Supporting Information

Itatani and Klump 10.1073/pnas.1321487111

SI Text

van Rossum Metric Analysis with Additional Decay Time Constants τ . In this study, we analyzed the temporal representation of spike responses using the van Rossum (vR) distance measure (1). This measure has a decay time constant as a parameter that alters the weighting of coincident firing for quantifying the temporal differences between two spike trains. Previous studies of auditory processing in the bird forebrain have used a range of time constants (2) and found time constants of approximately 10 ms optimal for the neural representation of birdsong.

To evaluate the effect of the value of the time constant (τ) on the neuronal sensitivity, we calculated vR distances for $\tau = 1$ ms and $\tau = 10$ ms in addition to those for $\tau = 3.16$ ms and $\tau = 31.6$ ms that were presented in *Results* and compared the neuronal sensitivity obtained for the different time constants ranging from 1 ms to 31.6 ms. Similar to the results presented in *Results*, the neurometric functions based on a vR distance measure with $\tau = 1$ ms (Fig. S1, *Left*) and $\tau = 10$ ms (Fig. S1, *Right*) showed that sensitivity, *da*, increased significantly as the time shift of the B tone was increased [$\tau = 1$ ms, *F*(5, 1,053) = 134.5, *P* < 0.001; $\tau = 10$ ms, *F*(5, 1,053) = 155.0, *P* < 0.001; generalized linear mixed models (GLMM) ANOVA] and dropped significantly as the frequency separation between A and B tones (Δf) was increased [$\tau = 1$ ms; *F*(2, 1,051) = 36.8, *P* < 0.001; $\tau = 10$ ms; *F*(2, 1,051) = 32.3, *P* < 0.001; GLMM ANOVA].

The overall sensitivity obtained with $\tau = 1$ ms was significantly lower than that obtained with $\tau = 3.16$ ms (P < 0.001, Bonferronicorrected t test), whereas the difference between the $\tau = 10$ ms and $\tau = 3.16$ ms conditions was not significant (Bonferronicorrected t test); thus, used a short τ of 3.16 ms and a long τ of 31.6 ms. Investigation of the sensitivity da comparing hit versus miss responses revealed no significant deviations from 0 for decay time constants of $\tau = 1$ ms and $\tau = 10$ ms (GLMM ANOVA), which was similar to the results for $\tau = 3.16$ ms and $\tau = 31.6$ ms reported in *Results*.

Spike Rate Change and Recovery from Suppression. The average neurometric functions based on the rate response showed an increase in activity during the ongoing B tone with an increasing onset time shift, possibly due to suppression. To evaluate the effects of suppression, we analyzed the spontaneous activity in a 40-ms time window immediately before B tone onset. As shown in Fig. S2A, suppression of spontaneous activity was reduced with increasing onset time shift and increasing Δf , with GLMM ANOVA showing significant main effects of Δf [F(2, 1,051) = 44.3, P < 0.001] and time shift [F(5, 1,051) = 20.8, P < 0.001] on the spontaneous rate. No significant two-way interaction was noted. The spontaneous rate was significantly greater in the 12 semitone condition compared with the 0 and 6 semitone conditions

- 1. van Rossum MCW (2001) A novel spike distance. Neural Comput 13(4):751-763.
- Narayan R, Graña G, Sen K (2006) Distinct time scales in cortical discrimination of natural sounds in songbirds. J Neurophysiol 96(1):252–258.
- Fishman YI, Arezzo JC, Steinschneider M (2004) Auditory stream segregation in monkey auditory cortex: Effects of frequency separation, presentation rate, and tone duration. J Acoust Soc Am 116(3):1656–1670.

(all P < 0.001, Bonferroni-corrected t test), and did not differ between the 0 and 6 semitone conditions. Given the absence of interaction between B tone onset shift and Δf on the suppression of activity before the B tone, we conclude that suppression per se has little effect on the steepness of the neurometric functions and thus on threshold. Suppression also could provide the basis for the small change in response magnitude in the time-shifted analysis window that was applied in the rate measure. Suppression effects in the forebrain have been observed for interstimulus intervals of up to 100 ms, with stronger effects at shorter interstimulus intervals (3, 4). This suggests that the time shift could lead to reduced suppression, resulting in an increased response to the B tone with increasing time shift. However, the shallow neurometric rate sensitivity functions suggest that such an effect is of less importance than the change in the temporal response patterns represented by the vR analysis.

The reduction in sensitivity with increasing Δf and the associated increase in time shift detection threshold can be attributed in part to the reduced rate response when A and B tone frequencies are moved away from the CF (Fig. S2B). If the average spike rate is reduced while the spike rate variance remains the same, then the neurons' sensitivity for detecting the precise spike timing will be diminished (see also ref. 5). There was little change in the spike rates of A and B tones in the 0 and 6 semitone conditions, but a considerable reduction in spike rate in the 12 semitone Δf condition. At the same time, the SE of the response was hardly changed. We found significant effects of the position of the tone in the triplet and the Δf condition on the rates during tone presentation, with GLMM ANOVA showing significant main effects of $\Delta f [F(2, 504) = 48.4, P < 0.001]$ and tone position in the triplet [F(2, 504) = 6.7, P = 0.001], with no significant two-way interaction. Relative rates dropped after the initial A tone in the triplet (with a significant difference in the rates of the first and second tones in the triplet; P = 0.001, Bonferronicorrected t test), whereas the rate of the second A tone showed no significant difference from the rates of both the first A tone and the first B tone. Rates of all three tones in the target triplet dropped significantly in the 12 semitone condition (P < 0.001 for all comparisons, Bonferroni-corrected t test), but did not differ between the 0 and 6 semitone conditions.

The observed drop in the rate during the tone presentation that may be related to adaptation and suppression effects (see also the analysis of spontaneous activity above) are both expected to reduce the sensitivity of the neurometric functions based on vR distances. The prediction of this change in sensitivity corresponds well to the observation of little change in the neurometric vR sensitivity function from 0 to 6 semitones and a greater change in this sensitivity function from 6 to 12 semitones.

Bee MA, Klump GM (2005) Auditory stream segregation in the songbird forebrain: Effects of time intervals on responses to interleaved tone sequences. *Brain Behav Evol* 66(3):197–214.

Bee MA, Klump GM (2004) Primitive auditory stream segregation: A neurophysiological study in the songbird forebrain. J Neurophysiol 92(2):1088–1104.



Fig. S1. Average neurometric functions based on the vR distance. Data were obtained from a total of 64 recording sites in four birds. Data for two different time constants, $\tau = 1$ ms (*Left*) and $\tau = 10$ ms (*Right*) were used in this additional analysis. For a comparison with the results for time constants of 3.16 ms and 31.6 ms, see *Results*. Open symbols show the mean values (n = 64 for each Δf condition and time shift). Error bars represent \pm SEM.



Fig. S2. Spiking activity in relation to Δf and B tone onset time shift. Open symbols show the mean values (n = 64 for each Δf condition and time shift). Error bars represent \pm SEM. (A) Spontaneous spike rate before B tone onset in test target triplets in relation to onset time shift and Δf . (B) Spike rate in response to each tone in the sham target triplet—first A tone in triplet (*Left*), B tone (*Center*), and second A tone in triplet (*Right*)—in relation to Δf for the same recording sites shown in A.