

## Comments

### Comment by Wang:

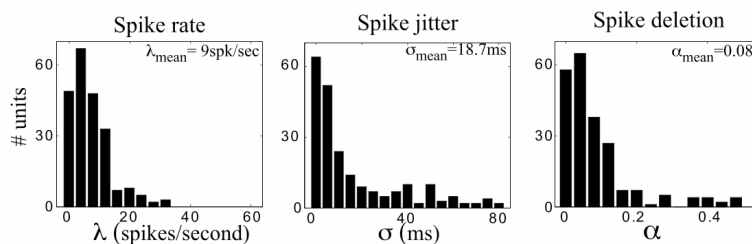
Your paper seems to ignore the evidence from other studies that auditory cortex neurons have different discharge patterns in response to time-varying signals when animals are awake or anesthetized (e.g., Goldstein *et al.* 1959; Lu and Wang 2000; Lu *et al.* 2001). In particular, we have shown in recent studies that neurons in the awake marmoset auditory cortex exhibit prominent discharges that are not time-locked to stimulus waveform or envelope at rapid modulate rates (Lu *et al.* 2001; Liang *et al.* 2002). Such rate-responses may not be adequately captured by your analyses that lumped together data from both anesthetized and awake preparations. In your data collected from awake ferrets, what is percentage of units from which you were able to produce significant STRFs? For those units that did not yield STRFs, were they driven by your stimuli?

- Goldstein M. H. Jr, Kiang N. Y-S., and Brown R. M. (1959) Response of the auditory cortex to repetitive acoustic stimuli. *J Acoust Soc Am* 31, 356–364.
- Lu, T. and Wang, X. (2000) Temporal discharge patterns evoked by rapid sequences of wide- and narrow-band clicks in the primary auditory cortex of cat. *J. Neurophysiol.* 84, 236-246.
- Lu T., Liang L. and Wang X. (2001) Temporal and rate representations of time-varying signals in the auditory cortex of awake primates. *Nat Neurosci.* 4, 1131-1138.
- Liang, L., Lu, T. and Wang, X. (2002) Neural representations of sinusoidal amplitude and frequency modulations in the primary auditory cortex of awake primates. *J. Neurophysiol.* 87, 2237-2261.

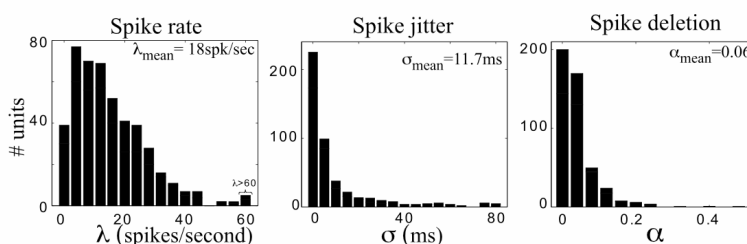
### Reply:

It is indisputable that neuronal responses in A1 exhibit various differences under awake and anesthesia conditions. Other than a more vigorous spike rate (Fig. A1, leftmost panel), awake recordings exhibit a more complex spectro-temporal response pattern captured by their spectro-temporal receptive fields (STRFs). Nevertheless, there are substantial similarities between the two populations. In our data set, we observe that TORC stimuli possess a strong response-driving capability under both anesthetized and awake conditions. This property enables us to successfully derive STRFs from over 2/3 of the cells. Particularly, using a basic estimate of reliability of cells' responsiveness to TORC spectro-temporal modulations, we find that a reliable response (and STRF measurement) can be obtained from 70% of awake and 69% of anesthetized units (from a total of 473 awake and 341 anesthetized single units). These findings of comparable STRF reliability under the two conditions translate also to the analysis of temporal precision in cortical responses. The distribution of precision parameters in awake and anesthetized populations are shown below:

### A. Anesthetized Experiments



### B. Awake Experiments



**Fig. A1.** Distribution of correlation model parameters.

The population distributions, shown in Fig. A1, exhibit apparent similarities between the anesthetized and awake experiments. The distribution of spike deletion ( $\alpha$ ) is strikingly similar in the two populations (rightmost panels). Additionally, spike jitter ( $\sigma$ ) is very comparable, despite a slightly heavier tail in the anesthetized compared to the awake condition (middle panels). This slight bias in the awake condition does not refute our overall finding of remarkable accuracy of phase-locking to the stimulus fine-structure. The similarities between two distributions are indeed more profound, with a mean of 18.7 vs. 11.7 ms in a range of 0–80 ms.

Overall, the striking similarities between the anesthetized and awake populations justify our analysis of temporal precision under the two conditions without distinguishing between experimental setups.

### Comment by de Cheveigné and Pressnitzer:

Maass (1997, 1998) has shown that formal neural networks based on spike times are more powerful (in terms of the number of neurons required for a given task) than networks that use spike rate to represent data. The representation is also efficient in that the amount of information carried by a spike is limited only by its temporal accuracy. Thorpe *et al.* (1996) argue that such a representation is used in the visual system, and the same principle makes sense in hearing, an eminently temporal sense. One could make the conjecture that sound properties are coded as relative spike times within a group of neurons. For example, a reference spike might be triggered within a neuron sensitive to the *occurrence* of events (regardless of their nature) while specific properties would be coded by the times of subsequent spikes within the group. If a stationary property such as periodicity is coded in this

way, the code need not be repeated unless the property changes. For example one does not expect the cortical response to a periodic tone to be periodic. Interspike time intervals within the group must be accurate, and the emission of the group of spikes is expected to follow reliably (and possibly with fixed latency) the sound event that it codes. If so, this coding principle might produce a pattern of cortical responses similar to that reported in your paper. The sparse nature of a temporal code fits well also with Barlow's (1961) principle of "redundancy reduction" (see comment to Nelken *et al.*, this volume).

- Barlow HB (1961) Possible principles underlying the transformations of sensory messages. In Rosenblith WA (Ed) *Sensory Communication*. Cambridge Mass: MIT Press, 217-234.
- Maass, W. (1997) Networks of spiking neurons: the third generation of neural network models. *Neural Networks* 10, 1659-1671.
- Maass, W. (1998) On the role of time and space in neural computation. *Lecture notes in computer science* 1450, 72-83.
- Thorpe, S., Fize, F., and Marlot, C. (1996) Speed of processing in the human visual system. *Nature* 381, 520-522.

### **Comment by Nelken on the comment by de Cheveigné and Pressnitzer:**

In general, I agree with this comment. In the responses of cortical neurons to some sounds, there are components that are highly precise but which may appear at a considerable latency after the onset of the sound (e.g. Bar-Yosef *et al.* 2002). These could serve the role of the spike groups you mention in your comment. However, the situation is really more complicated than that. Whereas some cortical spikes are highly precise, others seem to be much more variable in their timing. This is true even when using 'frozen' stimuli. Thus, sound coding in auditory cortex have both highly precise and highly variable spikes, and both are informative (when decoded at the appropriate time scales). The multiplicity of time constants apparent in cortical activity is probably one of its most difficult aspects, both for experimental and theoretical treatment (e.g. Nelken *et al.* 2003).

- Bar-Yosef, O., Rotman, Y., Nelken, I. (2002) Responses of neurons in cat primary auditory cortex to bird chirps: effects of temporal and spectral context. *J. Neurosci.* 22 8619-8632.
- Nelken, I., Fishbach, A., Las, L., Ulanovsky, N., Farkas, D. (2003) Primary auditory cortex of cats: feature detection or something else? *Biol. Cybern.* (in press).