Representation of a low-frequency tone in the discharge rate of populations of auditory nerve fibers

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Discharge rates for populations of single auditory nerve fibers in response to 1.5 kHz tone bursts were measured in anesthetized cats. Separate plots of average rate vs. best frequency (rate-place profiles) were made for high, medium and low spontaneous rate (SR) auditory nerve fibers. At the lowest sound levels studied (34 dB SPL), all three SR groups show a peak in the rate-place profile centered around 1.5 kHz. At the highest sound levels studied (87 dB SPL), the average rates of the high and medium SR fibers are saturated across a wide range of best frequencies, but a peak around 1.5 kHz is maintained in the rate-place representation of the low SR fibers. These results show that in addition to the temporal information present in the discharge patterns of auditory nerve fibers, a rate-place representation of a single low-frequency tone exists in the auditory nerve over a wide range of sound levels.

Introduction

At low sound pressure levels, a plot of average discharge rate versus best frequency (BF) for the population of auditory nerve fibers responding to a single pure tone shows a peak centered around the frequency of the tone (Evans, 1981; Kim and Molnar, 1979; Pfeiffer and Kim, 1975). We refer to such a plot as a rate-place profile (Sachs and Young, 1979). The peak in the rate-place profile is maintained over a wide range of sound pressure levels for high-frequency tones (Evans, 1981), but not for low-frequency tones (Kim and Molnar, 1979; Pfeiffer and Kim, 1975). The difference in the population behavior for high- and low-frequency tones is presumably related to the sharper tuning curves of high-frequency auditory nerve fibers (Evans, 1981). One interpretation of this result is that tone frequency can be encoded by average rate at high frequencies, while at low frequencies temporal information must be used.

On the other hand, studies with more complex stimuli such as tones in noise (Barta, 1985; Costalupes, 1985) and steady-state vowels (Sachs and Young, 1979) have shown that a rate-place representation of the stimulus spectrum is preserved over a wide range of sound pressure levels by the low spontaneous rate (SR) population of auditory nerve fibers. Low SR auditory nerve fibers have higher thresholds (Liberman, 1978) and wider dynamic ranges (Evans and Palmer, 1980; Sachs and Abbas, 1974; Schalk and Sachs, 1980) than do high SR auditory nerve fibers. In addition, low and high SR fibers have different morphological characteristics (Fekete et al., 1984; Liberman, 1982; Liberman and Oliver, 1984; Rouiller et al., 1983). The earlier studies of Pfeiffer and Kim (1975) and Kim and Molnar (1979) did not separate low SR fibers in a way which would enable us to determine if a rate-place representation of a low-frequency tone is maintained at high stimulus levels in these fibers. Therefore, we have re-examined the rate representation of a single low-frequency tone and analysed the contributions of low, medium and high SR fibers separately.

Methods

Two adult cats (2.0 and 3.4 kg) whose middle ears were free of infection were used. They were
injected intramuscularly with 0.3 mg of atropine to suppress mucous secretions and initially anesthetized with an intramuscular injection of ketamine (100–120 mg). The saphenous vein was cannulated and cats were maintained under anesthesia with intravenous injections of sodium pentobarbital. A tracheotomy was performed. Cats were placed in a sound-proof room (IAC-1204A) and their body temperature was maintained between 36 and 38°C. The external meatus was exposed and transected. The bulla was exposed and a small hole was drilled through the wall. A long piece of 0.86 mm I.D. polyethylene tubing (approximately 90 cm in length) was cemented to the hole in order to vent the bulla and prevent the development of negative pressure in the bulla (Guinan and Peake, 1967). The cranium between the tentorium and nucal ridge was removed and the cerebellum was gently retracted to expose the auditory nerve. Glass micropipettes filled with 3 M NaCl (10–40 MΩ) were used to record single auditory nerve fibers.

Acoustic stimuli were delivered from an electrostatic driver (Sokolich, 1977) through a hollow ear bar. Sound pressure at the eardrum was measured with a probe tube for each animal. This system typically has a flat frequency response (±5 dB) from 20 Hz to 20 kHz. Search stimuli consisted of 50 ms broadband noise bursts with 10 ms rise/fall times. The test stimulus was a digitally synthesized 1.5 kHz tone burst (400 ms duration; 10 ms rise/fall times) presented once per second.

When a fiber was isolated, its best frequency (BF) and threshold were determined with audiovisual cues. Single fiber thresholds at BF of the sampled population were used to monitor the physiological state of the cochlea. Spontaneous rate was estimated as the average rate over an interval of at least 3 s in the absence of any controlled acoustic stimuli. The 1.5 kHz tone was presented at four standard sound pressure levels, and average driven discharge rate was estimated on-line for the interval between 20 and 400 ms after the onset of the tone. Approximately 1000 spikes were collected in response to the 1.5 kHz tone at each level studied.

Results

Rate profiles of the sampled populations of auditory nerve fibers to a 1.5 kHz tone burst are shown in Fig. 1 for two cats. These profiles are plots of average discharge rate versus fiber BF. Average rates were computed for the last 380 ms of the 400 ms tone bursts. Data from high SR fibers (SR greater than 19 spikes/s) are plotted with crosses; data from medium SR fibers (SR between 1 and 19 spikes/s) are plotted with triangles; and data from low SR fibers (SR less than 1 spike/s) are shown by squares. The solid lines in Fig. 1 show a moving window average of the rate of only the high SR auditory nerve fibers. For both cats, there is a peak in the rate profile of the high SR population centered around 1.5 kHz at the lowest sound pressure levels we presented (Fig. 1A, C). However, at higher sound pressure levels (Fig. 1B, D) there is no clear peak around 1.5 kHz,
and the discharge rate is roughly constant across a range of BFs from 1.0 to 6.0 kHz. In order to study more fibers with BFs near 1.5 kHz, we did not study fibers with BFs greater than 10.0 and generally not greater than 7.0 kHz. Note also that at the low sound pressure levels (Fig. 1A, C) the average rate around 1.5 kHz is the same as the average rate at high levels (Fig. 1B, D), suggesting that the high SR auditory nerve fibers with BFs near 1.5 kHz are already saturated at these low levels. This result is similar to that previously reported by Kim and Molnar (1979) for a 1.0 kHz tone.

The behavior of the low SR auditory nerve fibers is clearly different from that of the high SR population. The dotted line in Fig. 1 shows a moving window average of the rate of only the low SR auditory nerve fibers. At the higher sound pressure levels where the discharge rate of the high SR fibers is saturated across a wide range of BFs (Fig. 1B, D), the rate profile of the low SR fibers shows a clear peak near 1.5 kHz.

The effect of increasing sound pressure level on the rate profiles for the three populations of auditory nerve fibers is further illustrated in Fig. 2. Here we show only the moving window averages for the low, medium and high SR populations of

![Fig. 2. Plots showing the moving window averages for the average discharge rate as a function of best frequency at the sound pressure levels indicated for experiments 2/21/85 and 3/12/85. Moving window averages are shown for high (---), medium (----) and low (-----) SR auditory nerve fibers.]

![Fig. 3. Scatter diagram showing the thresholds for low (O) and high (x) SR auditory nerve fibers. Thresholds were determined from audiovisual cues. Thresholds for medium SR fibers have been omitted for clarity. Mean thresholds of high and low SR fibers with BFs between 3 and 6 kHz are 6.2 dB SPL and 17.1 dB SPL, respectively.]

auditory nerve fibers with dotted, dashed and solid lines, respectively. At 34 and 37 dB SPL, the lowest level studied in each cat (Fig. 2A, E), all three populations of auditory nerve fibers show a peak in average rate near 1.5 kHz. At intermediate sound pressure levels (Fig. 2B, F), the peak near 1.5 kHz is lost in the high SR population as excitation begins to spread, and fibers with BFs above and below 1.5 kHz begin to saturate. The 1.5 kHz tone is still represented in terms of average rate by a clear peak in both the low and medium SR populations of auditory nerve fibers at 54 and 57 dB SPL (Fig. 2B, F). As sound pressure level is further increased to 84 and 87 dB SPL (Fig. 2C, D, G, H), the peak at 1.5 kHz is lost in the medium SR population as fibers with BFs removed from 1.5 kHz begin to respond and are driven into saturation at the highest levels. Nevertheless, at these high sound pressure levels a clear peak around 1.5 kHz remains in the rate profile for the low SR population.

Discussion

The results of the present study show that a 1.5 kHz tone can be represented in terms of average discharge rate over a wide range of sound levels. At high sound pressure levels where the driven rates of the high SR auditory nerve fibers are saturated across a wide range of BFs, the low SR population maintains a peak in the average rate profile around 1.5 kHz. This peak at high sound levels in the rate profile of the low SR auditory nerve fibers reflects the higher thresholds (Liberman, 1978) and wider dynamic ranges (Evans and Palmer, 1980; Sachs and Abbas, 1974; Schalk and Sachs, 1980) of these fibers relative to those of the high SR group.

In one case, at the highest level studied (Fig. 2H), the average rate of the low SR auditory nerve fibers in the 3–6 kHz region approaches that of the high and medium SR fibers. However, in the BF range of 3–6 kHz where the spread of excitation occurs, the mean thresholds for high SR fibers is 6.2 dB SPL and is 17.1 dB SPL for low SR fibers, and there are no fibers included in this sample with thresholds greater than 20 dB above the mean high SR thresholds (Fig. 3). On the other hand, Liberman (1978) reports low SR fibers with thresholds close to 40 dB above those of the high SR group for normal cats. Liberman found such high threshold fibers with electrical stimulation through the recording electrode; we did not search for fibers with electrical stimulation. Spread of excitation in these very high threshold fibers would be expected to be less than that observed in our sample. Nevertheless, even in the population shown in Fig. 2H, the discharge rate for low SR fibers with BFs around 1.5 kHz is still higher than those fibers with BFs between 3 and 6 kHz where the spread of excitation occurs. Even such a small peak could be sharpened and amplified by inhibitory sideband mechanisms in the cochlear nucleus.

The suggestion that frequency is encoded in average rate across the population of low SR fibers at high levels requires that the responses of these fibers be heavily weighted at high sound levels. Such a weighting has been proposed and modeled by Delgutte (1982) for responses to speech sounds. The low SR fibers represent approximately 15% of the auditory nerve population (Liberman, 1978).

In this regard it is interesting that low and medium SR fibers show more complex branching patterns (Fekete et al., 1983) within the cochlear nucleus and have a significantly greater number of bouton terminals and en passant swellings (Rouiller et al., 1983) within the cochlear nucleus than do high SR fibers. Furthermore, Shofner and Young (1985) have found that some non-spontaneous units in the cochlear nucleus characterized by chopper discharge patterns to tone bursts have BF rate–level functions similar to those of low SR auditory nerve fibers, i.e. they have sloping saturation (Sachs and Abbas, 1974; Schalk and Sachs, 1980). These observations suggest that the rate representation present at high levels in low SR auditory nerve fibers might be preserved in at least some subvssystems in the cochlear nucleus.

In summary, we have shown that a rate–place representation for the frequency of a single low frequency tone is maintained at high stimulus levels by the low SR population. This result and similar ones for more complex stimuli (Barta, 1985; Costalupes, 1985; Sachs and Young, 1979) emphasize the importance of considering average rate codes as seriously as codes based on temporal properties of discharge patterns (Young and Sachs, 1979).
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References


