100-click trials. When activity resumed, it had a characteristic pattern, as described by others (4, 18), of brief bursts of firing at multiples of approximately 100 msec superimposed on a biphasic, positive-negative slow-wave complex (Fig. 3). The discharge pattern is most likely specific to transient acoustic stimuli as light flashes were without effect in 10 units tested with both clicks and light stimuli; steady tonal signals in the units' excitatory region could evoke sustained discharges without evidence of the periodic groupings seen with clicks. There were several features of the late periodic discharge that can be noted. 1) The click rate needed to be relatively

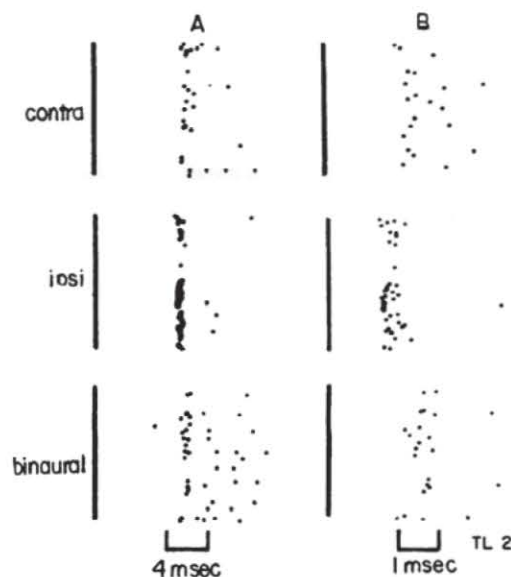


FIG. 2. Dot display of responses for a medial geniculate unit excited by either ear. Response to 100 clicks in each photograph. A: slow time base; clicks presented at the solid line to the left. B: fast time base; clicks presented 8 msec prior to solid line at the left. Interaural delay 0 μ sec for the binaural presentation. Note that responses to ipsilateral input occur about 1 msec earlier than to either contralateral or to binaural input.

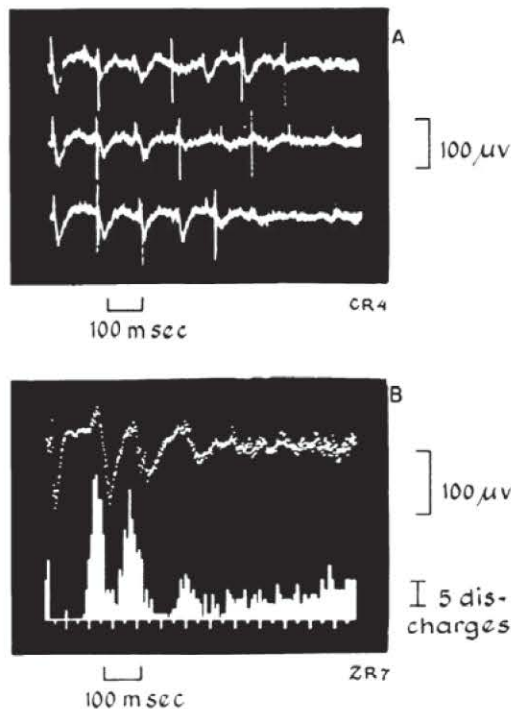


FIG. 3. *A*: individual traces showing unit CR4 discharging periodically in relation to a positive/negative slow-wave complex. *B*: same phenomena for unit ZR7; slow-wave responses to 100 clicks averaged in the top trace, the poststimulus time histogram of the spikes below. Medial geniculate; positivity at the recording electrode is up.

slow (approximately 1/sec) to elicit the periodic activity. Rates faster than 4/sec were accompanied by a suppression of unit activity. 2) There was a tendency for the contralateral input to elicit more clearly the periodic activity than the ipsilateral input. 3) Click intensity did not appear to be a factor as long as the unit's threshold for the periodic firing was exceeded. 4) The degree of synchrony of the late discharges would often fluctuate over a 15-min period in contrast to the constant occurrence of the initial period in which the unit was suppressed. Alterations in the level of anesthesia cannot entirely account for variations in the late discharges as similar fluctuations were encountered in one animal studied in an unanesthetized but paralyzed (gallamine triethiodide) condition. And 5) the occurrence of long-latency periodic discharges was not solely a feature of units with an initial period of suppres-

sion following clicks as it was seen occasionally in some of the 93 units securely driven at short latency by monaural clicks.

The classification of the remaining six units was diverse: three were unaffected by clicks presented to either ear, one was suppressed by contralateral stimulation with ipsilateral stimulation having no effect, one was suppressed by ipsilateral input while contralateral stimuli were without effect, and one unit could not be classified.

Responses to binaural time differences (Δt)

Of the 205 cells studied, 100 were systematically examined for sensitivity to Δt parameters. The measure employed was the total number of discharges occurring in an interval from 5–25 msec after each binaural click for a total of 100 trials. In units suppressed by monaural clicks, discharges were summed during one of the cyclic periods of activity (usually the initial epoch extending from 70–120 msec). Table 2 summarizes the types of binaural responses obtained, and examples are shown in Fig. 4. Judgments were made by visual inspection of the binaural response functions. The sample studied cannot be considered representative of the population of units encountered in medial geniculate body as most of the units inhibited by both ipsilateral and contralateral clicks were not examined in detail (compare Tables 1 and 3). This selection was intentional as binaural sensitivity was difficult to demonstrate in this class of units (see Table 3). Fifty-nine units were sensitive to binaural time differences and showed a differential response to binaural clicks as a function of the Δt interval (Fig. 4*A*). Eleven units were

TABLE 2. *Medial geniculate binaural response classification*

| | Type (see Fig. 4) | n |
|----------------------|-------------------|----|
| Binaurally sensitive | A. Δt | 59 |
| | B. facilitated | 11 |
| | C. depressed | 2 |
| No binaural effect | D. monaural | 28 |

n = 100 cells.

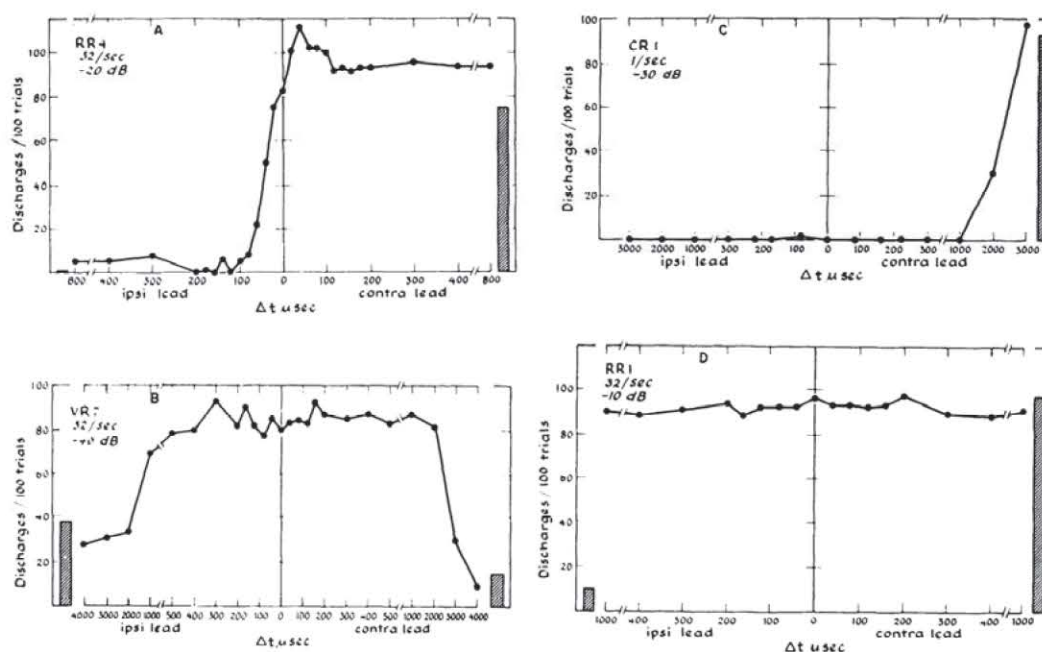


FIG. 4. Four principal types of binaural responses to interaural time differences (Δt) encountered in the present experiment. Bars at edges of each graph in both this and all subsequent figures represent the level of activity evoked by monaural stimulation. See text for description.

facilitated above their monaural response levels relatively independent to the Δt parameters (Fig. 4B). Two units showed the converse: a depression of responses below monaural levels relatively independent of the Δt parameters (Fig. 4C). And, 28 units were insensitive to binaural time-varying signals (Fig. 4D). When binaural sensitivity was examined as a function of the monaural-click groups (Table 3), it was apparent that all had a high proportion (ranging from 67 to 100%) of binaural sensitivity except for the class of units suppressed by monaural clicks. Of the 12 units in this class that were systematically examined, only 1 showed evidence of binaural interaction.

Characteristics of binaural interaction

Figure 5 is an example of a unit sensitive to the Δt parameters of a binaural click. The unit responded at short latency (7–8 msec) to a contralateral click and had a suppression of spontaneous activity from 7–20 msec after an ipsilateral stimulus. The number of discharges evoked for 100 click pairs varied in an orderly fashion as a

function of the Δt interval ranging from almost complete suppression when the ipsilateral ear led by 100–200 μ sec to a maximum number of discharges when the contralateral ear led by 300 μ sec. The function over the intervening Δt intervals measured in 20- μ sec steps appeared remarkably continuous. The poststimulus time histograms indicate that the change in discharge frequency was not accompanied by changes in the unit's latency or firing pattern. Note that discharges did not entirely reappear even when the ipsilateral signal led at intervals as long as 1,600 μ sec.

The shape of the Δt functions in binaurally sensitive units varied. In general,

TABLE 3. Binaural sensitivity as a function of monaural responses*

| | | Contra Ear | | |
|----------|---|------------|------|-----|
| | | + | – | 0 |
| Ipsi Ear | + | 28/36 | NT | NT |
| | – | 6/6 | 1/12 | NT |
| | 0 | 35/43 | NT | 2/3 |

+ = excitatory, – = inhibitory, 0 = no apparent effect, NT = not tested. * Number of binaural cells/number of cells tested.

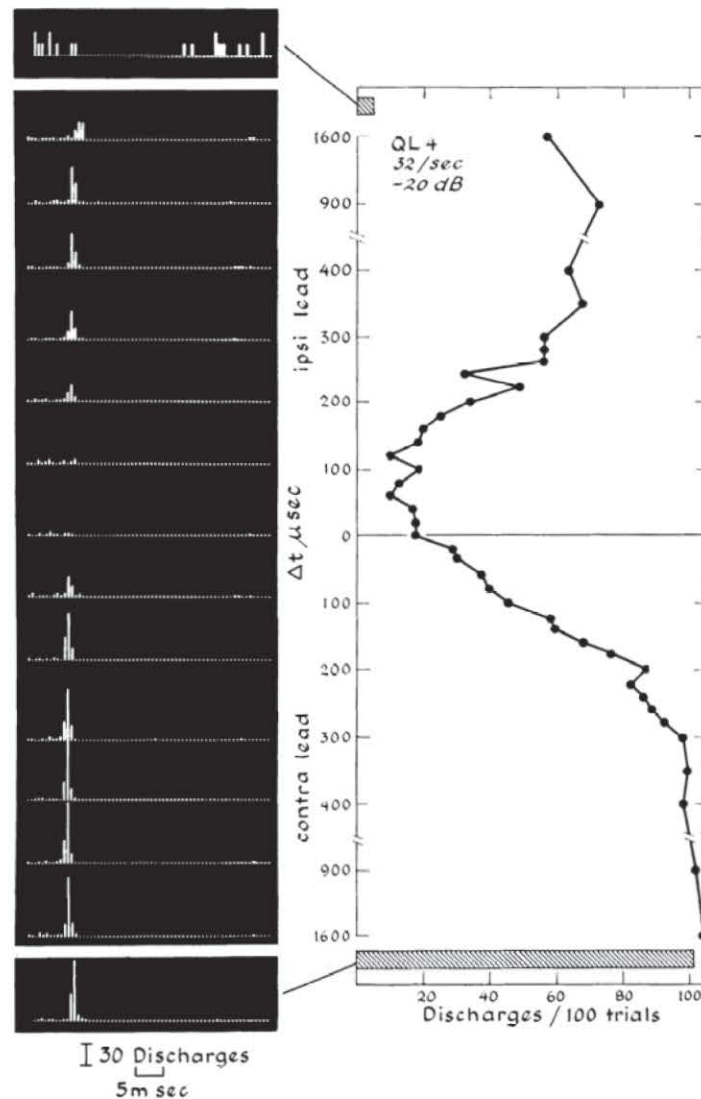


FIG. 5. Poststimulus time histograms of 100 presentations (*left*) and binaural response function for interaural time differences (Δt) (*right*) for unit *QLA* in medial geniculate. Histograms are aligned with the appropriate portion of the Δt function. The amplitude bar represents one discharge for the top histogram. Note that the effect of varying Δt is on the number of discharges and not on the discharge pattern or latency.

all had portions of the Δt continuum over which a gradual change in responding could be defined. Selected examples of the distribution of binaural sensitivity along the Δt continuum are shown in Fig. 6. All of the units were tested at the same intensity level (-10 dB).

Click intensity could affect both the shape of the Δt function and the portion of the Δt range over which graded inter-

action occurred. In 20 of the 29 units studied at two or more intensities, the region in which there is a change in discharge shifted toward the ipsilateral ear as intensity was raised (three examples are shown in left side of Fig. 7). All of these units had response functions that changed in a smooth manner over a limited portion of the Δt range. Of the nine units not showing a shift with changes in click in-

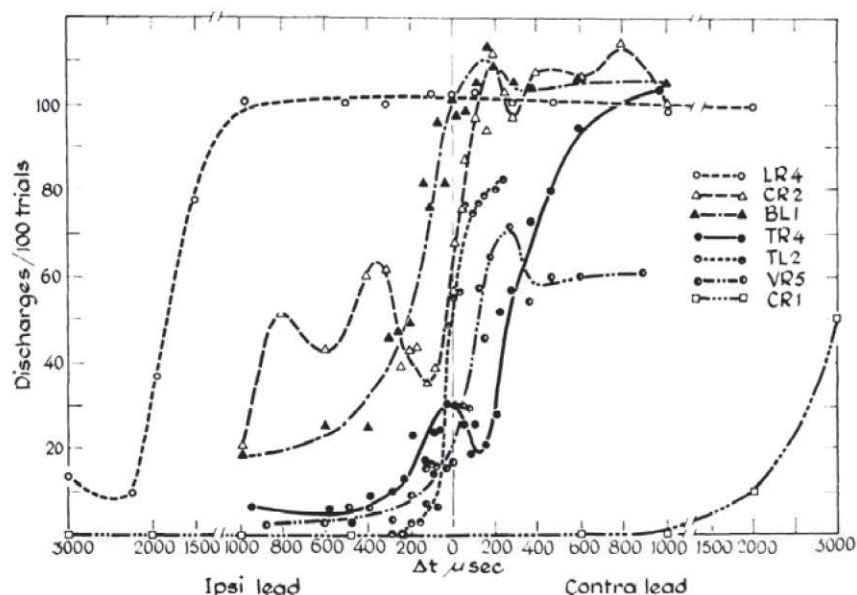


FIG. 6. Binaural Δt functions of seven medial geniculate units from the population studied showing their distribution across the Δt continuum.

tensity, two had sinusoidal Δt functions (Fig. 7, top right), two showed binaural interaction at only one of the intensity levels tested (Fig. 7, bottom right), four had Δt functions of complex form that extended over a wide range of Δt values (Fig. 7, middle right), and only one unit had a response function that changed in a smooth fashion over a restricted portion of the Δt continuum.

The effect of click rate on Δt interaction was examined in 10 units. For eight of these units, the number of discharges decreased as click rate increased, but the portion of the Δt continuum over which interaction occurred as well as the shape of the function remained unchanged (Fig. 8, top). If the click rate were close to the unit's ability to follow, the number of responses evoked might be too small to adequately judge whether interaction occurred. In the other two units, binaural interaction was insignificant at slow click rates (4/sec) and only became evident when the click rate increased to 16/sec (Fig. 8, bottom).

An examination of discharge patterns during the course of 100 click trials revealed some inconsistencies between the beginning and end of the click train in

four units tested at 32 clicks/sec. Three units (*R-R4*, *R-R5*, *C-R2*) discharged only occasionally during the first 5–10 click presentations relatively independent of the Δt condition, though the remainder of the click trials demonstrated clear-cut Δt sensitivity. One unit (*T-R7*) ceased discharging for several hundred milliseconds during the train of clicks independent of the Δt parameters. Twelve other units, however, did not show any particular trend in discharge pattern during the train of stimuli.

Binaural intensity differences (ΔI)

Sensitivity to binaural intensity differences was assessed in 37 units. Our procedure was to set $\Delta t = 0$ μ sec and to change the intensity of one of the clicks (usually decreasing the ipsilateral side) in 2-dB steps while maintaining the intensity of the other click at a constant level. The number of discharges occurring for 100 click trials was summed in a manner similar to the Δt measurements. Twenty-eight units sensitive to binaural time differences were also sensitive to binaural intensity differences. In 19 of these units there were sufficient data to compare relative sensitivities by superimposing the two response functions on the same graph (Fig. 9). A close approxi-

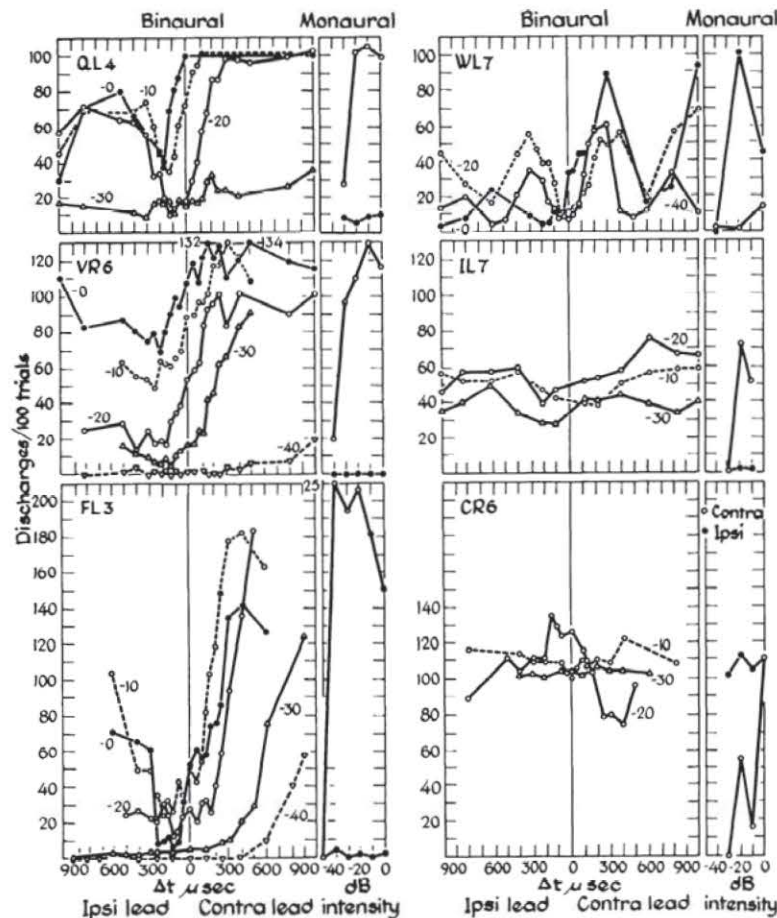


FIG. 7. Effect of click intensity on the binaural Δt function of six medial geniculate units. The three units on the left side show a shift of Δt sensitivity toward the ipsilateral ear as click intensity is increased; the three units on the right side show no orderly change. The monaural intensity function is shown to the right of each Δt graph. Details are in the text.

mation of the functions was obtained with values ranging from 1 dB = 5 μ sec (3 units) to 1 dB = 100 μ sec (1 unit) with the majority of units showing values between 1 dB = 10–20 μ sec (13 units). The modal values of 1 dB = 10–20 μ sec correspond to the values obtained for time-intensity relationships in human lateralization experiments (30). The effect of click intensity on relative binaural time and intensity sensitivities was not systematically explored. However, in one well-studied unit click intensity did differentially effect binaural time and intensity sensitivities. The data from this unit are graphed in Fig. 10 and show that a decrease in click intensity was accompanied by a much smaller shift in sensitivity to binaural intensity differences than to binaural time differences.

Five units were clearly shown to be sensitive to binaural intensity differences but to be insensitive to binaural time differences. Data from one of these are graphed in Fig. 11 (lower). Since our protocol biased us to explore ΔI interactions less completely than Δt interactions, we feel the estimate of the proportion of units sensitive to only binaural intensity difference is low.

Finally, there were four units that were sensitive to binaural time differences but insensitive to binaural intensity differences (one of these units is also in Fig. 11 (upper)). Thus, our results support, to some extent, the concept of two separate neural mechanisms for handling interaural time and interaural intensity differences (9, 41). While most units tested were sensi-

tive to both time and intensity parameters, a significant proportion was sensitive to just one of these features.

Anatomical correlates

There did not appear to be any orderly relationship between a unit's monaural or binaural response characteristics (described in Tables 1 and 2) and its location in the medial geniculate nucleus. The only possible suggestion of cell clusters occurred with units in which spontaneous activity was initially suppressed by monaural clicks and then recurred at 100-msec periods. They were the only kind of units detected on passes located at the rostral and medial edges of the nucleus.

Detection of apparent motion of sound source

Thirty units in three additional animals were tested for sensitivity to the apparent direction of sound movement. The signals were trains of binaural clicks whose Δt interval changed in a stepwise manner from a maximum value (Δt_{\max}) on click 1 to a minimum value on clicks 10 and 11 (Δt_{\min}) and then back up again to the Δt_{\max} value at click 20. The microphone that received the lead stimulus of the binaural pair was reversed between the 10th and 11th steps. We heard the signals as a train of clicks that moved in a smooth fashion from one side of the head to the other. The click rate could be varied from 0.5 to 20/sec to influence the velocity of apparent motion. The direction of movement (right to left or left to right) was determined by the ear that received the leading stimulus on the first click. Δt_{\max} was usually between 400 and 1,000 μ sec and the magnitude of each Δt step was $1/10$ of the value of Δt_{\max} . A computer was used to quantify unit responses to the signals. The number of discharges occurring 5–25 msec after each binaural click pair was stored in the memory location appropriate to the order of the click in the train (bin 1 represented click 1, etc.). Fifty repetitions of the click train were summed on the computer for movement in each direction. Visual inspection of the histograms did not reveal sensitivity to the direction of movement of the sound source in any of the units tested. The units all showed mirror symmetry of

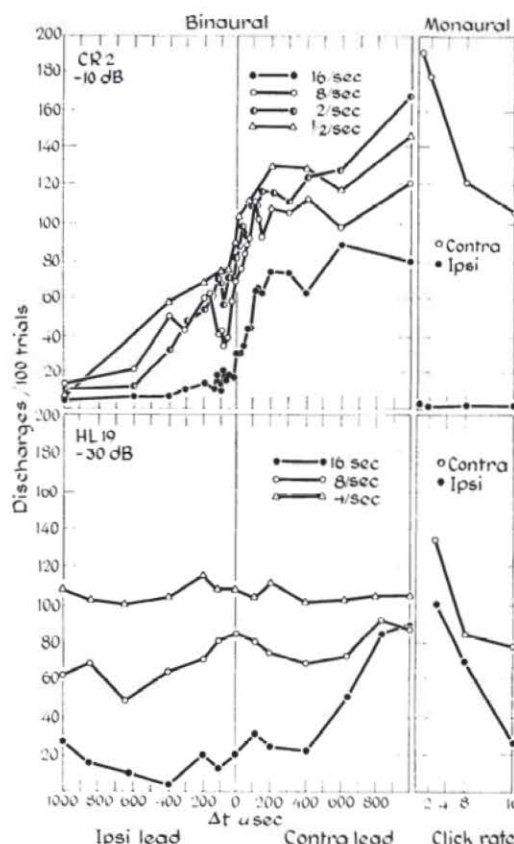


FIG. 8. The effect of click rate on the binaural Δt functions of two medial geniculate units. The monaural rate function is shown to the right of the Δt graphs. Note that number of discharges decreases as the click rate increases. Unit HL 19 shows sensitivity to the Δt parameter only at the fastest click rate (16/sec).

the response reflecting the unit's sensitivity to a particular range of Δt intervals independent of the apparent direction of sound movement. Our results differ from those of Altman et al. (6) who detected directional sensitivity in approximately 22% of units in the medial geniculate of chloralose-anesthetized cats. The failure to replicate Altman's results may be due to differences in the species of animals used in the two experiments (monkeys vs. cats) or in the anesthesia employed (pentobarbital vs. chloralose).

Inferior colliculus

Seventy-eight inferior colliculus units in five animals were studied to monaural and binaural click signals in a manner similar to that used in the medial geniculate study

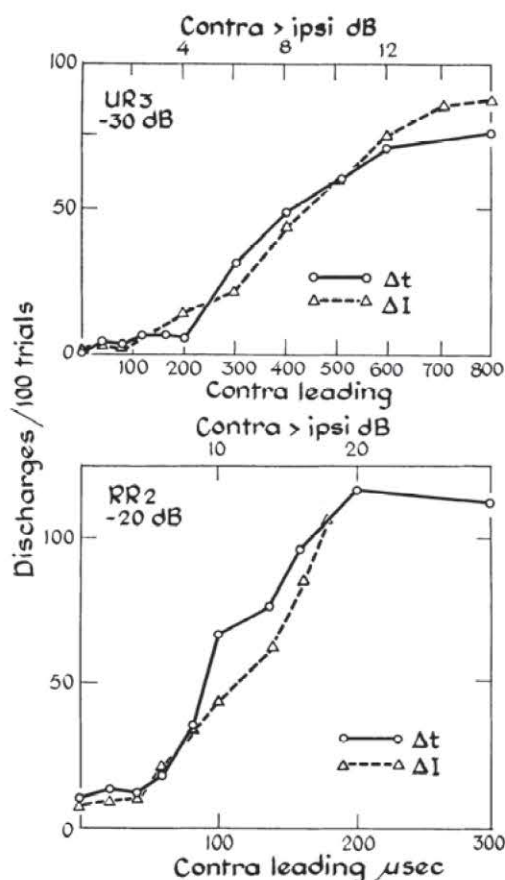


FIG. 9. A comparison of binaural Δt and binaural ΔI functions for two units. The abscissa has been adjusted to achieve superimposition of the two functions with values of 2 dB = 100 μ sec for the unit graphed at the top of the figure, and 2 dB = 20 μ sec for the unit graphed at the bottom.

so that binaural processes might be compared in these two nuclei. A major difference between the two auditory sites was in the class of units suppressed by monaural clicks to either ear. The majority of units in medial geniculate (53%) was of this type but only 10% of the inferior colliculus units could be so classified. Furthermore, the periodic firing pattern that characterized these units in medial geniculate was never observed in any inferior colliculus cell. Table 4 summarizes the relative frequency of the different monaural response categories encountered in inferior colliculus.

Responses to binaural Δt signals were assessed in 48 of the 78 inferior colliculus units. Twelve units (25%) were sensitive

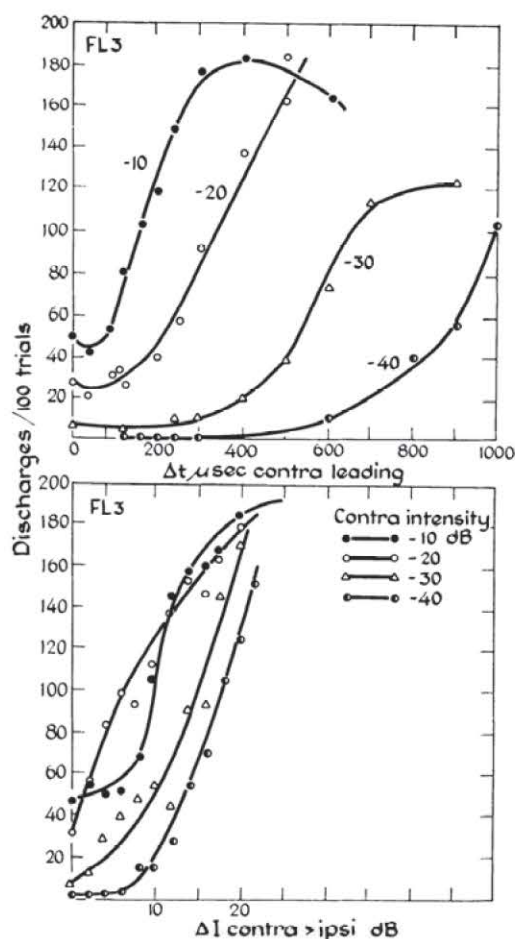


FIG. 10. Effect of a 40-dB range in click intensities on binaural Δt (upper graph) and ΔI (lower graph) functions in unit FL3. The scale for intensity was adjusted so that the Δt and ΔI functions were superimposed at -10 dB. Note the large shifts in Δt functions compared to ΔI functions with changes in overall click level.

to binaural time differences and showed a differential response to binaural clicks as a function of the Δt interval. The shapes of the binaural functions were similar to those observed from medial geniculate units. Five units (10.5%) were facilitated above their monaural response levels relatively independent of the Δt parameters. Two units (4%) showed a depression of responses below monaural levels relatively independent of the Δt parameters. And 29 (60.5%) units were insensitive to time varying binaural clicks employed. The high proportion of monaural units may reflect our use of just one type of acoustic

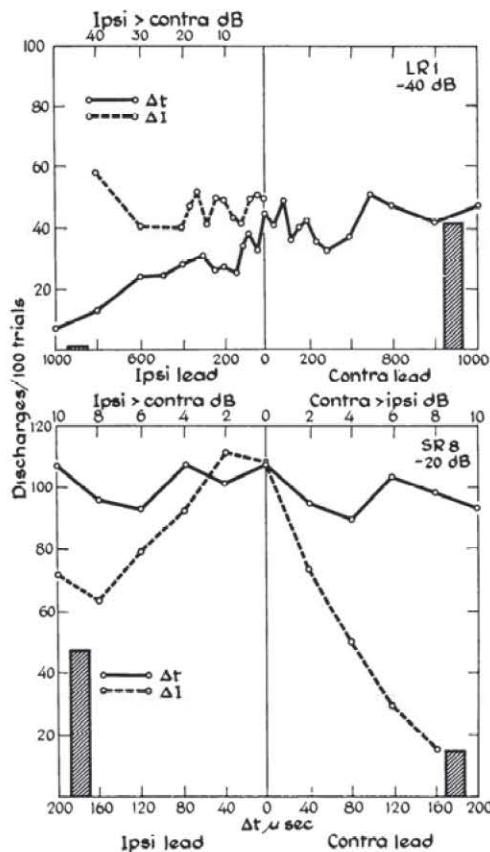


FIG. 11. Two medial geniculate units, one sensitive to Δt alone (above) another to ΔI alone (below).

signal (i.e., click), as Stillman (37) has found in the kangaroo rat that more than 90% of inferior colliculus units are binaurally sensitive if a variety of acoustic signals (tones, noises, clicks) are utilized.

DISCUSSION

Information about the position of a sound source in space may be contained in the discharge frequency of cells in medial

geniculate body. Forty percent of the units studied in the present experiments showed orderly changes in their firing frequency as a function of the binaural time and/or intensity parameters of the click signals employed. These results are in accord with previous studies demonstrating the relevance of discharge frequency or probability for encoding binaural features of acoustic signals at several levels of the auditory pathway (superior olive (23), lateral lemniscus (11), inferior colliculus (9, 34), medial geniculate body (6), and auditory cortex (12)). The results of the present experiment provide some new details about binaural processes. First, there appears to be two distinct populations of cells in medial geniculate with regard to sensitivity to binaural cues. One group comprising about 55% of the population sampled was insensitive to binaural cues and had a characteristic response to monaural clicks consisting of an initial suppression of spontaneous activity followed by alternating periods of activity and silence at intervals of approximately 100 msec. It must be emphasized that clicks were the only signals used in this study and binaural interaction might have become apparent in this class of units if other types of acoustic signals had been employed. The periodic firing pattern had been shown by Aitkin and Dunlop (3) to be most compatible with inhibitory processes occurring at the level of the medial geniculate body itself. The failure in the present study to detect such a cyclical firing pattern in cells in the inferior colliculus lends support to Aitkin and Dunlop's hypothesis. In contrast, approximately 80% of medial geniculate cells not showing this periodic firing pattern did show sensitivity to binaural time or intensity cues.

In the present study sensitivity to binaural time or intensity differences could be strongly influenced by the parameters of the click signals. In some cells, binaural sensitivity could only be demonstrated at a single intensity or within a small range of click-repetition rates. In other cells the portion of the Δt continuum over which sensitivity could be demonstrated shifted with changes in overall click intensity. The definition of cells with sensitivity to one

TABLE 4. *Inferior colliculus monaural response classification*

| | | Contra Ear | | | Total |
|----------|---|------------|----|----|-------|
| | | + | - | 0 | |
| Ipsi Ear | + | 12 | 0 | 1 | 13 |
| | - | 8 | 8 | 2 | 18 |
| | 0 | 36 | 4 | 7 | 47 |
| Total | | 56 | 12 | 10 | 78 |

+ = excitatory, - = inhibitory, 0 = no apparent effect.

particular Δt range independent of stimulus parameters, the so-called "characteristic delay" described by Rose et al. in the cat (34), was the exception in our experience (only 3 of the 29 cells tested at two or more intensities showed such a characteristic delay). This difference may reflect the choice of signals employed in the two experiments. We used clicks while Rose et al. (34) used steady-state low-frequency tones. Geisler et al. (20) have recently shown marked differences in the coding of binaural cues between the onset response and the sustained discharge portions of the same noise burst at the level of the inferior colliculus in cat.

The overall similarity of the types of binaural interaction found at the medial geniculate level in the present study to those obtained in lower auditory stations (9, 23; *Inferior colliculus* in the present study) is striking and may suggest that the medial geniculate serves merely to "relay" afferent auditory information to cortex. There is evidence from our data, however, indicating a more active role for medial geniculate. First, there were several cells which responded to monaural ipsilateral input at a shorter latency than to monaural contralateral input. These cells were sensitive to binaural time differences and surprisingly showed a suppression of activity when the ipsilateral ear led. Furthermore, when responses did occur, they appeared at the longer latency characteristic of the monaural contralateral input alone. Aitkin and Dunlop (2) also observed two units showing these characteristics in medial geniculate and postulated that monaural stimulation evoked subliminal inhibitory processes as well as excitatory events. With binaural stimulation there was an effective summation of the inhibitory events and a suppression of firing below that evoked by monaural clicks. The present results with varying Δt intervals indicate, in addition, that the inhibitory processes have temporal features that are important for binaural interaction.

Nelson and Erulkar (32), using intracellular techniques, have demonstrated the occurrence of IPSPs in medial geniculate body to click signals. In the present experiments there were occasions in which the

electrode appeared to be closely adjacent to a cell, a recording condition called quasi-intracellular (27), as judged by the occurrence of large-amplitude (10–20 mv) positive cell discharges and slow potential shifts presumed to be synaptic potentials. One well-studied example showed a marked disparity between the frequency of the slow positive-potential shifts and the frequency of spike discharges as a function of Δt parameters of binaural stimulation (Fig. 12). The slow potential shifts representing the cell's excitatory input occurred with almost equal probability across the Δt continuum, whereas the cell's discharge representing its output changed remarkably over the same Δt range (see Fig. 7, unit FL3, for details of spike-count functions).

Relation of unit data to binaural judgments

In a companion study (14) we examined the ability of squirrel monkeys to utilize interaural time or intensity cues for lateralizing trains of binaural click signals. There was a linear relation between correct performance on the lateralization task and the magnitude of the interaural time or intensity differences up to the criterion level (85% correct judgments) at Δt values of 60–180 μ sec and ΔI values of 6–10 dB. Correspondingly, a linear change in discharge frequency over a limited portion of the Δt or ΔI continuum was the most common type of binaural interaction encountered both in the present study as well as in earlier studies at the level of the superior olive (23) and inferior colliculus (9). How do the data fit with two commonly considered neural models of auditory localization, the "place" theory of Jeffress (26), and the population theory of van Bergeijk (10)? In the place theory the locus of a sound source is essentially converted to a locus of activity in the central nervous system. The units described above might serve in this capacity by signaling information about the position of a sound source within their particular Δt or ΔI domain. If these neurons were then arranged in some orderly fashion according to their Δt or ΔI sensitivities, information about a sound's position could be specified by activity of

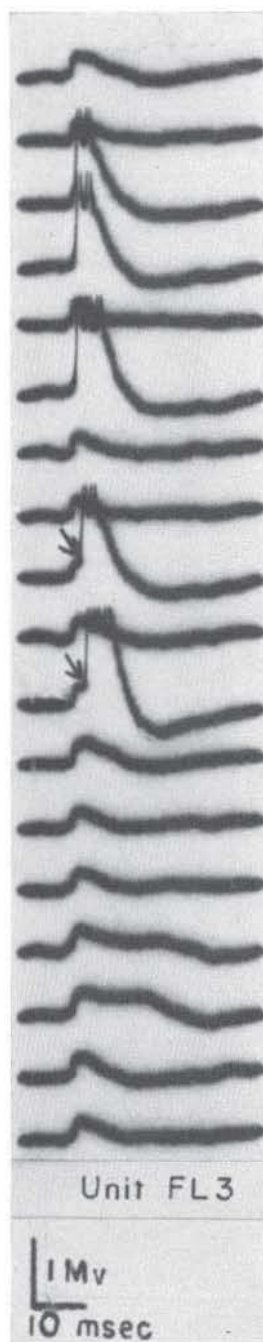


FIG. 12. Quasi-intracellular recordings from unit FL3. Each trace is triggered by a binaural click signal in which the ipsilateral input preceded by 120 μ sec. A slow positive-potential shift occurs with each stimulus, whereas cell spikes occasionally occur. Arrows in two of the trials indicate the point of origin of the spike discharges from the slow potential shifts.

particular groups of cells. Our data raise several problems with this model in addition to those commented on by Goldberg and Brown (22). First, the portion of the Δt continuum over which cells were sensitive ranged from 100 to more than 2,000 μ sec, with the modal value being between 200 and 400 μ sec. It is difficult to conceive of any of these cells functioning as detectors of a specific locus since their Δt sensitivities often exceeded the maximum Δt interval that a squirrel monkey would encounter naturally, i.e., approximately 200 μ sec. Second, the portion of the Δt range to which a unit was sensitive could shift by 50–200 μ sec with changes in overall signal intensity, thus requiring a separate neural system to correlate changes in sound intensity with changes in Δt sensitivity to preserve the cell's capacity to signal a specific sound locus.

An alternative hypothesis, first formulated by von Békésy (8) and then enlarged on by van Bergeijk (10), 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 medial superior olivary nuclei, and comparisons of the relative activities of the two nuclei would be made at some higher auditory station. Hall (23) used this model to analyze his unit data from the medial superior olivary nucleus of cat and found results that would be in keeping with several psychophysical parameters of binaural judgments in man. The results from the present experiment were also subjected to a population analysis. The discharge frequencies of 40 binaurally time-sensitive units tested at the same intensity (–10 dB) were averaged together over Δt values of 400 μ sec on either side of $\Delta t = 0$ μ sec. By specifying the recording site for each unit in terms of the ear receiving the initial click (contralateral or ipsilateral to the unit under study), the population can be considered as originating from just one of the paired medial geniculate nuclei. The results are plotted in Fig. 13 and show a gradual and continuous increase in dis-

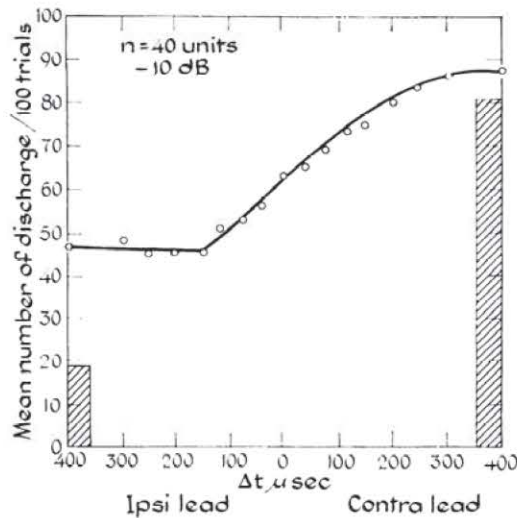


FIG. 13. Mean discharge frequency of 40 medial geniculate units from 12 animals as a function of interaural time differences (Δt) tested at the same intensity level (-10 dB). The variance was approximately 40 discharges/100 trials at each of the Δt values tested. Points have been fitted by a smooth curve.

charge frequency as Δt values shift from an ipsilateral lead of 160 μ sec to a contralateral lead of 300 μ sec. The curve is remarkably smooth considering the variability in discharge rates across the population. Thus, even using the small number of units sampled, information about the locus of a sound source appears to be contained in the average level of activity of the population of cells in the nucleus. The animal's lateralization judgments only encompass a portion of the Δt range over which the population of units in medial geniculate had a gradual change in discharge frequency. A better correspondence of the curves might have resulted had we been able to define the azimuth of the lateralized image as a function of the Δt parameters. The relevance of the overall behavior of populations of cells has been obtained in other neural systems as well. DeValois and Jacobs (13) have shown a good relationship between average discharge rates of cells in lateral geniculate nucleus of the macaque and the animals' psychophysical function to lights of different spectral content, while Humphrey et al. (25) have shown that the combined firing pattern of groups of motor cells in primate motor cortex corresponds to

several parameters of the animal's motor output. There could be difficulties in relying on the absolute level of activity from just one of the medial geniculate nuclei to localize a sound source, since discharge frequencies of both individual units (Fig. 7) and the population (Fig. 14) are strongly influenced by overall intensity. A solution to this problem proposed by van Bergeijk was that a comparison would be made at some higher auditory site of the relative difference in activity between the paired nuclei. The inferior colliculus units described by Rose et al. (34) with maximum sensitivity to one Δt range independent of signal frequency or intensity, their so-called characteristic delay, could be the neural equivalent of such a comparator mechanism. However, the rarity of these characteristic delay units in our results (only 10% of the population sampled at two or more intensities) suggests that the comparison has still not taken place at the level of the medial geniculate. If such a comparison were to be made of the levels of activity in the two medial geniculate nuclei, a different function based on the data from 40 units would have the form shown in Fig. 15. It would be of interest to know whether there are a significant number of units in auditory cortex that show such a response function.

An alternative approach to this problem

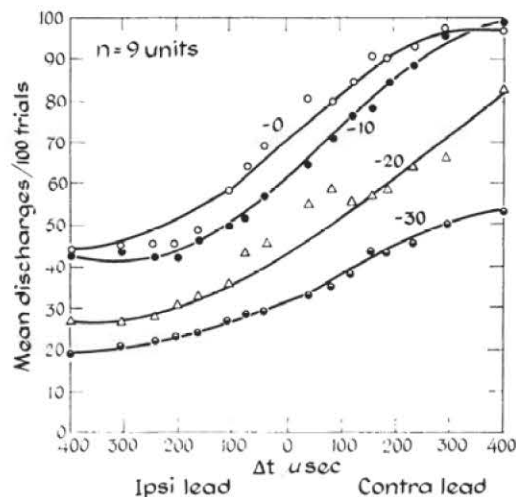


FIG. 14. Mean discharge frequency of nine medial geniculate units from seven animals as a function of interaural time differences (Δt) tested at four intensity levels.

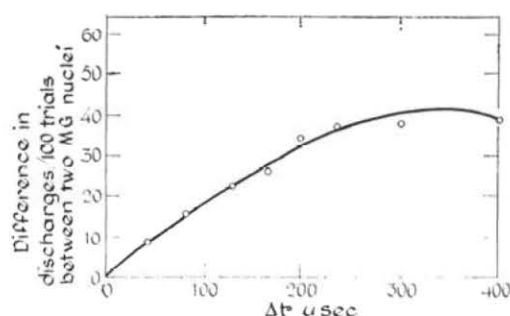


FIG. 15. Difference in discharge rates between the two medial geniculate nuclei as a function of the interaural time differences. Each plotted point is obtained by subtracting equivalent points along the average discharge function of the 40 units plotted in Fig. 13 (i.e., discharges/100 trials, 40 μsec , etc.).

is based on both anatomical and physiological (17, 29, 33) evidence of lateralized sensorimotor interactions at multiple sites along the auditory pathway affecting middle ear muscle activity (brain stem), 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 (7, 16). For instance, middle ear muscles respond more to ipsilateral than to contralateral inputs (28), whereas pinna, head, neck, and eye movements directed to one side occur with stimulation of the contralateral inferior colliculus nucleus (39) or medial geniculate nucleus (21). 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 Békésy 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 (23) in superior olive and hinted at by Benevento et al. (9) 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 (36). 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."

SUMMARY

The response of 205 units to both monaural and binaural clicks were studied in medial geniculate nucleus of pentobarbital-anesthetized squirrel monkeys. Two principal types of monaural response categories were observed. The larger group, consisting of 106 units, had an initial suppression of ongoing activity after a monaural signal to either ear followed by a characteristic clustering of cell discharges at intervals of approximately 100 msec. The second group, consisting of 93 units, responded at short latency (6–30 msec) to monaural clicks and only rarely showed a later periodicity in discharge pattern.

One hundred of these units were tested to binaural clicks with varying interaural time differences. Four binaural categories were observed: 1) Δt sensitive (59 units), showing a systematic change in discharge frequency over a limited portion of the interaural time domain; 2) facilitation (11 units), showing an increased level of activity above their monaural discharge rate relatively independent of the Δt parameters; 3) depression (2 units), showing a decreased level of activity below their monaural discharge rates relatively independent of the Δt parameters, and 4) binaural insensitivity (28 units), showing no difference in response to the binaural signals than to monaural inputs. Sensitivity to the binaural parameters was restricted almost entirely to units showing an early response to monaural clicks.

Click repetition rate and overall intensity had profound effects on Δt interaction. Of the 29 units tested at two or more

intensity levels, 20 showed a shift in sensitivity to Δt parameters toward the ipsilateral ear as click intensity was raised. Nine units failed to show a shift in Δt sensitivity with changes in signal intensity.

Of 33 Δt -sensitive units, 28 were also sensitive to interaural intensity differences. A comparison of the Δt and ΔI sensitivities revealed equivalence ratios ranging from 2 dB = 10 μ sec to 2 dB = 200 μ sec, with the mode occurring at 2 dB = 20–40 μ sec. Nine units were sensitive only to ΔI or Δt .

There did not appear to be any orderly distribution of units in medial geniculate with regard to binaural characteristics.

No evidence of sensitivity to the direction of apparent motion of a train of clicks could be found in 30 units.

The types of binaural interaction encountered in 78 inferior colliculus units were similar to those observed for medial geniculate.

Analysis of the medial geniculate data suggested that information about the locus of the sound source may be contained in the mean discharge frequency of the population of cells.

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