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Spatial Profiles of Correlation in Spike Timing to Broadband Noise Across Auditory Nerve

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Background

The cat auditory nerve (AN) contains ~50000 neurons innervating ~2500 inner hair cells across the cochlear basilar membrane. We are interested in the extent to which these neurons carry correlated temporal patterns, which depends on both the acoustic stimuli and intrinsic properties of the auditory periphery. Due to cochlear filtering, even Gaussian broadband noise (BBN) – for which adjacent frequencies have random phase – can produce correlated responses in fibers originating from nearby cochlear positions. We studied the spatial profile and extent over which correlated responses to broadband noise are found in the AN.

Methods

Neural responses to repeated presentations of a single token of BBN (frozen noise, 50-30.000 Hz, 0.6 or 1s in duration) were obtained from all fibers encountered in a given nerve. We collected spike trains from 149 AN fibers in 4 cats at 50dB SPL and 168 fibers in 5 cats at 70dB SPL. Spike trains from each fiber ("reference fiber") were compared with spike trains of all other fibers ("test fibers") of the same animal in order to obtain normalized same-stimulus cross-correlograms (SCC) (Figure 1C). As reported earlier [2], such SCCs show maxima at delays that depend on the distance between cochlear positions of the two fibers (Figure 2). We measured correlation in two ways: a) as the height of the largest peak of the SCC ("PH"), and b) as the SCC value at zero delay ("T0") (Figure 3A). The spatial correlational profiles were quantified in two ways: a) as the full-width at the half maximum (FWHM or "half-width"), and b) as the correlation area under the spatial profile (CA) (Figure 3B)

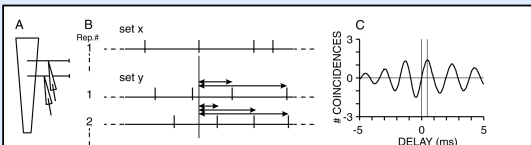


Fig. 1 A) Consecutive recordings from pairs of AN fibers. Trapezoidal shape represents uncoiled basilar membrane. B) Counting of spike coincidences between responses from a pair of AN fibers. C) Cross-correlogram for a pair of fibers with CFs of 522 Hz and 617 Hz. No smoothing or fitting has been applied. [From 2]

Same-stimulus cross correlograms SCC

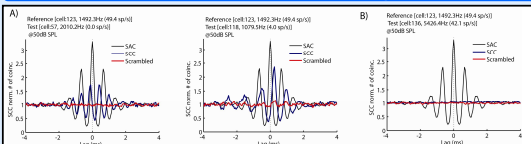


Fig. 2 Same-stimulus cross-correlograms (blue lines, SCC) of the reference fiber (CF=5.5 kHz) with A) two fibers with similar CF (2 kHz and 1 kHz) and B) a fiber with high CF (5.4 kHz). Notice the shifts of the SCC compared to the auto-correlogram of the reference fiber (black lines) caused by traveling wave delays in the cochlea.

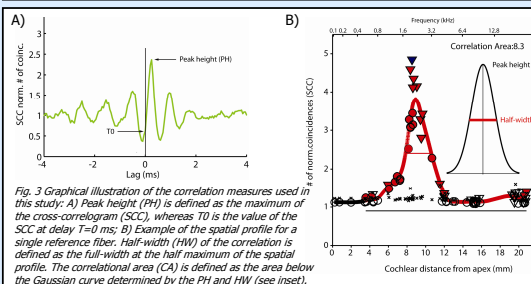


Fig. 3 Graphical illustration of the correlation measures used in this study. A) Peak height (PH) is defined as the maximum of the cross-correlogram (SCC), whereas T0 is the value of the SCC at delay T=0 ms; B) Example of the spatial profile for a single reference fiber. Half-width (HW) of the correlation is defined as the full-width at the half maximum of the spatial profile. The correlation area (CA) is defined as the area below the Gaussian curve determined by the PH and HW (see inset).

Spatial profiles of single AN fibers

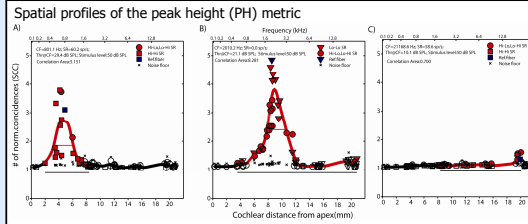


Fig. 4 Spatial profiles of the PH metric for three reference AN fibers located at an apical, central and basal position in the cochlea. Their position is estimated from the characteristic frequency (CF) of the tuning curve. A) low-CF fiber (CF=0.8 kHz); B) mid-CF fiber (CF=2.0 kHz) and C) high-CF fiber (CF=21.2 kHz).

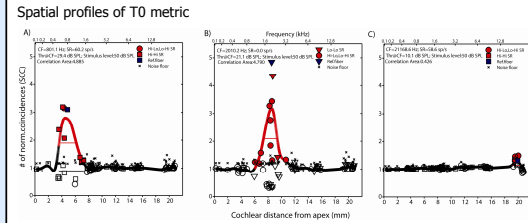


Fig. 5 Spatial profiles of the T0 metric of the same AN fibers as in the previous figure. Notice sharpening of the T0 spatial profile compared to the PH curve. The noise floor for the T0 metric has been estimated from the noise floor to PH.

A & B experiment

Unexpectedly, significant correlation re. scrambled ("scr") spike trains, were observed over widely separate cochlear locations (Fig. 3B). To understand the source of this correlation, we collected spike times to a noise ("A") and an uncorrelated noise ("B"). We compared the noise floor (see box "Noise floor") in the scrambled condition with the noise floor in the uncorrelated noise condition (spike times to noise A vs. spike times to noise B). Blue = correlated noise. Red = uncorrelated noise. Black = scrambled control.

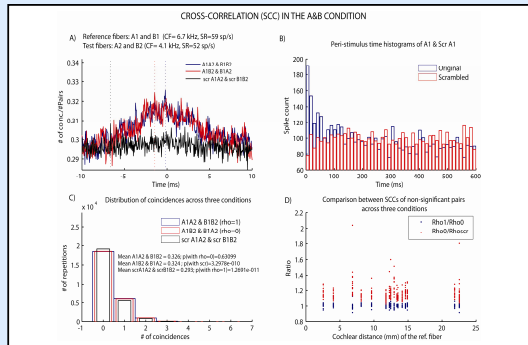


Fig. 6 A) The SCC for a pair of fibers with different CF (fiber 1: CF=6.7 kHz; fiber 2: 4.1 kHz). The SCC to the uncorrelated noise (red line) is similar to the SCC to the correlated noise (blue line), which indicates the real noise floor. B) Scrambling of spike times removes the adaptation pattern in peristimulus time histograms which removes a source of stimulus-induced correlation (black line in A). C) Distributions of coincidences in correlated, uncorrelated and scrambled conditions. D) Ratios between correlated and uncorrelated noise floors (blue dots) and ratios between uncorrelated and scrambled noise floors do not change with CF.

Population analysis

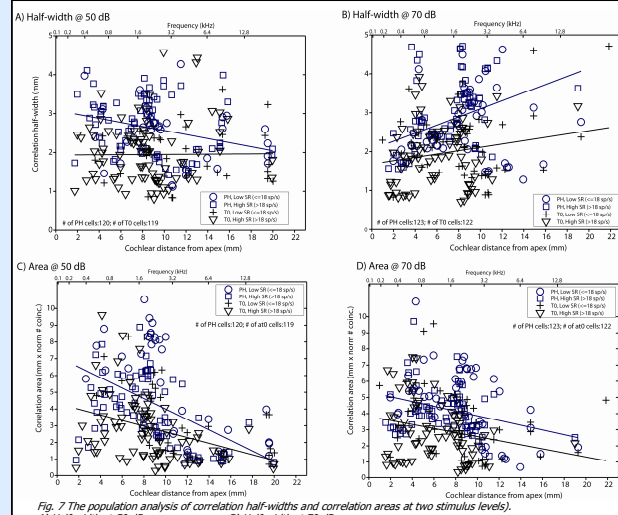


Fig. 7 The population analysis of correlation half-widths and correlation areas at two stimulus levels. A) Half-width at 50 dB. B) Half-width at 70 dB. C) correlation area at 50 dB. D) correlation area at 70 dB. At 50 dB (left), using the PH metric (blue), the half-widths of spatial profiles were large for apical cochlear regions and decreased towards the base. Using the T0 metric (black), half-widths were much smaller and remained constant towards the base, so that at the most basal locations half-widths were similar for PH and T0.

Global spatial profiles

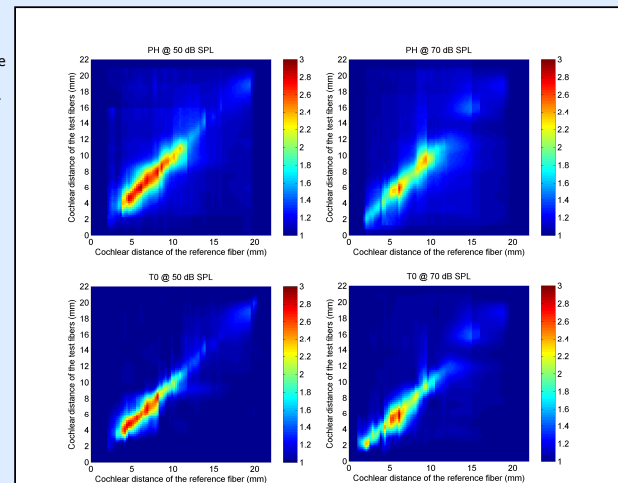


Fig. 8 Global spatial profiles of peak height (PH) and T0 metrics at two stimulus levels. These global spatial profiles were obtained by superimposing and averaging spatial profiles of single fibers (e.g. as in Fig. 4) of all animals onto an interpolated mesh-grid

Noise floor of correlations

In order to identify significant cross-fiber correlations, the noise floor was estimated by scrambling of spike times (keeping the same first-order inter-spike interval statistics) using a bootstrap method (with N=50 trials). The observed distribution of correlation values yielded confidence intervals. Noise floor was set to the upper confidence limit (at p=0.05). As shown in Figure 6, scrambling removes the adaptation pattern in the peri-stimulus time histograms, which lowers the noise floor compared to the correlations of the spike trains in response to the uncorrelated noise (A and B noise token with rho=0). In the AB experiments, where the spike times were collected for A and B noises, we estimated the ratio of the noise floors between the AB and scrambled condition (1.07 for 50 dB SPL, and 1.17 for 70 dB SPL stimulation). These ratios were used to adjust the noise floor for cases where the spike times to the B tokens were not collected.

Conclusions

The observed spatial profiles (Fig. 7) show broad regions of correlation (several mm) centered on the reference fiber, at all CFs.

The half-width of the magnitude of correlation is surprisingly invariant with cochlear position, particularly when measured at a delay of 0 ms (T0, black symbols, Fig. 7A,B).

The correlation area, which provides a more global measure of level of correlation ("correlation energy"), clearly decreases towards the base, reflecting the gradual decline of temporal coding with increasing CF (Fig. 7C,D).

Global spatial profiles (Fig. 8) reveal that 1) spatial profiles are narrower in shape when the range of delays is restricted to 0 ms, compared to when it is unconstrained 2) an increase in stimulus level is not accompanied by a broadening in extent of cross-fiber correlations, despite the known broadening in cochlear filter shape.

The results show that availability of monaural delays in the central nervous system (e.g. in cochlear nucleus) is an important factor in the spatial extent of correlation.

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