Discharge Patterns of Neurons in the Ventral Nucleus of the Lateral Lemniscus of the Unanesthetized Rabbit

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INTRODUCTION

The ventral nucleus of the lateral lemniscus (VNLL) is a major auditory nucleus that sends a large projection to the inferior colliculus. Despite its prominence, the responses of neurons in the VNLL have not been extensively studied. Previous studies in nonecholocating species have used anesthesia, which is known to affect discharge patterns. In addition, there is disagreement about the proportion of neurons that are sensitive to binaural stimulation. This report examines the responses of neurons in the VNLL of the unanesthetized rabbit to monaural and binaural stimuli. Most neurons responded to contralateral tone bursts at their best frequency and had either sustained or phasic discharge patterns. A few neurons were only inhibited. Most sustained neurons were classified as short-latency sustained (SL-sustained), but a few were of long latency. Some SL-sustained neurons exhibited multiple peaks in their discharge pattern, i.e., they had a “chopper” discharge pattern, whereas other SL-sustained neurons did not exhibit this pattern. In ordinary chopper neurons, the multiple peaks corresponded to the evenly spaced action potentials of a regular discharge. In unusual chopper neurons, the action potential associated with a particular peak could fail to occur during any one presentation of the stimulus. Unusual chopper neurons had a relatively irregular discharge. Phasic neurons were of two types: onset and transient. Onset neurons typically responded with a single action potential at the onset of the tone, whereas transient neurons produced a burst of action potentials. Transient neurons were relatively rare. About half the neurons also were influenced by ipsilateral stimulation. Most binaurally influenced neurons were either sensitive to interaural temporal disparities (ITDs) or excited by contralateral stimulation and inhibited by ipsilateral stimulation. Neurons sensitive to ITDs were mostly of the onset type and were embedded in the fiber tract medial to the main part of the nucleus. Neurons inhibited by ipsilateral stimulation could be of the sustained or onset type. The sustained neurons were located on the periphery of the main nucleus as well as in the fiber tract. Most of the monaural neurons were in the main, high-density part of VNLL. The present results demonstrate that the VNLL contains neurons with a heterogeneous set of responses, and that many of the neurons are binaural.

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tion, we have not distinguished distinct nuclei in this region. The VNLLl and VNLLm correspond to the compact ventral region and the neurons intercalated in the medial limb of the lateral lemniscus, respectively. The VNLLd comprises neurons between VNLLl and the dorsal nucleus of the lateral lemniscus, which are distributed with a density intermediate between VNLLl and VNLLm.

Because the principal input to the VNLL is from the contralateral VCN, a major question is to what degree the sustained and onset responses in the VNLL reflect these inputs. The sustained responses are reported to be similar to those observed in the VCN (Covey and Casseday 1991; Guinan et al. 1972a,b). In both the VNLL and the VCN, they include a primary-like discharge pattern that resembles the pattern produced by auditory nerve fibers and a chopper discharge pattern consisting of multiple peaks (responses in the VCN reviewed by Rhode and Greenberg 1992). In the VCN, neurons with a primary-like discharge pattern are characterized by a more irregular discharge than those with a chopper pattern (Blackburn and Sachs 1989; Young et al. 1988). Despite apparent agreement on the types of discharge patterns encountered in the VNLL, there is disagreement as to the proportions of neurons displaying different patterns. It is possible that this disagreement is a consequence of the use of anesthesia, which is known to influence discharge patterns (Brownell et al. 1979; Kuwada et al. 1989; Ritz and Brownell 1982).

The present study examines the discharge patterns of neurons in the VNLL of the unanesthetized rabbit and compares these patterns with those observed in other studies of the VNLL and in the VCN.

METHODS

Surgery and recording

Six female Dutch-belted rabbits (~2 kg) with clean external ears were used in these experiments. The preparatory surgery already had been described (Batra and Fitzpatrick 1997). Each rabbit was prepared for recording in two steps. During both steps, the rabbit was anesthetized with a mixture of ketamine and xylazine (35 and 5 mg/kg im). In the first step, the dorsal surface of the skull was exposed surgically using aseptic techniques, and a short metal rod was mounted on it. After the surgery, while the animal was still anesthetized, custom ear molds were made by inserting a short metal rod into the external meatus and pressing ear impression compound (Audalin, Esschem, Essington, PA) in around it. Later, the rod was replaced with a plastic meatus and pressing ear impression compound (Audalin, Esschem, Essington, NI) connected to the tubes that ran through the ear molds.

Acoustic stimulation and calibration

Pure tone bursts (4 ms rise and fall times, typically 75 ms long, repeated every 200 ms) were produced digitally using dual synthesizers designed at the University of Wisconsin, one for each ear (Rhode 1976). These synthesizers were controlled by a PDP-11 computer, which also controlled data collection. The tone bursts were delivered through DT-48 earphones (8 Ω, Beyerdynamic, Hicsville, NY) connected to the tubes that ran through the ear molds. Acoustic calibration was performed in one of two ways. In the first two animals, the intensity of the stimuli was set relative to a standard calibration. After the last recording session with each rabbit, the animal was deeply anesthetized, and the true calibration in dB SPL (re 20 μPa) was measured using a calibrated microphone and probe. The probe was inserted through a hole drilled in the wall of the bony external meatus, opposite the tympanum. The gap around the hole was sealed before calibrations were performed. With this method of calibration, it was not possible to maintain a constant intensity while testing a neuron at different frequencies, because the true intensities were only determined after experiments on each rabbit were concluded. For this reason, tuning characteristics were not determined for neurons studied in these animals.

In the remaining animals, the tube through the ear molds was made of stainless steel rather than plastic and incorporated a fine probe for calibration which extended ~1 mm beyond the sound delivery tube. When inserted, the tip of the probe was ~2 cm from the tympanum. In these animals, calibrations were performed through the probe before recordings were initiated, and intensities were set relative to this calibration.

Localization of recording sites

For each electrode penetration, the position of the electrode was set relative to a reference mark on the skull. The depth at which each neuron was studied was recorded. In three animals, locations of recording sites were reconstructed chiefly from reference marks that were made at selected sites during the last recording session. In one of these animal, the marks were made electrolytically (10 μA for 10–20 s). In the other two animals, the marks were made by injecting biotinylated dextran or fluorescein conjugated latex microspheres through a micropipette which also could be used to record neural activity.

In the remaining animals, most recordings were made with micropetites (tip diam ~1–1.5 μm) that were loaded with phosphate-buffered saline containing 10% dextran tagged with one of a variety of fluorescent labels or with biotin (Molecular Probes, Eugene OR; D1817, D1820, D1956, D1976, D3312, D7153). Many recording sites in these animals were marked directly by iontophoretic injection of the label (2.5 μA × 1.25–5 min).

On conclusion of recordings from an animal, it was anesthetized deeply and perfused with a washout followed by a fixative containing 4% paraformaldehyde and 0.2% glutaraldehyde, according to the procedures of Hill and Oliver (1993) for rats. The brains were blocked in the plane of the electrode tracks, placed in 30% sucrose for several days and frozen-sectioned (50 μm). In brains with injections of markers, alternate sections were mounted for visualization of the fluorescent markers (in, e.g., Fluoromount G, Southern Biotechnology Associates, Birmingham, AL). The remaining sections were processed using an avidin-biotin-horseradish peroxidase (HRP) complex (ABC
neurons were divided further into onset and transient categories, based on PSTH shape. Sustained neurons were subdivided into long-latency, short-latency sustained (SL-sustained) and strongly adapting categories. Phasic neurons were considered to be of long latency if their latency was \( > 7 \text{ ms} \) greater than the median of neurons in our sample at similar best frequencies (see Fig. 16A). Strongly adapting neurons were distinguished based on the shape of their PSTHs.

### Analysis of Variability
The analysis of variability to determine whether the discharge of a neuron was regular or irregular was performed in a manner similar to that previously described by others (Blackburn and Sachs 1989; Bourk 1976; Young et al. 1988). Our parameters were identical to those of Young et al. (1988) with two exceptions. First, the binwidth was \( 0.5 \) or \( 1 \) ms (compared with \( 0.1 \) or \( 0.2 \) ms), and no smoothing was used. Second, the average coefficient of variation (CV) was calculated over the interval \( 35–65 \text{ ms} \) (as compared with \( 12–20 \) ms) or somewhat less if spontaneous activity after the offset of the tone influenced the analysis (Young et al. 1988).

### Tuning Curves
Tuning curves were calculated as isoresponse contours for neurons for which responses were measured over a sufficient range of intensities and frequencies. First, from the responses at each intensity, a contour was constructed by interpolating the response linearly at 100 equally spaced frequencies. Second, visual examination of response areas and PSTHs was used to determine the minimum discharge rate at which responses could be consistently observed above variations in spontaneous activity. Finally, the intensity at which the response passed the selected discharge rate at each of the 100 frequencies was determined by linear interpolation.

### Analysis of Adaptation
To assess the amount of adaptation in individual neurons, a measure similar to that of Blackburn and Sachs (1989) was used. The mean discharge rate during 14–18 ms after the median latency was compared with that during 0–4 ms after the median latency.

### Results
The results in this report are based on the responses of 174 neurons and 1 multiunit cluster in and around the VNLL that were tested with contralateral tone bursts and other stimuli. The multiunit cluster was included because it had a discharge pattern not reported in lower centers and because its location was marked. The responses of two neurons at marked recording sites in the rostral periolivary region also have been included for comparison. The responses of some of these neurons were the subject of a previous report (\( n = 17 \)) (Batra and Fitzpatrick 1997).

The neurons typically responded to contralateral tone bursts (\( n = 170/175 \)). Most neurons had either sustained (\( n = 74 \)) or phasic (\( n = 86 \)) responses to tones at their best frequency (for details of classification scheme, see METHODS). A few neurons were inhibited by contralateral stimulation (\( n = 10 \)). Neurons that were not responsive to contralateral tones were excited by binaural low-frequency stimuli and were sensitive to interaural temporal disparities (ITDs) at low frequencies (\( n = 5 \)). Sustained neurons were subdivided into SL-sustained, long-latency, and strongly adapting categories. Phasic neurons were subdivided into onset and transient categories. In the following text, the locations of different types are described, and then sustained, phasic, and inhibited neurons are discussed in turn.

### Locations of response types
The locations of most neurons were reconstructed based on a few lesions or marking injections made after weeks or months of recording. Based on these reconstructions, the neurons included in this study appeared to be located in the VNLL, the adjacent reticular formation, and in the rostral superior olivary complex immediately adjacent to the VNLL. However, such localization is subject to considerable error. To more accurately determine the locations of different response types, locations of recording sites in a few animals were marked directly with dye injections. Figure 1 illustrates the locations of these sites collapsed onto three sections through the VNLL (see
METHODS). These sections are in the plane of the electrode penetrations that is pitched forward from the transverse, so that upper portions of each panel are more anterior as well as more dorsal. A is most posterior, C is most anterior. ○, □, △, , and ○: neurons with monaural responses; ●, ■, ▲, and ◆: neurons with binaural responses. Binaural onset category includes 5 neurons sensitive to interaural temporal disparities (ITDs) previously illustrated in Batra and Fitzpatrick (1997). Data from 3 animals have been pooled. BN, nucleus of the brachium of the inferior colliculus; LL, lateral lemniscus; MCP, middle cerebellar peduncle; MTB and VTB, medial and ventral nuclei of the trapezoid body; PN, pontine nuclei; Pyr, pyramids; Sag, sagulum; V, trigeminal nerve; c, d, l, m, medial, lateral, and dorsal divisions of the ventral nucleus of the lateral lemniscus (VNLL).

FIG. 1. Locations of marked recording sites. Each panel depicts a section through the brainstem of the rabbit in the plane of the electrode penetrations that is pitched forward from the transverse, so that upper portions of each panel are more anterior as well as more dorsal. The section in Fig. 1A is the most posterior. The ventral part of this section shows the caudal parts of VNLLl and VNLLm (l and m) where the lateral lemniscus merges with the trapezoid body. More dorsally, VNLLd (d) is present where the lateral lemniscus has turned posteriorly toward the inferior colliculus. Figure 1B is a section through the main part of VNLL. Figure 1C shows the rostral limb of the lateral lemniscus that lies anterior to VNLLl. The rostral limb contains a sparse population of neurons, much like VNLLm.

The marked sites were within the boundaries of the lateral lemniscus (Fig. 1, A–C), in a rostral portion of the ventral nucleus of the trapezoid body (VTB, Fig. 1A), and in more caudal olivary nuclei (not shown). None of the sites were in the reticular formation adjacent to the lateral lemniscus. Penetrations were made medial to the marked sites in the VNLL, but responses to acoustic stimulation were not encountered in this region. Thus neurons sensitive to tones appear to be rare or absent in this part of the reticular formation. Otherwise, the distribution of the marked sites was similar to that of the indirectly reconstructed recording sites.

The VNLLm and VNLLl contained different complements of neurons. The VNLLm and its anterior continuation contained chiefly onset neurons (10/13) (Fig. 1, ○ and ●), most of which (8/10) were sensitive to ITDs at low frequencies, as described previously (Batra and Fitzpatrick 1997). The VNLLl contained a large proportion of SL-sustained neurons (6/10) (Fig. 1, △ and ▲). Binaural neurons within VNLLl (3/10) appeared to be on its periphery. The one marked site in VNLLd was associated with a neuron that had an SL-sustained discharge pattern and that was inhibited by ipsilateral stimulation.

The responses of neurons in the rostral portion of the ventral nucleus of the trapezoid body appeared similar to those of neurons in the VNLL. Two SL-sustained neurons were located within this region. Their latencies and response patterns were similar to other SL-sustained neurons encountered in this study. Thus although most of the neurons in this study were in VNLLm and VNLLl, a few were located more dorsally in VNLLd or more ventrally.

Sustained neurons

The most common type of sustained neuron (n = 61/74) had a short latency (see METHODS) and a discharge pattern that consisted of an initial peak that declined, or adapted, to a steady level (Fig. 2, A–D). Such SL-sustained neurons were widely distributed in the VNLL, but the majority of marked sites (6/10 neurons) were located in VNLLl (Fig. 1). The extent of the adaptation in SL-sustained neurons could be large (Fig. 2, A–C). These neurons (10/74) had latencies varied among neurons (compare Fig. 2, A and B with C and D). Some SL-sustained neurons exhibited a brief “dip” in the response after the initial transient (Fig. 2, A and B), similar to what has previously been observed in the cochlear nucleus (Blackburn and Sachs 1989; Pfeiffer 1966).

A few neurons had responses that declined throughout the tone burst to near zero (Fig. 2E). These neurons were excluded from the SL-sustained category and instead were classified as strongly adapting (3/74 neurons). The only marked site associated with a strongly adapting neuron was in the VNLLl (Fig. 1B). Still other sustained neurons were of long latency (Fig. 2, F–H). These neurons (10/74) had latencies >7 ms greater than that appropriate for their best frequency (see Fig. 16A). They exhibited two types of discharge patterns in response to tone bursts. The more common type of long-latency neuron (7/10) discharged with a low discharge rate (<100 action potentials/s) (Fig. 2, F and G). One of these neurons exhibited a chopper pattern (Fig. 2G). The less common type of long-latency neuron (3/10) produced a response that gradually built to a peak and then declined (Fig. 2H). Examination of raster plots confirmed that this pattern was not the result of a single action potential occurring with variable latency.

To quantify the proportion of SL-sustained neurons that
adapted, the average discharge rate late in the response was compared with that early in the response (see METHODS). For all neurons the discharge rate changed by >5% (61/61 neurons), indicating that their discharge rate was not constant during the stimulus. Most neurons showed a decrease in the discharge rate (53/61 neurons).

To determine whether SL-sustained neurons were similar to, or different from, short-latency sustained neurons in the VCN such as primary-like and chopper neurons, the initial portion of the response of the SL-sustained neurons was examined on a time scale similar to that commonly used in studies of that nucleus (Figs. 3–5). Some SL-sustained neurons in the VNLL responded to contralateral tone bursts with a chopper pattern similar to that observed in the VCN (Fig. 3, A and B, top). In such ordinary chopper neurons, the multiple peaks of the chopper pattern were the result of action potentials occurring at regular intervals during each repetition of the stimulus (Fig. 3, A and B, 2nd row). Each peak was associated with one action potential per repetition. In some neurons the chopping frequency was more rapid than in others (compare Fig. 3, A and B). The chopper pattern in the PSTH was occasionally relatively sustained (Fig. 3A, top) but was typically more transient (Fig. 3B, top).

In the VCN, neurons with a chopper pattern have a regular discharge. The degree to which the regularity of the discharge was maintained throughout the stimulus was assessed using an analysis of variability (Fig. 3, 3rd and 4th rows) (see METHODS). For ordinary chopper neurons, the standard deviation of the interspike interval (Fig. 3, 3rd row, dotted line) was typically less than the mean (Fig. 3, 3rd row, solid line) throughout the stimulus. This was reflected in the CV (Fig. 3, 4th row), which is the ratio of the standard deviation to the mean.

Other SL-sustained neurons in the VNLL showed an unusual chopper pattern (Fig. 4). Like the ordinary chopper neurons, these neurons also exhibited multiple peaks at the onset of the response to tone bursts (Fig. 4, top). However, in some of these neurons the width of the peaks did not increase gradually as in ordinary chopper neurons, but instead later peaks were much broader than the immediately preceding peaks (Fig. 4B, top). In unusual chopper neurons, the initial action potential of the response sometimes corresponded to the second or later peaks, the first peak having been “missed” (Fig. 4, 2nd row, →).

Some unusual chopper neurons discharged irregularly, with the standard deviation of the interspike interval considerably less than the mean (Fig. 4A, 3rd and 4th rows). However, most discharged irregularly, with the standard deviation more comparable to the mean (Fig. 4B, 3rd and 4th rows).

Still other SL-sustained neurons did not exhibit a chopper pattern (Fig. 5, top). Some of these nonchopper neurons produced a well-timed initial action potential that was followed by a brief pause (Fig. 5B). Most nonchopper neurons discharged rather irregularly (Fig. 5, A and B, 3rd and 4th rows).

Ordinary chopper neurons were the most numerous (20/44), and unusual chopper neurons the least (10/44). Nonchopper neurons were the most numerous (20/44), and unusual chopper neurons the least (10/44). Nonchopper
neurons were intermediate in number (14/44). Other SL-sustained neurons (n = 17) could not be classified in one of these groups because they had a low discharge rate, were of low frequency and phase-locked, or because the number of presentations was too small to make an adequate assessment.

The CVs of SL-sustained neurons were broadly distributed around a value of 0.5 (Fig. 6, dashed line). Nearly all ordinary chopper neurons had CVs $< 0.5$, indicating a regularity in their discharge, whereas most unusual chopper neurons and non-chopper neurons discharged more irregularly, with CV $\geq 0.5$.

**Phasic neurons**

Phasic neurons were of two types: onset and transient. Most phasic neurons exhibited an onset pattern (78/86; Fig. 7, A–C), which consisted of a large peak at onset, followed by no (Fig. 7A) or few (Fig. 7B) action potentials. Sometimes, the response after the initial peak was suppressed below the spontaneous rate (Fig. 7C). A few phasic neurons exhibited a transient pattern (8/86), consisting of a burst of action potentials that could last up to $\sim 20$ ms (Fig. 7D). Most marked sites associated with onset neurons were in VNLLm or its continuation in the rostral limb of the lateral lemniscus (10/11 neurons; Fig. 1). The two marked sites associated with transient neurons were in VNLLl.

Some phasic neurons also produced a discharge associated with the offset of the stimulus. Off discharges were most common in transient neurons (4/8) and were only occasionally present in onset neurons (6/78). In transient neurons, this off response occurred with a latency of $> 20$ ms (relative to sound offset) near best frequency, considerably more than the latency of the response to the onset of the tone. In onset neurons, the off discharge was usually of short latency, i.e., comparable with that of the onset response. It is unlikely that this short-latency off discharge was a result of spectral splatter, because it was rarely seen and often was associated with a nonmonotonic rate-level function (see following text), which is more consistent with the presence of an inhibitory input.

The latency of the long-latency off response could differ at frequencies other than best frequency. Figure 8 illustrates one neuron in which this was observed. At best frequency the latency of the off response was long (Fig. 8A). At higher frequencies, the latency was shorter (Fig. 8B) and comparable with the latency of the initial phasic response (see also different neuron in Fig. 12C). For the neuron of Fig. 8, the off response was larger above best frequency (note change in scale), but this was not always the case (Fig. 12C). The change in latency with frequency was relatively abrupt, suggesting that the off responses at the different frequencies reflect rebound from different sources of inhibition.

When viewed on an expanded time scale, the discharge pattern of onset neurons showed considerable variety, but
differed from the pattern displayed by transient neurons (Fig. 9). Most onset neurons responded with a single action potential to all or most repetitions of the tone (Fig. 9, A and B). This action potential could be locked tightly to the onset of the sound (Fig. 9A) or it could be locked loosely (Fig. 9B). Other onset neurons responded with two or three action potentials (Fig. 9C). These action potentials were spaced regularly, resulting in two or three peaks in the PSTH. The interval between the peaks typically was unrelated to the frequency of stimulation. Transient neurons responded with a burst to each presentation of the stimulus (Fig. 9D). The burst could contain as many as seven or eight action potentials. These action potentials did not produce multiple peaks in the PSTH (Fig. 9D, top), even though the intervals between them appeared relatively regular (Fig. 9D, bottom).

Inhibited neurons

Some neurons were inhibited by contralateral stimulation (n = 10/175; Fig. 10). In half of these, the discharge rate gradually recovered to spontaneous levels after the tone (Fig. 10A), but in the remainder, there was an off discharge after termination of the tone (Fig. 10B). Inhibited neurons were not excited by ipsilateral stimulation. One of the two marked sites associated with an inhibited neuron was in VNLLm, the other was in the limb of the lateral lemniscus that was lateral to VNLLl (Fig. 1).

Tuning

The tuning of SL-sustained neurons (n = 12) tended to be narrower for neurons with higher best frequencies (Fig. 11A). The tuning of the onset neurons tested (n = 8) did not appear to depend on best frequency and was quite broad (Fig. 11B, solid line and dashed line). Transient neurons (n = 4) tended to have relatively sharp tuning (Fig. 11B, Tr).

Constancy of the discharge pattern

The discharge pattern of a neuron was usually maintained at all frequencies to which it was responsive (Fig. 12). Examples are shown of an SL-sustained neuron, an onset neuron, and a transient neuron (Fig. 12, A–C, respectively). The response of some SL-sustained neurons and of some transient neurons was suppressed below the spontaneous rate at frequencies surrounding the best frequency (Fig. 12A, top, and C, bottom, respectively). Such sideband suppression was typically more pronounced below the best frequency in SL-sustained neurons and above best frequency in transient neurons.

Most neurons displayed their characteristic discharge patterns across a range of intensities as well. Figure 13 shows the responses of a SL-sustained neuron (Fig. 13A), an onset neuron (Fig. 13B), and a transient neuron (Fig. 13C) from threshold (Fig. 13, top) to intensities well above threshold (Fig. 13, bottom). Each neuron maintained its discharge pattern at all intensities.
There was a small group of neurons that formed a notable exception to the rule that the discharge pattern was similar across frequency. These neurons had high best frequencies (i.e., ≥2 kHz, the upper limit for phase-locking) when assessed at a low intensity, but produced a vigorous sustained discharge at low frequencies when stimulated with tones of high intensity. The responses of one neuron of this group are illustrated in Fig. 14. When tested with best-frequency tones of low intensity (40 dB in this example), this neuron produced a SL-sustained response consisting of a well-timed onset followed by a relatively weak sustained discharge (Fig. 14A, left). This discharge pattern was maintained at higher intensities (70 dB, Fig. 14A, right). Other neurons in this group responded with an onset discharge to best-frequency tones (not shown). There was no response to low-frequency tones when the intensity was low (Fig. 14B, left), but at higher intensities the response was vigorous (Fig. 14B, right) and was typically stronger than that at best frequency. The low-frequency response was phase-locked (Fig. 14C). The vector strength for phase-locking (Goldberg and Brown 1969) was typically 0.8, which is similar to that observed in the auditory nerve (Johnson 1980; Joris et al. 1994). Thus these neurons had a low-frequency sustained discharge that appeared to be independent of the discharge pattern at best frequency, which could be either SL-sustained or onset.

**Dynamic range**

The dynamic range, or the range of intensities above threshold over which the response is graded, was assessed in neurons for which responses were recorded from threshold to either saturation or 40 dB above threshold. Most of these neurons were either SL-sustained neurons (n = 30) or onset neurons (n = 16).

The response of most neurons increased monotonically from...
threshold until saturation was reached (Fig. 15A, ●, ▲, and ◆: Fig. 15B). A few neurons (n = 7/54), displayed a nonmonotonic increase in the response (Fig. 15A, ○). Most of these neurons were phasic neurons (n = 5/7: 4 onset, 1 transient). Most of the nonmonotonic phasic neurons had a short-latency off response, consistent with the notion that the nonmonotonicity was a consequence of an inhibitory input.

Onset neurons tended to have shorter dynamic ranges than SL-sustained neurons (compare Fig. 15, A with B). The average dynamic range of onset neurons was ~20 dB (23 ± 15 dB, mean ± SD; Fig. 15C, □). For SL-sustained neurons, the average dynamic range was almost 50 dB (48 ± 15 dB) (Fig. 15C, ◆). The difference was significant (t = 5.4, P < 0.01, df = 44). The dynamic range of most SL-sustained neurons was underestimated, because responses were not typically measured up to saturation.

Latency

Most neurons with excitatory responses had latencies of ~5–9 ms to contralateral stimulation (7.0 ± 1.4 ms, median ± SIQR, n = 160; Fig. 16A). Some neurons had latencies >7 ms greater than the average for a particular frequency (Fig. 16A, --- vs. ---). All of these long-latency neurons (Fig. 16A, ■) had sustained responses.

For many neurons, the SD of the latency of the first action potential was not representative of the variability in latency. An example, by no means the most extreme, is shown in Fig. 16B. During most responses, the latency was close to 7.4 ms (Fig. 16B, histogram), except for a single repetition during which the latency was ~50 ms. A Gaussian curve with an equivalent SD (5.2 ms) was far broader than the main peak (Fig. 16B, --). In contrast, a Gaussian curve with an equivalent SIQR (0.31 ms) had a width similar to that of the main peak (Fig. 16C, ---). For this reason, the SIQR rather than the SD was used as a measure of variability.

There was an overall trend for longer latencies to also be more variable. Some onset and SL-sustained neurons had extremely short, tightly-locked latencies (Fig. 16C, ○ and ▲, respectively). Others had longer latencies that were also not as well locked to the onset of the stimulus. The latencies of transient neurons (Fig. 16C, ◆) were more closely clustered than those of SL-sustained and onset neurons, but the variability in the latency was similar to that of other neurons with similar latency. Long-latency neurons (Fig. 16C, ■) had the most variable onset times.

The latencies of most neurons decreased appreciably with increasing intensity. The shift in latency was calculated over a range of 10–30 dB, beginning at 10 dB above threshold. Onset and SL-sustained neurons showed a similar range of shifts in latency with increasing intensity (Fig. 16D) as did transient and long-latency neurons (not shown).

To establish whether any neurons in the VNLL of the rabbit could be considered to have “constant latency” as described in the bat Eptesicus (Covey and Casseday 1991), we tested neurons in our sample with two criteria similar to those used in the earlier study of Eptesicus (for a comparison of the criteria in the rabbit and Eptesicus see DISCUSSION). The first criterion was that the SIQR of the latency be <0.67 ms (Fig. 16C, →). Most neurons (112/160) met this
criterion. The second criterion was that as the intensity was raised the latency should shift by no more than 33 μs/dB (Fig. 16D). Fewer neurons (21/98) met this criterion. Overall, about an eighth of the neurons tested met both criteria (12/98) and could be considered to have a constant latency. Some of these constant-latency neurons had onset discharge patterns (8/12) and others had sustained discharge patterns (4/12). If an SD <1 ms was used as the first criterion, then fewer neurons met both criteria (4/98).

Binaural influences

Although most neurons in the VNLL responded to contralateral stimulation, many were influenced by ipsilateral stimulation as well. Some neurons were sensitive to ITDs at low frequencies and were located chiefly in the medial part of the nucleus. The properties of these already have been described (Batra and Fitzpatrick 1997) and will not be discussed in detail here. The four neurons of Fig. 17 illustrate other influences of ipsilateral stimulation. In Fig. 17, A–C, ipsilateral tone bursts (bar) were presented during the response of SL-sustained neurons to contralateral tone bursts. The neuron of Fig. 17A was facilitated by ipsilateral stimulation, whereas those of Fig. 17, B and C, were suppressed. In some neurons (Fig. 17B), the suppression was relatively weak, whereas in other neurons (Fig. 17C), it was stronger. Onset neurons also could display binaural influences. The response of the neuron of Fig. 17D to contralateral tones (1st panel) was progressively reduced as the

![Diagram](http://jn.physiology.org/Downloadedfromhttp://jn.physiology.org/pdf/)

FIG. 9. Discharge patterns of 4 phasic neurons viewed on an expanded time scale. Top: PSTH (bin-width: 0.2 ms); bottom: raster of 30 stimulus presentations. Repetitions averaged in each case: 100. Frequencies (kHz) and intensities (dB): 22.0, 70 (A); 3.0, 80 (B); 8.0, 70 (C); and 1.0, 64 (D).

FIG. 10. Discharge patterns of 2 inhibited neurons. Same format as Fig. 2. Frequencies (kHz), intensities (dB), and number of repetitions: 22.0, 64, 100 (A) and 8.0, 80, 150 (B).
The intensity of simultaneously presented ipsilateral tones was increased (I = 55–75 dB).

The distribution of neurons in the sample across binaural categories is illustrated in Fig. 18A. Slightly less than half of the neurons (40%) responded to only contralateral stimulation. Of these, most were excited by contralateral tones (E0), but a few were inhibited (I0). The major categories of binaural influences present were ipsilateral suppression combined with contralateral excitation (EI) and sensitivity to ITDs at low frequencies. Most EI neurons had a SL-sustained discharge pattern (23/41), but several had an onset discharge pattern (14/41). Most ITD-sensitive neurons had an onset discharge pattern (36/44). Two high-frequency onset neurons that were sensitive to ITDs at low frequencies were classified as being ITD sensitive. About 10% of neurons tested were sensitive to ITDs in the envelopes of sinusoidally modulated best-frequency tones, and most of these were EI.

Among the EI neurons, the strength of suppression was widely distributed. To quantify the strength of ipsilateral inhibition, the percent suppression of the response at the highest ipsilateral intensity tested was calculated, relative to the response to contralateral stimulation alone (Fig. 18B). Neurons were more or less uniformly distributed by this measure. This indicates that among EI neurons the ipsilateral inhibition could vary from being very weak to near total.

**DISCUSSION**

Neurons in the VNLL of the unanesthetized rabbit responded to pure tone bursts at the contralateral ear with a variety of discharge patterns. In agreement with earlier studies (Adams and Mugnaini 1990; Aitkin et al. 1970; Covey and Casseday 1991; Guinan et al. 1972a,b), most exhibited sustained or phasic patterns, and a lesser number were only inhibited. Both the sustained and phasic groups contained some subgroups not previously described. These include long-latency and strongly adapting neurons in the sustained group and transient neurons in the phasic group.

Many neurons in the VNLL were influenced by ipsilateral stimulation as well as being driven by contralateral stimulation. The two major types of binaural interaction were suppression of contralateral responses by concomitant ipsilateral stimulation and sensitivity to ITDs. Both sustained and onset neurons could exhibit binaural suppression, but sensitivity to ITDs occurred chiefly in onset neurons. The evidence indicates that onset neurons sensitive to ITDs, inhibited neurons, and some sustained neurons exhibiting binaural suppression are located in VNLLm, whereas VNLLl contains transient neurons, monaural sustained neurons, and, at its margins, some neurons exhibiting binaural suppression.

**Discharge patterns in the VNLL**

It is unlikely that the discharge patterns observed in the present study represent those of axons ascending in the lateral lemniscus rather than those of neurons in the VNLL itself. The axons of the neurons in the medial and lateral superior olives that are the primary encoders of ITDs are known to ascend in the lateral lemniscus. Although neurons sensitive to ITDs were found in the VNLL, none of these neurons displayed the signature phase-locking and sensitivity to ITDs of primary encoders of ITD (Batra et al. 1997b). The absence of any recordings from the axons of neurons in the medial and lateral superior olives suggests that the responses reported here were from cell bodies and not axons.

The proportions of neurons with different discharge patterns found in the present study differ from those in previous studies of the VNLL. Several small populations have not been reported previously. These include transient neurons, inhibited neurons, long-latency neurons, and strongly adapting neurons. The proportion of sustained neurons that display a chopper pattern is lower than in earlier studies (Adams 1997; Guinan et al. 1972a,b). This most likely reflects the use of anesthesia in the earlier work which is known to influence the discharge pattern (Brownell et al. 1979; Kuwada et al. 1989; Ritz and Brownell 1982). There is evidence in the lateral superior olive that anesthesia decreases the proportion of neurons with chopper discharge patterns (Batra et al. 1997b; Brownell et al. 1979). The proportion of onset neurons is also higher in the present study than previously reported. However, this is probably due to an oversampling of VNLLm, which contains chiefly onset neurons.

**Sources of discharge patterns**

The different subtypes of SL-sustained discharge patterns that are present in the VNLL also are observed in the VCN (reviewed by Rhode and Greenberg 1992). At first glance, the chopper neurons in the VNLL appeared broadly similar to those in the VCN. A few neurons in the VNLL exhibited what appeared to be sustained chopper patterns, whereas others exhibited transient chopper patterns. Similarly, the nonchopper neurons of the VNLL produced discharge patterns that were similar to the primary-like and primary-like-with-notch patterns reported in the VCN.

Despite these similarities, there were differences. The dy-
namic range of SL-sustained neurons was considerably larger than that of most neurons in the VCN. Most neurons in the VCN have dynamic ranges of ~25 dB (Rhode and Smith 1986). An exception are the Oc neurons (which, despite their name, do have substantial sustained discharge rates). These neurons have an average dynamic range of 57 dB, similar to the SL-sustained neurons of the VNLL. However, it is unlikely that the wide dynamic range of the SL-sustained neurons is inherited from the Oc neurons or from sustained neurons in medial periolivary regions that also have a wide dynamic range and are sensitive to contralaterally presented sounds (Kuwada and Batra 1999). The axonal terminations of Oc neurons within the VCN contain pleomorphic vesicles (Smith and Rhode 1989), suggesting they are inhibitory. There is also evidence that, for the most part, the Oc neurons project only to the contralateral cochlear nucleus (P. H. Smith, personal communication). The projection from medial periolivary regions to the VNLL is sparse (Glendenning et al. 1981). Thus it is more likely that the wide dynamic range of neurons in the VNLL is a result of neural processing in the VNLL itself and is a consequence of the convergence of inputs from the VCN that encode different ranges of intensity. Some sustained neurons in the VNLL of Eptesicus also have wide dynamic ranges (Covey and Casseday 1991).

Another way in which SL-sustained neurons differed from sustained neurons in the VCN was in the significant proportion of unusual chopper neurons. These neurons likely correspond to “unusual neurons” in the VCN that exhibit a multipeaked discharge pattern but do not fire an action potential for each peak during each presentation of the stimulus (Blackburn and Sachs 1989). In the VCN, they are reported to be rare (~3% of neurons). It is unlikely that the responses of unusual chopper neurons arise by the cellular mechanisms usually considered to give rise to chopper discharge patterns in the VCN. Models of chopper discharge patterns in the VCN typically do not assume an internal oscillator (e.g., Arle and Kim 1991). Instead, they assume a steady synaptic input that is integrated to generate an action potential. The timing of action potentials then is determined by the level of synaptic input and the time of the preceding action potential. Without an internal oscillator, or a
periodic input, it is difficult to see how the periodicity could be maintained without the generation of an action potential. It is, however, possible that unusual chopper neurons in the VNLL get input from the ordinary chopper neurons of the VCN.

As with the SL-sustained neurons, onset neurons are present in both the VCN and the VNLL. There is evidence that some of the onset responses in the VNLL are inherited via inputs from the VCN octopus cells, which appear to project to the VNLL and terminate there in calyceal endings (Adams 1997; Joris et al. 1992; Schofield and Cant 1997). Such endings would serve to faithfully reproduce the onset discharge pattern of octopus cells in neurons of the VNLL. Some of the neurons encountered in the present study did have properties similar to those posited for octopus cells (Godfrey et al. 1975; Joris et al. 1992). They had a well-timed onset and a discharge pattern that was onset or sustained with a relatively low sustained discharge rate. They also synchronized strongly to low-frequency tones. These neurons could well have received their input from octopus cells of the VCN.

Many other onset neurons encountered in the present study did not appear to have inherited their discharge pattern from octopus cells. These onset neurons were of low best frequency, were sensitive to ITDs, and were located chiefly in VNLLm. At low frequencies, octopus cells do not produce an onset response but instead a sustained, phase-locked discharge. Furthermore the calyceal endings that are believed to come from octopus cells have been reported only in VNLLl. Thus there appear to be multiple populations of onset neurons within VNLL.

In contrast with the SL-sustained and onset neurons, transient neurons appear to be novel to the VNLL. Such responses may be the consequence of unusual membrane properties of these neurons or may reflect an inhibitory input following an excitatory input by 10–20 ms. The presence of an off response in some of these neurons is consonant with the presence of an inhibitory input. The decrease of the latency of the off response at higher frequencies suggests that there may be two different off responses generated by inhibitory rebound from two different sources of inhibition. The short-latency off response present at higher frequencies may be a consequence of rebound from an inhibitory input active during the stimulus. The long-latency off response present near best frequency may be the result of rebound from a delayed inhibitory input or one that lasts longer. Alternatively it may be rebound from an inhibitory input that is activated transiently at the offset of a stimulus. Neurons with a strong, short-latency off response are present in the superior olivary complex (Kuwada and Batra 1999), most likely in a region surrounding the medial superior olive. It is possible that these neurons provide inhibition to the VNLL, although, as remarked earlier, input from this region to the VNLL appears sparse (Glendenning et al. 1981).

The inhibited discharge pattern also does not appear to be inherited via the input from the VCN. Such responses could be the result of inhibitory projections from the superior olivary complex. One possible source of inhibition in this region is the medial nucleus of the trapezoid body. The principal neurons of this nucleus receive contralateral input (e.g., Cant and Casseday 1986; Stotler 1953; Tolbert et al. 1982; Warr 1972, 1982) and are immunoreactive to glycine, a known inhibitory transmitter (Adams and Mugnaini 1990; Wenthold et al. 1987). They are known to project to the VNLL (Casseday et al. 1988; Glendenning et al. 1981; Sommer et al. 1993; Spangler et al. 1985). Glycinergic endings occur in the VNLL (Oliver and Bishop 1998; Saint Marie et al. 1997; Vater et al. 1997; Winer et al. 1995).

![FIG. 13. Discharge patterns of 3 neurons as a function of intensity. A: SL-sustained neuron. B: onset neuron. C: transient neuron. Binwidth: 2 ms. Frequencies (kHz), number of repetitions: 42.0, 25 (A); 5.5, 25 (B); and 19.0, 20 (C).](http://jn.physiology.org/)

Constancy of latency

In the VNLL of the rabbit, there did not appear to be distinct populations of constant latency and variable latency neurons. Instead there appeared to be a continuum such that neurons with less variable latencies responded sooner than those with more variable latencies. This relationship appears to be at least partially inherited from the auditory nerve (Heil and Irvine 1997). Thus the VNLL of the rabbit differs from that of Eptesicus.

In Eptesicus, distinct populations of constant and variable latency neurons occur, and constant latency neurons have shorter latencies than variable latency neurons (Covey and Casseday 1991). Despite this difference between the two species, some of the neurons in the rabbit appeared to qualify as constant latency responders as defined in Eptesicus.

Our criteria for constant latency responders differed from those employed in the study of Eptesicus (Covey and Casseday 1991). In that study, constant latency neurons were defined as “having a SD in first-spike latency of <1.0 ms and a change of <1.0 ms in first-spike latency as SPL was increased from 10 dB above threshold to 40 dB above threshold.” A problem with such a definition is that the SD of the latency is sometimes a poor descriptor of the variability because of the occurrence of a few long-latency responses (cf. Fig. 16B) or the presence of spontaneous activity, or both (Heil and Irvine 1997; Young et al. 1988). This problem was absent in the study of Eptesicus because in the VNLL of that animal constant-latency responders have no spontaneous activity (Covey and Casseday 1991) and no long-latency responses (E. Covey, personal communication). In the present study, a somewhat different criterion was substituted, based on the SIQR of the latency (SIQR < 0.67). Our criterion corresponds to the first criterion of the study in Eptesicus when the distribution of latencies of individual neurons is Gaussian.

Our second criterion also differed from that in the earlier study. The shift in latency with intensity was not measured 40 dB above threshold in neurons with higher thresholds because such high intensities could startle the unanesthetized rabbit. If a linear decrease in latency with level is assumed over the 30 dB range, then 1.0 ms of shift in the study on Eptesicus corresponds to a shift of 33 μs/dB (Fig. 16D, †). This assumption probably underestimates the number of neurons that meet this criterion for having a constant latency because shifts in latency are typically not linear with level and are larger at lower intensities. A smaller proportion of neurons met this criterion than the first criterion (see Fig. 16C).

Regardless of the particular criteria used, there appeared to be a small proportion of constant-latency neurons in the rabbit.

FIG. 14. Responses of a neuron that synchronized to low-frequency tones of high intensity. A: discharge patterns at best frequency (3.25 kHz). B: discharge patterns at a low frequency (707 Hz). Binwidth: 2 ms. C: phase histogram depicting synchrony to 707 Hz at 70 dB.

This suggests that the large population of such neurons in *Eptesicus* arose by differential amplification of neurons that are common to other species as well. In the rabbit, such neurons appear to represent part of a continuum, whereas in *Eptesicus* the continuum appears to have been differentiated into constant- and variable-latency types.

**Localization of response types**

Most of the neurons studied here were localized directly or indirectly to VNLLl or VNLLm and a few were localized to VNLLd. Recordings from neurons in the superior olivary complex and from neurons in more rostral structures were excluded as far as possible. The region we and others have called VNLLd (Adams 1979, 1997; Whitley and Henkel 1984) also has been referred to as the intermediate nucleus of the lateral lemniscus (Glendenning et al. 1981; Saint Marie et al. 1997; Schofield and Cant 1997). We have selected the present nomenclature partly because the majority of the neurons in our sample were from the more ventral portions of VNLL and it was convenient to refer to the entire region with a single name and partly because the boundary between the two regions was not sharply delineated in our material.

Different response types were partly segregated within the VNLL. Sustained neurons predominated in the VNLLl, whereas onset neurons predominated in the VNLLm. Also, the majority of neurons in VNLLl were monaural, whereas the majority in VNLLm were binaural and often sensitive to ITDs. Although we consider VNLLm and VNLLl to be divisions of the VNLL, they may be more properly considered separate nuclei because of the differences in cytoarchitecture and neural responses.

**FIG. 16.** Analysis of latency for neurons in the vicinity of the VNLL. *A:* median latency as a function of best frequency. —: smooth curve, constructed by first calculating median latencies across neurons in half-octave bands of best frequency from 0.71 to 32 kHz, and then fitting these values by eye. - - - : same curve shifted upward 7 ms. Neurons with latencies above - - - were considered to be of long latency. *B:* difference between SD and semi-interquartile range (SIQR) as a measure of variability of the latency. Histogram: latency distribution for a sample neuron (repetitions: \( n = 100 \); responses: \( n = 69 \)). —: Gaussian curve with SD equal to that of latency distribution. - - - : Gaussian curve with SIQR equal to that of latency distribution. *C:* variability of the latency. Line is a power function least-squares fit to the data. Multiplier: 0.957; exponent: 1.90; \( r = 0.72 \). Each symbol in A and C is a different neuron. *D:* shift in latency with intensity for SL-sustained and onset neurons. \( \rightarrow \) and \( \uparrow \) in C and D, respectively, are criterion levels for constancy of the latency. Latency measurements have not been corrected for the acoustic delay of 0.2 ms.

**FIG. 17.** Responses of 4 binaural neurons. *A:* SL-sustained neuron facilitated by ipsilateral stimulation. *B:* SL-sustained neuron weakly suppressed by ipsilateral stimulation. *C:* SL-sustained neuron strongly suppressed by ipsilateral stimulation. *D:* onset neuron suppressed by ipsilateral stimulation. In A, B, and C a 300-ms contralateral tone is presented at 0 ms. Lines under each panel denote ipsilateral stimulation. In D, each PSTH depicts the response 4–8 ms after onset of a 75-ms tone burst. *Left panel in D:* contralateral stimulation alone at 60 dB. *Other panels:* binaural stimulation with progressively higher ipsilateral intensity levels, given in dB. Frequencies (kHz): 1.3 (A); 8.5 (B); 5.0 (C); and 4.0 (D). Ipsilateral/contralateral intensities (dB): 49/64 (A); 67/77 (B); and 64/74 (C).
binaural neurons (35%). Neither of these studies specifically state
whereas Guinan et al. (1972a,b) found a substantial number of
were in conflict over the proportion of binaural neurons in the
vides a possible reconciliation between two earlier reports that
present only at its margins. Aitkin et al. (1970)
were not sensitive to ITDs but were instead EI. In a few of
these weakly suppressed neurons are excluded, there is still
number of binaural neurons. At least
if these weakly suppressed neurons are excluded, there is still
provided histological and technical assistance.
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REFERENCES
ADAMS, J. C. Ascending projections to the inferior colliculus. J. Comp. Neurol.
ADAMS, J. C. Projections from octopus cells of the posteroventral cochlear
nucleus to the ventral nucleus of the lateral lemniscus in cat and human.
ADAMS, J. C. AND MUGNAINI, E. Dorsal nucleus of the lateral lemniscus: a
nucleus of GABAergic projection neurons. Brain Res. Bull. 13: 585–590,
1984.
ADAMS, J. C. AND MUGNAINI, E. Immunocytochemical evidence for inhibitory
and disinhibitory circuits in the superior olive. Hear. Res. 49: 281–298,
1990.
AITKIN, L. M., ANDERSON, D. J., AND BRUGGE, J. E. Tonotopic organization and
discharge characteristics of single neurons in nuclei of the lateral lemniscus
ARLE, J. E. AND KIM, D. O. Neural modeling of intrinsic and spike-discharge
BATRA, R. AND FITZPATRICK, D. C. Neurons sensitive to interaural temporal
disparities in the medial part of the ventral nucleus of the lateral lemniscus.
BATRA, R., KUWADA, S., AND FITZPATRICK, D. C. Sensitivity to interaural
temporal disparities of low- and high-frequency neurons in the superior
1236, 1997a.
BATRA, R., KUWADA, S., AND FITZPATRICK, D. C. Sensitivity to interaural
temporal disparities of low- and high-frequency neurons in the superior
olivary complex. II. Coincidence detection. J. Neurophysiol. 78: 1237–1247,
1997b.
BLACKBURN, C. C. AND Sachs, M. B. Classification of unit types in the
anteroventral cochlear nucleus: PST histograms and regularity analysis.
BOURK, T. R. Electrical Responses of Neural Units in the Anteroventral
Cochlear Nucleus of the Cat (PhD dissertation). Cambridge, MA: MIT,
1976.
BROWNEll, W. E., MANIS, P. B., AND RITZ, L. A. Ipsilateral inhibitory re-
CANT, N. B. AND CASEDADAY, J. H. Projections from the anteroventral cochlear
nucleus to the lateral and medial superior olivary nuclei. J. Comp. Neurol.
CASEDADAY, J. H., COVEY, E., AND VATER, M. Connections of the superior
olivary complex of the rufous horseshoe bat Rhinolophus rouxi. J. Comp.
COVEY, E. Response properties of single units in the dorsal nucleus of the
lateral lemniscus and paralemniscal zone of an echolocating bat. J. Neuro-
COVEY, E. AND CASEDADAY, J. H. The monaural nuclei of the lateral lemniscus
in an echolocating bat: parallel pathways for analyzing temporal features of
FIG. 18. Binaurality of neurons in the vicinity of the VNLL. A: number of
neurons in each binaural category. For explanation of categories, see text. n = 159.
B: Histogram depicting degree of suppression in neurons that showed
binaural suppression. Percent suppression is the response at the highest ipsi-
laral intensity level (typically 10–20 dB above the level at the contralateral
car), relative to the response to contralateral stimulation alone. Contralateral
intensity level was typically 50–70 dB SPL. n = 37.

The VNLL of other species also contains regions similar to
what we have termed VNLLm in the rabbit. The VNLLm
probably corresponds to the “lateral tegmentum” of the cat (Glenden-
nning et al. 1981). However, for reasons we have already given
(Batra and Fitzpatrick 1997), we prefer the term VNLLm. The
VNLLm also appears cytoarchitecturally similar to the VLLs of
the guinea pig (Schofield and Cant 1997), in that both are inter-
stitial nuclei embedded in the fibers of the lateral lemniscus. The
VLLs, however, is located anterior to the main column of neurons
that constitute the VNLL. This may be because the medial limb of
the lateral lemniscus in the guinea pig is considerably less prom-
inent than in the rabbit. The anterior limb of the lateral lemniscus of
the rabbit appears to contain fewer neurons than the medial
limb, but these neurons appear to have similar responses to those
encountered in VNLLm.

The VNLLm does not correspond to the paralemniscal zone
as originally defined in the cat (Henkel 1981; Henkel and
Edwards 1978; May et al. 1990) and later used in mustache and
horseshoe bats (Covey et al. 1987; Metzner 1989). This
paralemniscal zone lies rostral to VNLL and medial to the
medial lemniscus and appears to be part of a pathway mediat-
ing motor responses to acoustic stimuli. The VNLLm also does
not correspond to the paralemniscal zone as defined by some
later authors in Eptesicus and mustache bats (Covey 1993;
Zettel et al. 1991) for reasons we have given previously (Batra
and Fitzpatrick 1997).

Many of the binaural neurons encountered in the VNLL
were not sensitive to ITDs but were instead EI. In a few of
these neurons the strength of suppression was weak and may
have been an artifact due to acoustic cross-talk. However, even
if these weakly suppressed neurons are excluded, there is still
a large number of binaural neurons in our sample. At least
some of these do lie in the VNLL, although they may be
restricted to the margins of this division. Aitkin et al. (1970)
also reported that binaural neurons in VNLL appeared to be
present only at its margins.

The partial segregation of monaural and binaural neurons pro-
vides a possible reconciliation between two earlier reports that
were in conflict over the proportion of binaural neurons in the
(1970) found that few neurons in the VNLL were binaural (11%),
whereas Guinan et al. (1972a,b) found a substantial number of
binaural neurons (35%). Neither of these studies specifically state
whether the region we call VNLLm was included in their defi-
nition of VNLL. Guinan et al. (1972b) do, in fact, illustrate several
binaural onset neurons near the medial border of VNLL. These
neurons may have been in VNLLm. Conceivably the two studies
sampled different populations, resulting in different estimates of
the number of binaural neurons.

In sum, the VNLL contains different groups of neurons with
a variety of monaural and binaural response properties. The
responses of many neurons reflect the prominent input from the
VCN, but some response properties are emergent in the VNLL.


