Single-Unit Responses in the Inferior Colliculus of Decerebrate Cats
I. Classification Based on Frequency Response Maps

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Ramachandran, Ramnarayan, Kevin A. Davis, and Bradford J. May. Single-unit responses in the inferior colliculus of decerebrate cats. I. Classification based on frequency response maps. J. Neurophysiol. 82: 152–163, 1999. This study proposes a classification system for neurons in the central nucleus of the inferior colliculus (ICC) that is based on excitation and inhibition patterns of single-unit responses in decerebrate cats. The decerebrate preparation allowed extensive characterization of physiological response types without the confounding effects of anesthesia. The tone-driven discharge rates of individual units were measured across a range of frequencies and levels to map excitatory and inhibitory response areas for contralateral monaural stimulation. The resulting frequency response maps can be grouped into the following three populations: type V maps exhibit a wide V-shaped excitatory area and no inhibition; type I maps show a more restricted I-shaped region of excitation that is flanked by inhibition at lower and higher frequencies; and type O maps display an O-shaped island of excitation at low stimulus levels that is bounded by inhibition at higher levels. Units that produce a type V map typically have a low best frequency (BF: the most sensitive frequency), a low rate of spontaneous activity, and monotonic rate-level functions for both BF tones and broadband noise. Type I and type O units have BFs that span the cat’s range of audible frequencies and high rates of spontaneous activity. Like type V units, type I units are excited by BF tones and noise at all levels, but their rate-level functions may become nonmonotonic at high levels. Type O units are inhibited by BF tones and noise at high levels. The existence of distinct response types is consistent with a conceptual model in which the unit types receive dominant inputs from different sources and shows that these functionally segregated pathways are specialized to play complementary roles in the processing of auditory information.

INTRODUCTION

The central nucleus of the inferior colliculus (ICC) receives converging projections from most, if not all, of the auditory nuclei in the brain stem and, in turn, provides nearly all of the input to the thalamocortical pathway (for review, Irvine 1986; Oliver and Huerta 1992; Oliver and Shneiderman 1991). Afferent projections to the ICC may be excitatory (e.g., cochlear nucleus, Oliver 1987; Semple and Aitkin 1980; superior olive, Glendenning et al. 1992) or inhibitory (e.g., dorsal nucleus of lateral lemniscus) (Adams and Mugnaini 1984; Roberts and Ribak 1987; Shneiderman and Oliver 1989; Shneiderman et al. 1988, 1993). The manner in which these inputs combine creates functionally distinct synaptic domains within ICC and presumably basic differences in ICC response types (Aitkin and Schuck 1985; Brunso-Bechtold et al. 1981; Maffi and Aitkin 1987; Oliver and Huerta 1992; Oliver et al. 1997; Roth et al. 1978; Ryugo et al. 1981; Shneiderman and Henkel 1987; Zook and Cassidy 1987).

ICC neurons have been classified previously according to excitatory response patterns, which are mapped in the frequency domain by recording single-unit responses to tone bursts across a range of frequencies and sound pressure levels (Aitkin et al. 1975; Bock et al. 1972; Ehret and Merzenich 1988; Fuzessery and Hall 1996; Ramachandran et al. 1997; Rose et al. 1963; Ryan and Miller 1978; Wang et al. 1996; Yang et al. 1992). The resulting frequency response maps exhibit three general patterns of excitatory tuning: open tuning curves that are V-shaped; level-tolerant tuning curves that remain narrow with level; and upper threshold (or closed) tuning curves that respond to a circumscribed range of stimulus frequencies and levels. At the present time, the inhibitory influences that shape ICC frequency response maps are not well characterized because most prior studies were conducted with anesthetized preparations that lack the necessary spontaneous activity for a direct demonstration of inhibition.

This report provides the first extensive evaluation of the inhibitory patterns of ICC neurons by sampling single-unit responses in unanesthetized, decerebrate cats. Results obtained with the decerebrate preparation support previous observations that there are three basic types of frequency response maps in ICC; in addition, it is shown that these response types differ mainly in the strength and distribution of inhibitory inputs. Frequency response maps of units with open tuning curves exhibit no inhibition (so-called type V units); the narrow bandwidth of units with level-tolerant tuning curves is flanked by strong inhibition (type I units); and units with closed tuning curves show predominantly inhibitory responses at levels above their islands of excitation (type O units). Other basic differences between these ICC response types include rates of spontaneous activity, shapes of BF tone and noise rate-level functions, and relative responsiveness to narrowband versus broadband stimuli. A companion paper (Davis et al. 1999) describes the binaural response properties of ICC neurons in decerebrate cats.

METHODS

Surgical preparation

Adult male cats (n = 8) with clean external ears and middle ears free of infection were used under institutional animal care guidelines. Cats were anesthetized with xylazine (2 mg im) and ketamine (initial
dose 40 mg/kg im; supplemental doses 15 mg/kg iv) and given atropine sulfate (0.1 mg im) to minimize mucous secretions. The cephalic vein was cannulated to allow intravenous infusions of fluids, and a tracheotomy was performed to facilitate quiet breathing. A core temperature of 39°C was maintained with a regulated heating pad. A midline incision was made over the skull and the temporoparietal muscles reflected to visualize the top of the skull and the ear canals. A craniotomy (~1 cm wide) was performed over parietal cortex, then the underlying cortex and brain stem (between the thalamus and superior colliculus) was aspirated to create a complete supracollicular decerebration; anesthesia was discontinued. The ear canals were transected near the tympanic annulus to accept hollow ear bars for delivering closed-field acoustic stimuli. The bullae were vented with ~40 cm of PE 200 tubing to prevent build-up of pressure in the middle ear. The cat’s head was secured in a stereotaxic frame. A second craniotomy was performed over occipital cortex and tissue overlying the IC was aspirated to visualize the recording site. In most subjects, complete access to the ICC required partial removal of the tentorium.

Gallamine triethiodide was administered to some cats (n = 4) to reduce brain pulsations that compromised the stability of recording. These subjects were placed on a mechanical respirator and maintained at an end-tidal CO2 of 4%. Gallamine paralysis was never induced within 8 h of the initial surgical preparation to ensure that the decerebration procedure was complete (as judged by lack of voluntary movements).

The cat was euthanized with an overdose of pentobarbital sodium (26 mg/kg iv) at the end of the recording session (48–72 h after start of surgery). The brain was perfused transcardially with phosphate (26 mg/kg iv) at the end of the recording session (48–72 h after start of surgery). The brain was perfused transcardially with phosphate buffer saline and fixed with 10% formalin in phosphate buffer. Completeness of decerebration was verified by examination of the thalamus and brain stem (between the thalamus and superior colliculus) was aspirated to create a complete supracollicular decerebration; anesthesia was discontinued. The ear canals were transected near the tympanic annulus to accept hollow ear bars for delivering closed-field acoustic stimuli. The bullae were vented with ~40 cm of PE 200 tubing to prevent build-up of pressure in the middle ear. The cat’s head was secured in a stereotaxic frame. A second craniotomy was performed over occipital cortex and tissue overlying the IC was aspirated to visualize the recording site. In most subjects, complete access to the ICC required partial removal of the tentorium.

Electrophysiological recordings were made in a sound-attenuating chamber. Stimuli were delivered via electrostatic speakers that were coupled to the hollow ear bars; this closed acoustic system produced a uniform response (±5 dB) at frequencies from 40 Hz to 40 kHz. Acoustic calibrations were performed with a probe tube microphone that inserted into the ear bars near the tympanic membrane. All test stimuli were 200 ms in duration with 10-ms rise/fall times; presentation rates were 1 burst/s. Unit activity was recorded with platinum-iridium microelectrodes. The electrode signal was amplified 10,000–30,000 times and low-pass filtered at 5 kHz. A variable threshold stimulus was used to discriminate action potentials; spike times were recorded relative to stimulus onset. Discharge rates are described in terms of driven rates; that is, the total response rate during a stimulus presentation minus spontaneous activity. Response rates were computed during the final 150 ms of the stimulus-on interval (to reflect steady-state responses) and spontaneous rates were measured during the final 400 ms of the stimulus-off interval of each 1-s stimulation period. This choice of response window eliminated most effects of adaptation; informal analyses suggest that response magnitudes, and not the general patterns of excitatory/inhibitory responses, were affected by changes in the duration of the response window.

Electrodes were advanced dorsally into the IC using a remote-controlled hydraulic micromanipulator (Kopf Instruments, CA). Search stimuli included 50-ms tone or noise bursts presented to the contralateral ear. As the electrode advanced, the frequency that excited background activity first decreased (usually from 10 to 20 kHz at the surface to ~1 kHz) and then increased. This reversal in the sequence of BFs, observed 1–2 mm below the surface of the IC, indicated entry into ICC (Atick et al. 1975; Merzenich and Reid 1974). In addition, units in ICC tended to exhibit simple spikes and have sharp tuning, whereas units outside the ICC (e.g., in dorsal cortex, ICD, or the external nucleus, ICX) tended to respond with complex spikes, show offset responses, have long latencies, and exhibit poor tuning.

When a single ICC unit was isolated, its BF was determined audiometrically and the following characterization protocol was initiated. Rate-level functions were obtained by sweeping the level of BF tones or broadband noise bursts over a 100-dB range. Frequency response maps were created by sweeping the frequency of tone bursts over a four octave range centered on unit BF. These frequency sweeps were presented at multiple sound levels, ranging from ~10 dB below to ~70 dB above threshold. Each frequency–intensity combination was presented once.

**RESULTS**

Results are based on 146 units from eight cats. Within this sample, 56 units were localized to the ICC based on histological reconstruction of electrode tracks; the remaining units were inferred to be in the ICC based on the sequence of BFs within tracks and the similarity of their response properties to those of histologically localized units. The photomicrograph in Fig. 1 shows one recording track through the IC; the reconstructed track is marked by a line and the electrolytic lesion is enclosed by a circle. In this track, the electrode was placed on the caudal aspect of the IC and passed through the ICD before entering the ICC. Other recovered electrode tracks passed through the ICX before entering the ICC, suggesting that the full extent of the ICC was sampled. Response properties of ICC units fell into two broad categories: units with sustained
discharges \( (n = 134) \) and units that responded with a single onset spike at all frequencies and levels \( (n = 12) \). Responses of onset units are not considered further in this report.

**Frequency response maps**

Units with sustained responses were divided into three groups based on the patterns of excitation and inhibition revealed in their frequency response maps (Table 1). Representative data for each unit type are shown in Fig. 2. In these plots, excitatory areas \( (■) \) are defined as stimulus conditions that elicited responses \( ≥1 \) SD above spontaneous activity; similarly, inhibitory areas \( (□) \) indicate tone-driven rates \( ≥1 \) SD below spontaneous activity. Type V units \( (top) \) have a V-shaped excitatory area that widens about unit BF (vertical line) with increasing sound levels. These units do not show inhibitory responses to pure tones. Type I units \( (middle) \) generally have an I-shaped excitatory area that maintains its sharp tuning at higher levels; this level tolerant excitatory area is flanked on both sides by wide inhibitory areas. Some (predominantly low-BF) type I units show less pronounced inhibitory effects at lower frequencies and thus exhibit more V-shaped excitatory areas; nonetheless, these units are easily distinguishable from type V units based on the presence of strong above-BF inhibition. Type O units \( (bottom) \) are characterized by an O-shaped island of excitation around BF threshold that gives way to inhibition at higher sound levels. Type O units may exhibit additional excitatory areas, but the frequency location of these responses is highly variable between units. Type V units were the least abundant unit type in our sample \( (16/134) \); type O units were the most prevalent \( (71/134) \).

Figure 3 shows the distribution of BFs for the three response types. The BFs of type V units were always low \( (<3 \) kHz), whereas the BFs of type I and type O units spanned most of the cat’s range of audible frequencies. As in previous studies (Aitkin et al. 1975; Merzenich and Reid 1974), BFs increased as the electrode advanced from the dorsal to ventral limits of the ICC. Consequently, the unit types were not distributed uniformly across the dorsoventral axis of the ICC. Type V units typically were recorded during the initial dorsal progression of the electrode track, and type I units were recorded more ventrally. Type O units dominated our sample and could be found throughout the course of most tracks.

ICC unit types show differences in the range of frequencies that evoke excitatory responses. Frequency tuning was assessed by calculating each unit’s Q values \( (\text{BF divided by bandwidth of the excitatory area in the frequency response map}) \). At 10 dB above threshold (Fig. 4A), \( Q_{10} \) values increase with BF until \( ∼10 \) kHz, after which they remain relatively unchanged. Most data points fall within the range of values recorded from auditory-nerve fibers (ANFs) in our laboratory (Calhoun et al. 1997; Miller et al. 1997); therefore, low-level frequency tuning in the ICC appears to be determined by peripheral processes. At 40 dB above threshold (Fig. 4B), type V units continue to follow the tuning properties of ANFs (data taken from Liberman 1978), while type O units show no

**Table 1. Response properties of ICC units with sustained discharge rates**

<table>
<thead>
<tr>
<th></th>
<th>Type V Units</th>
<th>Type I Units</th>
<th>Type O Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of units</td>
<td>16</td>
<td>47</td>
<td>71</td>
</tr>
<tr>
<td>Spontaneous rate, spikes/s</td>
<td>1.25</td>
<td>9.8</td>
<td>11</td>
</tr>
<tr>
<td>BF-tone threshold re ANF, dB</td>
<td>12</td>
<td>4</td>
<td>1.5</td>
</tr>
<tr>
<td>Max rate for BF tone, spikes/s</td>
<td>58</td>
<td>101</td>
<td>34</td>
</tr>
<tr>
<td>Max rate for noise, spikes/s</td>
<td>72</td>
<td>63</td>
<td>40</td>
</tr>
<tr>
<td>Noise threshold re tone threshold, dB</td>
<td>3.7</td>
<td>4.1</td>
<td>2.2</td>
</tr>
<tr>
<td>Norm slope for tone, /dB</td>
<td>−0.0012</td>
<td>−0.0081</td>
<td>−0.052</td>
</tr>
<tr>
<td>Norm slope for noise, /dB</td>
<td>0.0008</td>
<td>0.0019</td>
<td>−0.032</td>
</tr>
</tbody>
</table>

Table entries are median values. ANF, auditory nerve fiber. Noise thresholds were computed over a bandwidth 10 dB above the best frequency (BF)-tone threshold for each unit.
The lateral inhibitory sidebands of type I units maintain a sharply tuned excitatory area at levels well above threshold, as indicated by their comparable $Q_{40}$ and $Q_{10}$ values. A few predominantly low-BF type I units showed reduced low-frequency inhibition, which allowed the bandwidth of their excitatory areas to expand to produce $Q_{40}$ values seen in the auditory nerve.

Traditional $Q$ measures provide an adequate description of the strictly excitatory response areas of ANFs but fail to capture the frequency tuning properties of the inhibitory responses that characterize type I and O units. The bandwidths of these inhibitory tuning curves were quantified by calculating $Q_{40}$ values across the total width of the lower and upper inhibitory response areas, assuming that they form a single V-shaped area centered on BF. This metric is designated the $Q_{40}$ of inhibition and is plotted in Fig. 4C; for comparison, excitatory $Q_{40}$ values of ANFs also are shown. In general, the $Q_{40}$ of inhibition for both type I and type O units was a third of ANF $Q_{40}$ values. This broad bandwidth is presumably established by the convergence of multiple inhibitory inputs with different BFs. It is likely that these events occur at a lower level of auditory processing because inhibitory bandwidth is only slightly changed by pharmacological manipulations within the ICC (Davis et al. 1999).

Responses to BF tones

ON-BF responses were characterized by obtaining rate-level functions for BF tone bursts. Figure 5A shows representative data for each unit type; for display purposes, the functions have been smoothed with a triangularly weighted moving window average. Responses of the representative type V unit climb to a maximum and then maintain a steady discharge rate at higher stimulus levels. By contrast, the rate-level function of the type O unit is strongly nonmonotonic; as the level of the tone grows, the unit exhibits a rate increase followed by strong inhibition. The type I unit also exhibits nonmonotonicity at higher tone levels, but unlike the type O unit, the neuron does not show actual inhibitory effects at BF (i.e., the decline in driven rate does not fall below levels of spontaneous activity).

The degree of nonmonotonicity shown by each unit can be quantified by calculating the normalized slope of the saturated component of BF rate-level functions (Davis et al. 1996; Young and Voigt 1982). This measure involves normalizing...
response rates by the maximum rate of each function and then fitting a best fit line (least squares) to the portion of the curve between the maximum (or the first sharp change in slope) and the next inflection point (or end of the data). As illustrated on the rate-level function of the type V unit in Fig. 5A (---), the best fit line included data spanning $\leq 10$ dB. Units having more negative normalized slopes exhibit stronger nonmonotonicity.

Figure 5B shows the distribution of normalized slopes for each unit type; median values are marked (*). The typical saturating monotonicity of type V units is indicated by the clustering of values near 0. A majority of type I units displayed monotonic properties that were quite similar to those of type V units, although slopes in this response type also could be nonmonotonic (negative values). Type O units, on the other hand, exhibited exclusively nonmonotonic rate-level functions. Nonparametric statistical tests indicated that rate-level functions of type I units were significantly less nonmonotonic than those of type O units ($P < 0.001$, Mann Whitney $U$ test). Type V units were excluded from these statistical analyses because of their small sample size; however, Fig. 5B clearly shows the opposite polarity of type V versus type O responses at high stimulus levels (---).

Rate-level functions like those in Fig. 5A also can be used to define basic trends in spontaneous rate, BF threshold, and maximum firing rate for units in each response type; these data are summarized in Table 1. As shown in Fig. 6, most type V units (10/16) exhibited spontaneous rates $<5$ spikes/s; whereas, most type I (38/47) and type O (63/71) units had spontaneous rates $>5$ spikes/s.

The relationship between the absolute threshold and BF of ICC units was essentially identical to trends previously observed in the auditory nerve (Fig. 7A), except that the range of thresholds at a particular BF was more compressed in ICC and tended to fall along the best threshold curve of ANFs (shown by line) (Calhoun et al. 1997; Miller et al. 1997). These results suggest that the lower limits of auditory sensitivity for CNS neurons are established in the periphery. Further support for this interpretation is provided by histograms in Fig. 7B, which plot the distribution of ICC thresholds relative to the ANF best threshold curve at the same BF; negative values indicate ICC units with lower thresholds than their auditory nerve counterparts. Type V units tended to fall among the least sensitive units; most ICC neurons in this response type (13/16) had thresholds $>5$ dB above the auditory nerve best threshold curve. In contrast, many type I and type O units displayed relative thresholds that were $<5$ dB above the best threshold curve of ANFs. A few of these units produced thresholds that
were ≤5 dB below the most sensitive auditory nerve responses. This apparent hypersensitivity most likely reflects differences in threshold criteria between previous ANF studies and present methods: ANF thresholds were obtained from tuning curves based on a 20-spikes/s rate increase criteria; ICC unit thresholds were obtained from rate-level curves based on a rate change of 1 SD from spontaneous rate.

The differing amounts of on-BF inhibition shown by response maps in Fig. 2, and rate-level functions in Fig. 5A can influence the maximum driven rates elicited by BF tones. Figure 8 shows the distribution of maximum BF tone-driven rates for each unit type. Strong inhibitory effects in type O units were correlated with low maximum driven rates (median 34 spikes/s); while the less inhibited type I units achieved much higher rates (median 101 spikes/s). Interestingly, some type V units reached driven rates approaching 200 spikes/s, whereas others exhibited maximum driven rates <100 spikes/s. This latter result is somewhat surprising given the fact that type V units are the only response type to show no obvious signs of inhibition. Two properties of type V units may account for this variability in responsiveness to contralateral BF tones: first, their maximum discharge rate has a tendency to shift to lower frequencies with increasing sound level (Fig. 2), and second, many type V units respond maximally to ipsilateral stimulation (Davis et al. 1999). For the subset of five type V neurons that are known to be contralaterally dominated (■ in histogram), the median maximum discharge rate for contralateral stimulation is 152 spikes/s.

Responses to broadband noise

Almost all ICC units (118/122) responded to bursts of broadband noise, and generally, the response functions were similar in shape to those evoked by BF tones. Figure 9A shows representative noise rate-level functions for each unit type. As for BF tones, the feature that distinguishes the noise rate-level functions of each unit type is the degree of nonmonotonicity at high stimulus levels. The function for the type V unit shows a monotonically increasing discharge rate. The noise-driven rates of the type O unit exhibit a severe nonmonotonicity that leads to strong inhibition at levels >20 dB above threshold.
The noise rate-level function of the typical I unit is monotonic and saturating.

The distribution of normalized slopes for each unit type is shown in Fig. 9B. Values for 11/16 type V units fall near zero, which is a reflection of the minimal inhibition that is apparent in type V response maps. The five remaining type V units showed high noise thresholds and failed to reach saturation at the highest noise levels tested (e.g., Fig. 9A); the slope value is undefined for these units and is plotted off the axis. Monotonic noise rate-level functions were seen in 32/41 type I units (units to the right of - - -); the remaining units in this response class exhibited nonmonotonicity at higher noise levels, but discharge rates never fell to levels approaching spontaneous activity. For the majority of type O units (59/65), high levels of noise produced sufficient inhibition to reduce noise-driven rates down to or below levels of spontaneous activity; consequently, rate-level functions for this unit class tended to be highly nonmonotonic (41/65 with slopes below - - -). Nonparametric statistical tests indicated that noise rate-level functions of type O units were significantly more nonmonotonic than those of type I units (P < 0.001, Mann Whitney U test).

The magnitude of nonmonotonicity for each unit’s noise and BF tone-driven responses is compared in Fig. 10A, which plots the normalized slope of the noise rate-level function against values obtained with BF tones; the — represents equal slopes. Units with undefined noise slopes (e.g., the type V unit in Fig. 9A) are plotted above the axis. Note that the majority of the data points for all three unit types are broadly distributed along the equi-response line, suggesting that the shape of a unit’s noise response is largely predictable from its tone response. In particular, a unit’s noise response is usually more monotonic than its tone response (the data points lie above the equi-response line; P < 0.001, sign test). However, some units show very different degrees of nonmonotonicity for tones and noise. For example, some type O and type I units produced strongly nonmonotonic rate-level functions for tones but not for broadband noise.

Thresholds for noise responses are plotted as a function of BF in Fig. 10B. To allow a comparison with tone thresholds (data from Fig. 7A), noise thresholds are specified in terms of the total noise power in the bandwidth of each unit 10 dB above threshold. The overall distribution of noise thresholds shows a tendency to decrease as BF increases, which is similar to the pattern observed in the ICC of anesthetized cats (Ehret and Merzenich 1988). The lowest noise thresholds were observed at BFs between 8 and 30 kHz; whereas, very sensitive tone thresholds extended from 1 to 12 kHz. These trends suggest a divergence of noise versus tone sensitivity at low frequencies; however, for the majority of units, tone thresholds provided a good estimation of noise thresholds, as indicated by the scatterplot of tone versus noise thresholds in Fig. 10D. In general, neurons in the type O response class were the most sensitive units for both tones and noise. As was observed for BF tones, type V units tended to show relatively high noise thresholds in particular when compared with type O units with similar BFs.

Each unit’s maximum discharge rate for noise is plotted against its maximum tone-driven rate in Fig. 10C. Type I units showed significantly lower discharge rates when tested with noise than with tones (P < 0.001, sign test); this reduced responsiveness is most likely due to the effects of noise energy falling into the inhibitory sidebands that surround the narrow excitatory area of type I units. Type V units, where lateral inhibitory effects are presumed to be weak or nonexistent, exhibited no significant difference in maximum driven rates for tones and noise (P > 0.05, sign test). The maximum noise-driven rates of type O units were also not statistically different from their maximum tone-driven rates (P > 0.05, sign test); however, the scatter in these data suggests groups of units that may be biased toward either broadband or narrowband stimuli. Ten type O units showed excitatory responses when tested with tonal stimuli but were inhibited (8...
cases) or unresponsive (2 cases) to noise; these data are plotted along the x axis in Fig. 10C.

DISCUSSION

The response types in this report were identified with monaural stimulation of the contralateral ear. Other studies have proposed alternative classification systems that are based on patterns of excitation and inhibition for binaural stimuli (Aitkin et al. 1984; Irvine 1986 for reviews). Davis et al. (1999) investigates the binaural response properties of ICC neurons in decerebrate cats and describes the systematic relationships between the two classification schemes.

Does the decerebrate preparation yield normal physiological response types?

The advantage of the decerebration procedure is that it provides a preparation for long-term stable recording without the confounding effects of anesthesia. The decerebration techniques used in this study were directed toward the thalamus, which is the primary target of ICC projections. An important concern with this surgical approach is that the decerebration procedure may have damaged the distal axons of our neural sample and therefore altered their physiological properties. One extreme consequence of axotomy is neuronal degeneration. When sections through the ICC of three cats were examined under light microscope, normal-looking cell bodies were observed throughout the inferior colliculus and gliosis was restricted to locations of electrode tracks (Fig. 1).

It is possible that axotomy altered the response properties of ICC units without producing obvious signs of neural degeneration. Several studies have looked at the effects of acute axotomy on neurons in sensory ganglia (Czeh et al. 1977; Gallego et al. 1987; for review, see Titmus and Faber 1990) or CNS (Faber and Zottoli 1981; Kuwada and Wine 1981); few changes in electrophysiological properties were noted during time courses that extended well beyond the duration of our recording experiments (48–72 h). Our own results support those observations in that no obvious differences were seen in the response properties of units studied near the beginning or end of experiments.

As a further test of the reliability of the decerebration preparation, control experiments were conducted without decerebration in intact barbiturate-anesthetized cats. Figure 11 provides examples of the three types of frequency response maps that were obtained in these experiments. The maps clearly show the basic excitatory response properties that constitute the classification system proposed in Fig. 2. That is, units with open tuning curves (top) have V-shaped excitatory areas that are only as sharp as ANFs at 40 dB re threshold ($Q_{40} = 0.7$); level tolerant units (middle) have I-shaped excitatory areas that maintain their sharp tuning at higher levels ($Q_{40} = 3.2 >$ ANFs); and upper threshold units (bottom) have O-shaped islands of excitation around BF threshold that give way at higher levels to regions of little-or-no response. The upper threshold unit in Fig. 11 also shows a region of excitation above BF; this feature is shared, in part, by the type O unit in Fig. 2. The conspicuous absence of inhibitory responses for the level tolerant and upper threshold units is a side effect of anesthesia. Other electrophysiological studies of ICC units in anesthetized cats show similar distributions of the shape and bandwidth of excitatory response areas (Aitkin et al. 1975; Ehret and Merzenich 1988; Ramachandran et al. 1997; Wang et al. 1996).

Another detrimental effect of the decerebration procedure is that it disrupts descending inputs to the inferior colliculus.
Anatomic studies suggest that the ICC of the cat receives only sparse projections from the thalamus and little, or no, direct input from the cortex (Adams 1980; Andersen et al. 1980; for a review, see Huffman and Henson 1990; Oliver and Huerta 1992). Effects of de-efferentation are best assessed by comparing our results to the limited ICC data that have been obtained in intact, awake preparations. Excitatory tuning characteristics in the ICC of decerebrate cats are very similar to results obtained in awake bats (Yang et al. 1992) and primates (Ryan and Miller 1978). The distribution of spontaneous rates in decerebrate cats (Fig. 6) also matches that seen in awake cats (Bock and Webster 1974; Bock et al. 1972) and primates (Ryan and Miller 1978). Patterns of inhibition resemble those observed in awake primates (Ryan and Miller 1978). Although these earlier studies did not address the relationship between response pattern and BF, it is interesting that all examples of units with broad tuning at higher levels had low BFs, whereas the level tolerant units and the upper threshold units had high BFs. Our population of type V units was confined to frequencies <3 kHz, whereas the type I and type O units were more prevalent at higher frequencies (Fig. 3). The good agreement of results obtained in awake and decerebrate animals lends additional support to the assumption that our surgical procedure did not introduce fundamental changes in ICC discharge patterns.

**Origins of the unit types**

Neurons in the ICC can be grouped into two major anatomic classes based on somatic shape and dendritic distribution. Disc-shaped cells have compact dendritic fields that are oriented along the path of lemniscal fibers; consequently, these cells are thought to receive inputs from afferent neurons with similar BFs. Stellate cells have more broadly distributed dendrites that presumably integrate inputs across a wide range of BFs (Oliver and Morest 1984). A similar morphological dichotomy has been described for two classes of stellate cells (called planar and radiate) in the anteroventral cochlear nucleus (AVCN) (Doucet and Ryugo 1997). Intracellular studies suggest that AVCN planar neurons are sharply tuned in frequency and show sustained responses to tones, whereas radiate neurons are broadly tuned and show onset responses (Smith and Rhode 1989). If a similar morphological/physiological correlation holds in ICC, then sustained responses may reflect the activity of disc-shaped cells, whereas onset responses may originate from stellate cells. This interpretation is given some credence by the independent observation that anatomically defined stellate cells and physiologically defined onset-responders represent a small minority of ICC neurons.

Given the assumption that sustained responses in the ICC originate from the same population of disc-shaped cells, it is likely that functional differences between the three unit types reflect heterogeneity in their inputs. Principal cells in the medial superior olive (MSO), lateral superior olive (LSO), and cochlear nuclei have unique response patterns and are primary sources of innervation for the ICC. When anterograde tracers are injected into LSO and dorsal cochlear nucleus (DCN) (Oliver et al. 1997), labeled axons from the two sources remain segregated in some regions of the ICC but overlap at other locations. This topographical organization suggests that synaptic domains within the ICC are created to perform the dual role of relaying information from individual sources of input to higher processing levels and integrating information across auditory nuclei (Semple and Aitkin 1981). From this perspective, responses of disc-shaped cells may be expected to reflect a mixture of the physiological properties of their ascending inputs and may even be essentially identical to their inputs within regions of the ICC where anterograde labeling indicates little convergence (Oliver and Huerta 1992).

Several lines of experimental evidence lead to the conjecture that type V response patterns are strongly shaped by inputs from the MSO. Type V units have broad excitatory areas without overt inhibition, low spontaneous discharge rates, and relatively high thresholds. Of the primary sources of input for inferior colliculus, these characteristics most closely match the response properties of MSO units (Goldberg and Brown 1969;
Guinan et al. 1972). More than 50% of the MSO is devoted to the processing of frequencies < 4 kHz; type V units in the ICC also reflect a strong bias toward low-frequency sensitivity. Injections of anterograde autoradiographic tracers in dorsal MSO (i.e., the low-frequency half of the nucleus) produce tonotopically organized labeling in dorsal-lateral ICC (Aitkin and Schuck 1985; Henkel and Spangler 1983); in the present study, type V units were recorded primarily at low BFs during the initial dorsal penetration of electrode tracks. Although most MSO neurons project to the ipsilateral ICC, binaural response properties are established before this one-sided distribution of MSO input. Like MSO neurons, type V units in the ICC show exclusively excitatory responses when stimulated with BF tones in either ear (EE) and are more sensitive to binaural than to monaural stimuli (Davis et al. 1999).

Type I units have high BFs and level tolerant excitatory areas that are flanked by inhibitory areas. These physiological characteristics suggest that the LSO is the primary source of ascending inputs for neurons of this response type (Caird and Klinke 1983; Guinan et al. 1972; Tsuchitani and Boudreau 1966), although the significant projection from stellate cells in the contralateral AVCN cannot be discounted as an additional or alternate source of ascending input (Adams 1979, 1983; Cant 1982; Osen 1972; Ryugo et al. 1981; Shofner and Young 1985). Rate-level functions of type I units show a mixture of monotonic and nonmonotonic responses that also is seen in the LSO of decerebrate cats (Brownell et al. 1979). In addition, type I units are excited by contralateral tones but inhibited by ipsilateral tones (EI) (Davis et al. 1999); neurons with these so-called EI binaural properties are found mainly in LSO (Guinan et al. 1972; Tsuchitani and Boudreau 1969).

Type O units have high BFs and receptive fields dominated by inhibition at high levels. These properties suggest that the inputs to this unit type are derived from the DCN (Spirou and Young 1991; Young and Brownell 1976). The ICC receives direct inputs from pyramidal and giant cells in the DCN (Adams 1979; Osen 1972; Ryugo et al. 1981). Like type O units in ICC, the DCN projection neurons have frequency response maps that show consistent BF excitation only at stimulus levels near threshold (the so-called type IV unit response). As a result, highly nonmonotonic rate-level functions are observed for both type IV and type O units if BF tones are used as stimuli. Although the binaural properties of the DCN have not been studied in great detail (Mast 1970, 1973), type IV units can show both EE and EI response patterns, which are also a property of type O units (Davis et al. 1999). Despite these basic similarities, the preponderance of type O units in our sample is at odds with the relatively minor DCN projection to ICC (Adams 1979). This apparent discrepancy suggests either a sampling bias (e.g., type O units are recorded from the larger disc-shaped neurons) (Oliver and Morest 1984) or that DCN afferents ramify widely in ICC (Oliver et al. 1997). Alternatively, these data suggest that type O unit properties are also created at the level of the ICC by a suitable convergence of excitatory and inhibitory inputs (Yang et al. 1992).

**Signal processing in the ICC**

The existence of three physiologically distinct response types (with sustained responses) suggests that ICC neurons may be specialized for different aspects of signal processing. Because type V units have low BFs and predominantly excitatory response patterns, their inputs are hypothesized to have origins in the MSO. Acoustic information is carried from the auditory nerve to the MSO through a pathway that is defined by its powerful synaptic coupling (Schwartz 1972, 1992). It has been suggested that this is the primary channel for transmitting the timing of spike discharge rates to higher levels of processing (Irvine 1986, 1992). Consequently, type V units may play an important role in auditory behaviors that require faithful transmission of temporal information such as the encoding of stimulus location based on interaural time difference cues (Kuwada and Yin 1983; Yin et al. 1986, 1987).

Level-tolerant tuning curves like those shown by type I units have been found at multiple levels in the bat auditory system and have been proposed as a mechanism for maintaining frequency selectivity at high sound levels (Olsen and Suga 1991; Suga and Tsuzuki 1985; Yang et al. 1992). In this interpretation, lateral inhibition attaches a specific frequency to a neuron by preventing expansion of excitatory bandwidth. Lateral inhibition also may make type I units ideal candidates for detecting narrowband signals in noisy environments either by reducing the effective bandwidth of masking noise at higher stimulus levels (the power spectrum model of masking) (Patterson and Moore 1986) or by reducing the responsiveness to wideband relative to narrowband stimuli. One potential difficulty in the latter case, however, is that the noise-evoked activation of the extensive inhibitory sidebands of the unit could result in complete inhibition of the excitatory response to the narrowband stimulus. Type I units do not appear to suffer from this drawback as their noise-driven rates are almost never reduced to zero (Fig. 10C), and preliminary observations suggest that type I units do provide the best representation of BF tones in noise (Ramachandran et al. 1997). In the visual system, retinal ganglion cells use a receptive field organization similar to type I units to reduce visual noise (Werblin 1974). Like their presumed LSO inputs, type I units are also sensitive to interaural level differences (Davis et al. 1999).

Type O responses are similar to the upper threshold units that have been described throughout the auditory system of bats (Suga and Manabe 1982; Yang et al. 1992); these units have been characterized previously as “feature detectors” because they respond under such a restricted set of stimulus conditions. It also has been suggested that units with strongly nonmonotonic rate-level functions may be specialized for intensity coding because unlike monotonic units they do not respond to an upwardly unlimited range of stimulus levels (Brugge and Merzenich 1973; Phillips et al. 1985; Suga and Manabe 1982). To represent all discriminable sound levels, it is expected that a population of level-tuned units would show different “best intensities,” which sum to encompass the full range of hearing. Our results do not support this interpretation in that all type O thresholds fell within 30 dB of the most sensitive neural thresholds. If the basic similarities between type O response pattern in ICC and type IV responses in DCN reflect a direct input, type O units also may be involved in sound localization. Young and his colleagues have shown that DCN type IV units respond selectively to peaks and notches in the spectrum of broadband sounds (Nelken and Young 1994; Young et al. 1992). In the normal behavioral repertoire of the cat, these sharp spectral features are created by the filtering properties of the pinnae (Rice et al. 1992) and must be present...
for accurate localization of complex sounds (Huang and May 1996).

The similarity of ICC response types to those of lower-level brain stem neurons, including their sensitivity to interaural level differences described by Davis et al. (1999), suggests that the parallel pathways evident in the cochlear nucleus and superior olive may remain segregated at the level of the inferior colliculus. Although the systems described in this paper resemble those at lower levels, the presence of convergent inhibitory inputs in the colliculus, such as projections from the dorsal nucleus of the lateral lemniscus, and the fact that there are several ascending inputs to the colliculus that were not considered earlier, such as the periolivary nuclei and nucleus of the lateral lemniscus, argue that the inferior colliculus is not merely relaying an unmodified representation from below. Some of the modifications in the ascending representation involve binaural properties (e.g., McAlpine et al. 1998), some involve temporal sensitivity (Delgutte et al. 1998; Langner and Schreiner 1988; Litovsky 1998), and others remain to be revealed by studies of complex natural stimuli.

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