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# Coding the temporal structure of sounds in auditory cortex

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**Auditory cortex in anesthetized animals responds poorly to rapid stimulus trains. In awake marmosets, rapidly repeating sounds are now shown to be represented by a rate code.**

Perceiving change in sounds over time is the most important function of human hearing. If all the fine spectral (frequency) information is omitted from speech, leaving only a relatively slow, amplitude modulation of 'white noise' by the speech envelope, we still hear remarkably well, scoring well above chance on phoneme identification[1]. Temporal coding also contributes in several ways in listening to simple, non-speech sounds, including pitch, space and pattern perception[2].

The auditory system has developed several specialized mechanisms to process rapidly time-varying stimuli. In the cochlea, direct, mechanically coupled ion channels in the stereocilia of hair cells are very rapidly opened and closed in synchrony with the displacement of the basilar membrane[3]. Single auditory nerve fiber discharges are able to follow these channel openings, or 'phase-lock', to frequencies up to 4 kHz in mammals and even up to 9 kHz in certain birds. At higher frequencies, filtering by the hair cell membrane prevents phase locking, and a 'place code', reflecting place of innervation along the cochlea, is thought to be responsible for very high-frequency hearing. Nevertheless, further specializations for time preservation are found in the auditory brainstem[4]. Auditory nerve fibers form giant, 'endbulb of Held' terminals onto some cochlear nucleus neurons, and transmitter-gated channels with extremely rapid kinetics are found postsynaptically. In contrast to the auditory periphery, neurons at higher levels of the auditory system seem to process time-varying signals with much less fidelity. Although most neurons in the auditory cortex respond precisely to the onset of a sound, the responses are usu-ally transient and cannot explain the perception of connected streams of sound. Lu, Liang and Wang[5] now show in this issue that two populations of neurons, in the primary auditory cortex of awake marmosets, process time-varying acoustic stimuli (clicks) using independent codes. One population shows sustained, synchronized responses for lower-frequency click trains, whereas a second, newly identified population shows non-synchronized increases in spike rate for higher frequency trains (**Fig. 1**) Many neurons in the 'synchronized' population actually show a decreased response rate for higher frequency stimuli.

Most previous research on auditory cortex physiology has used barbiturate anesthesia. The focus of the research has typically been on examining the responses of single neurons to variations in the (spectral) frequency of long-duration pure tones. This approach enabled maps to be made of the spatial distribution of the 'best frequency' of neurons across the surface of the cortex (tonotopicity). Whereas the transient responses of neurons in the anesthetized cortex are precisely timed to the stimulus onset, the capacity to follow repetitive, shorter duration stimuli is limited to relatively low frequencies. A major departure of the study by Lu and colleagues[5] was the use of an unanesthetized preparation. Neurons in the unanesthetized cortex were found to show much more sustained responses to trains of rapidly presented stimuli than those studied previ-ously in the anesthetized cortex. Although a smaller proportion of neurons in the awake cortex had synchronized responses, they discharged synchronously in response to higher rates of repetitive sounds. However, the major impact of the Lu et al. paper[5] is likely to be the discovery of the population of neurons having a non-synchronized, rate code for stimuli presented at high repetition rates (**Fig. 1**). In these neurons, increasing rates of stimulation (above about 30 Hz) led to increasing rates of discharge, up to a mean peak response rate of 30–40 spikes/second at 200–300 Hz, the fastest stimulus rates used. The discovery of this rate coding depended on the sustained firing of neurons found so much more commonly in the cortex of awake animals, but it was also due to the analytic rigor and insight of the authors. Overall, just under half of the click-responsive cortical neurons test-ed ($n = 190$) in the Lu et al. study[5] could be clearly classified as synchronized or rate-responsive. The remainder showed a variety of non-synchronized and rate-insensitive responses.

From perceptual experiments, it is clear that the auditory system processes
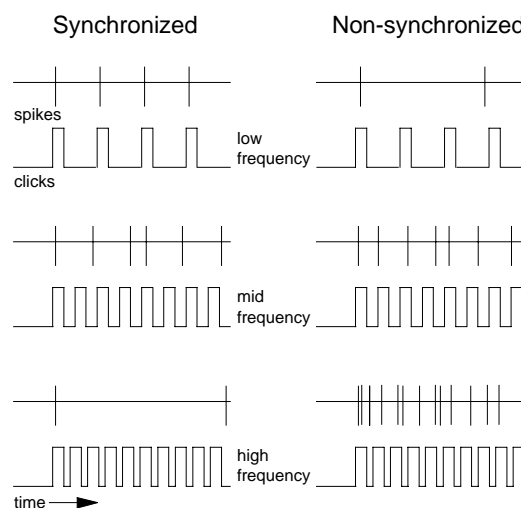


**Fig. 1.** Responses to click stimuli of hypothetical synchronized and non-synchronized auditory cortex neurons in the study of Lu and colleagues[5]. Synchronized neurons respond in a 'phase-locked' manner to inter-click intervals (ICIs) longer than about 20 ms. At slightly shorter ICIs (10–20 ms), they have non-syn-chronized, sustained discharges that decrease in rate with decreasing ICI (that is, increasing repetition rate). For very short ICIs, they discharge only at the onset and offset of the stimulus train. Non-synchronized neurons do not respond to clicks presented at low rates. As ICIs decrease from 50–30 ms, they show a gradually increasing, sustained response rate. Their response rate dramatically increases for ICIs shorter than about 30 ms.

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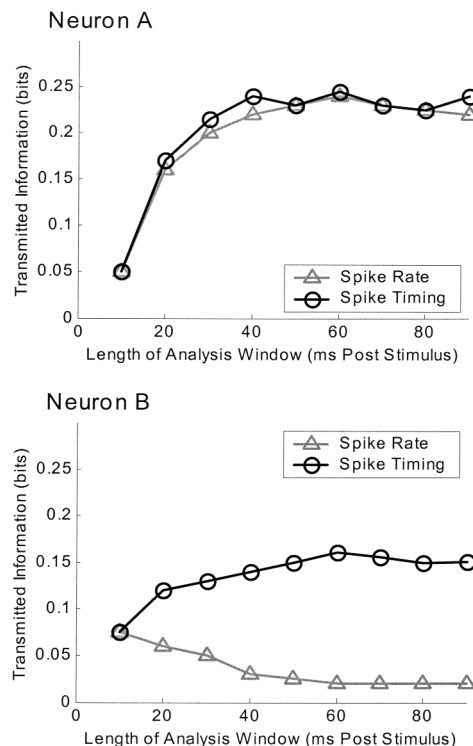
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### Neuron A



### Neuron B



**Fig. 2.** Amount of stimulus-related information of two neurons in rat somatosensory cortex, estimated using information theoretical measures under the assumption that the neuron uses either a rate or a spike timing code. The authors analyzed time windows of increasing length after stimulus onset. For a rate-coding neuron, one might expect the amount of information to increase for longer time windows, as firing rate estimates should improve when based on longer observation periods. For neuron A, this seems indeed to be the case. However, for neuron B, the rate-based information actually declined when longer analysis windows were considered, whereas the information derived from putative spike timing codes increased. Note that in both cases the amount of information transmitted by spike timing is at least equal to, if not greater than, that transmitted by rate. Based on data from Panzeri and colleagues[6].

and interprets fast and slow temporal fluctuations in a fundamentally different manner. Fast, periodic oscillations, of amplitude-modulated noise, for example, are perceived as one continuous sound. Thus, temporal fluctuations occurring on this fast time scale contribute to pitch. In contrast, temporal patterns that occur on a slower time scale (less than about 30 Hz) are perceptually resolved as individual auditory events, and may carry most of the information required to identify and characterize a sound source. The study cited above[1], showing the recognition of noise modulated by the speech envelope, is an example of this slow temporal perception. The existence of two separate temporal codes in the auditory cortex may help to explain these and other auditory perceptual phenomena, such as the ability to detect temporal gaps between noises separated by just a couple of milliseconds. As noted by Lu and colleagues[5], it is intriguing that several qualitative changes in temporal perception occur around the frequency (about 30 Hz) that separates the two populations of cortical neurons. For example, fast, periodic oscillations, such as those from

a fully revved motorcycle engine, are perceived as one continuous sound having a clear, high-frequency pitch. Slower oscillations (such as from an idling engine) are perceptually resolved as individual auditory events, each having a distinct pitch.

Although it is tempting to suggest that the temporal code and the spike rate code, each operating over a different range of stimulus rate, underlie perception, proving that connection is not straightforward. One way forward, as frequently used by visual neuroscientists, is to train the animal to make a perceptual decision while the activity of cortical neurons is being recorded. On each perceptual trial, the activity of the neuron is compared with the decision reached by the animal. Significant correlations have now been obtained in both the primary and non-primary visual cortex. This approach has been used with great success, for example, by Newsome, Shadlen and their colleagues in their studies of the cortical basis of visual motion discrimination[6,7]. In contrast, Lu and colleagues[5] recorded from A1 neurons in marmosets that were trained to sit quietly, but not to perform a behavioral task.

A final note of caution is signaled by some other recent studies using alternate modes of response analysis. For exam-

ple, the presence of continuous sounds might be encoded by the synchronization of low levels of background firing often observed in cortical neurons[8]. Thus, in the auditory cortex of anesthetized marmosets, deCharms and Merzenich showed that the correlation between the discharges of nearby clusters of neurons could signal stimulus features, even though the firing rate of the neurons did not change. It has been argued that the distinction between rate and spike timing codes may also not be as clear as it appears at first[9]. An interesting case in point is a study by Panzeri and colleagues[10] (**Fig. 2**). Single-neuron responses to whisker stimulation, recorded from rat somatosensory cortex, were analyzed using information theory, rather than more conventional approaches. The results of this analysis led to the perhaps counterintuitive observation that even neurons normally described as 'rate coding' often seemed to carry more information in spike timing than in firing rate.

The study of Lu and colleagues[5] has made a highly significant contribution to our understanding of auditory cortex function. However, its most important legacy may be to encourage the growing trend in auditory neuroscience away from anesthesia and thus allow psychophysical theories of auditory perception to be tested at a physiological level.

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