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SINGLE UNIT ANALYSIS OF THE POSTEROVENTRAL COCHLEAR NUCLEUS OF THE DECEREBRATE CAT

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Abstract—Single unit recordings were obtained in the cochlear nuclear complex of the unanesthetized, decerebrate cat. Sixty-six of 282 units were localized to the posteroventral cochlear nucleus, 17 from the multipolar cell area and 49 from the octopus cell area. Spontaneous rates ranged from less than 1 to 75 spikes per second in the multipolar cell area and from less than 1 to 135 spikes per second in the octopus cell area. Poststimulus time histograms revealed four response types, at the best frequency, in the posteroventral cochlear nucleus. These responses were: (1) primary-like (maximum response shortly after the stimulus onset, followed by a reduction in activity to a steady state); (2) chopper (similar to primary-like but with multiple peaks in the first 10–15 milliseconds); (3) onset-ex (onset response followed by a low level of excitation); and (4) onset-in (onset response followed by inhibition). The onset-in responses represented the first observations of inhibition, at best frequency, for onset units in the mammalian cochlear nuclear complex. Analysis of interspike interval distributions showed that both spontaneous and driven activity consisted of irregular intervals for all four response types.

Activity-intensity functions for primary-like, chopper and onset-ex units showed monotonic increases with increases in stimulus intensity. Activity-intensity functions for onset-in units were non-monotonic. Latency-intensity functions for primary-like, chopper and onset-ex units exhibited monotonic decreases with increases in intensity. Latency-intensity functions for onset-in units were non-monotonic. In contrast to primary-like, chopper and onset-ex units, onset-in units do not retain the intensity and temporal information coded in the eighth nerve, as least for stimuli above 2 kilohertz. It is hypothesized that a depolarization block, caused by the massive eighth nerve input to octopus cells, is responsible for the inhibition observed from onset-in units.

The posteroventral cochlear nucleus (PVCN), within the cochlear nuclear complex, can be parcelled into two divisions, one rostral and one caudal. Osen[35] referred to the rostral PVCN as the multipolar cell area (MCA); it consists of a heterogeneous group of multipolar and small cells.[24,35] The caudal pole of the PVCN, containing a relatively homogeneous population of octopus cells, with an occasional small cell,[24,28,35] was termed the octopus cell area (OCA) by Osen.[35] Kane's[24] Golgi and electron microscopic study demonstrated that primary (8th nerve) endings terminate on more than 70% of the somatic and proximal dendritic surface of octopus cells. Anterograde tracing studies, using labelled amino acids, confirmed the observations that octopus cells receive a massive somatic input from the cochlea.[23,27] In contrast, electron microscopic studies of multipolar (stellate) cells in the posterior region of the anteroventral cochlear nucleus have revealed that less than 15% of their somatic surface is covered by synaptic terminals.[44]

Godfrey, Kiang & Norris[17] conducted a systematic single unit investigation of the PVCN in the barbiturate anesthetized cat. These investigators classified their units according to the appearance of the poststimulus time histogram (PSTH) pattern to 25 ms tone bursts at the unit's best frequency, 10–15 decibels (dB) above threshold. On this basis three types of units were identified in the MCA: chopper units (a multipeaked response, whose peaks are not related to the frequency of the stimulus), primary-like units and 'extraordinary' units. Most units within the OCA displayed little or no spontaneous activity; the main response to a tone burst was a spike which shortly followed the onset of stimulus. The onset responses were of two types: on-type I, with no activity after an initial spike, and on-type L, with a low level of activity after the initial spike(s); these responses were presumed to come from octopus cells. Although high intensity stimuli did not affect the response of on-type I units, such stimuli elicited from on-type L units an increased number of discharges, leading to a chopper response at highest intensities. To high intensity, 900 ms tones, on-type L units showed a primary-like response or a dip response (similar to a primary-like

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Abbreviations: dB SPL, decibels sound pressure level; MCA, multipolar cell area; ms, millisecond; OCA, octopus cell area; PSTH, poststimulus time histogram; PVCN, posteroventral cochlear nucleus; onset-ex/in PSTH pattern of onset followed by excitation/inhibition.

response, but with a decrease in response rate between the onset transient and the steady state discharge). Romand[38] and Gisbergen, Grashuis, Johannesma & Vendrik[15] have also observed onset responses in the OCA of the anesthetized cat.

Most physiological studies of the cochlear nuclear complex, including all studies of the PVCN, have used anesthetized preparations. However, discharge patterns may differ between barbiturate and decerebrate preparations, as has been shown in the dorsal cochlear nucleus[14,55] and in the lateral superior olive.[6] Webster & Aitkin[50] have pointed out that units in several regions of the auditory system display higher spontaneous rates in the unanesthetized state than in the anesthetized state. Such findings led us to investigate whether there are similar differences between the response characteristics of PVCN neurons in the anesthetic-free cat and in the anesthetized cat.

EXPERIMENTAL PROCEDURES

Animal preparation

Units reported in this study came from 15 cats of either sex. Animals were anesthetized with halothane in a mixture of 67% nitrous oxide and 33% oxygen and were rendered decerebrate by a pre-collicular transection of the brainstem. Anesthesia was discontinued after decerebration. The posterior fossa approach was used to expose the caudal part of the cochlear nuclear complex, which could be viewed by aspiration or displacement of a small portion of the choroid plexus.

Glass-coated platinum-iridium electrodes[52] with tips 10–20 micrometers long and 15 micrometers wide, and with resistances of 1–15 megohms, were used. After positioning the electrode behind the PVCN, the exposure was flooded with 3% agar-agar in saline to reduce brainstem pulsations and to keep the nervous tissue moist. The electrode was advanced in a horizontal plane with a David Kopf hydraulic microdrive. Noise bursts were used to probe for units. The integrity of the peripheral auditory system was monitored by checking the neurophonic.[51,53] Measurements of the brain surface depth and the depth of a lesion made at the end of an electrode track were used for subsequent reconstruction of the track.

When a recording session was completed, the animal was perfused through the heart with 10% formalin, following a saline exsanguination. The brain was removed, prepared for frozen sectioning and cut in a horizontal plane (same plane as the electrode tracks). Serial sections through the cochlear nuclear complex were stained for Nissl substance with Cresyl-echt violet or thionine. Electrode track reconstruction, based on Osen's[35] classification, allowed for localization of the recording sites within the cochlear nuclear complex.

Stimulus presentation and data collection

Short tone presentations consisted of 50 repetitions of a 200 ms signal with a one second interstimulus interval or, at later stages of the study, 500 repetition of 25 or 50 ms duration with a 100 ms interstimulus interval. Long tones were 1000 ms in duration, at a 5 s interstimulus interval. All stimulus presentation, data collection, data storage and on-line data analysis were under the control of a Digital Equipment Corporation PDP 11/40 computer.[10] The computer controlled stimulus frequency (Krohn-Hite 4031R programmable oscillator); the stimulus envelope was shaped by a Grason-Stadler electronic switch. The stimulus had a rise-fall time of 2.5 ms, as in Godfrey *et al.*[17] and Adams.[1] The electrical signal was amplified by a CEG galvanometer amplifier and then attenuated by a Grason-Stadler programmable attenuator. Sound was produced at the eardrum by a Beyer DT-48 earphone. Calibration of sound intensity in the closed acoustic system was achieved with a probe tube and microphone (General Radio 1962-9602); output of the microphone was measured with an Ortholoc-SC 9505E lock-in analyzer. The probe tube was placed within one to two millimeters of the tympanic membrane.

Responses from the electrode were carried over a short lead to a preamplifier (Tektronix RM 122 or, in later experiments, to a Princeton Applied Research 113). Electrical activity was band pass filtered between 0.3 and 3 kilohertz and a Schmitt-trigger was used to generate pulses coincident with action potentials. The Schmitt-trigger pulses went to one channel of a six channel pulse interval timer, with 2 microsecond resolution. The pulse interval timer digitized the time intervals between successive Schmitt-trigger pulses for subsequent analysis.[9,10] Data were stored on magtape for off-line analyses.

Data analysis

Spontaneous rates were obtained from records of subthreshold and near threshold stimulation and were computed from a time window during the last half of the interstimulus period. Data collected during the tone burst were used to generate PSTHs and interspike interval histograms.[19,21] The variability in interspike intervals for spontaneous activity was indexed by the coefficient of variation, which is the standard deviation around the mean interval, divided by the mean interval.[19,20,49] Symmetry ratios[36] were determined from interspike interval histograms by finding the ratio between the time from the beginning of the histogram to the mode and the time from the mode to the end of the histogram, at a level of 10% of the height of the mode. The bin width was adjusted such that the largest bin contained 15% of the total spike count. In addition to analysis of spontaneous activity, interspike interval distributions were evaluated from driven activity during the last half of the stimulus. The coefficient of variation at a standard mean interval of 15 ms was calculated from a regression line through values of the mean interval *versus* standard deviation.[18,21] Activity-intensity functions, representing the summed driven activity minus the summed spontaneous activity, were plotted in counts (spikes) *versus* intensity.

Latency data were obtained for the first driven spike after the stimulus onset. All latency data were computed from the respone to tone presentations, which had a 2.5 ms rise-fall time. A conduction delay period, which takes into account time for air and bone conduction, inner ear mechanics, receptor transduction, synaptic delays and eighth nerve conduction delays, was excluded in the measure of latency. This value was based on the observations that onset units have latencies, to click stimulation, of approximately 2.0 ms.[17] Unit events occurring during a conduction delay period between 0–2.0 ms were excluded from latency calculations.

Statistical analyses included determination of the correlation coefficients between best frequency and spontaneous