combination of more accurate experimental measurements (Kremkow et al., 2016; Lee et al., 2016; Nauhaus et al., 2016) and computational models (Miller, 1994; Paik and Ringach, 2011; Swindale et al., 2000) may soon explain what we thought were complicated parameter relations with some simple connectivity rules.

A better understanding of visual cortical topography is likely to bring important new insights about cortical function. Knowing what and how image parameters are mapped in visual cortex and what parameter combinations are allocated the largest portion of cortical space can help to better understand the building blocks of visual cortical processing. Parameters that are mapped together may be more likely to be wired together in the form of local and long-distance neuronal networks, and knowledge of this topography may help to reveal new rules of cortical connectivity. Visual cortical maps are also closely related to visual function. For example, humans maximize the visual processing of detail and color by dedicating half of their primary visual cortex to a small fraction of their central retinas while using the rest of the visual cortex to map the binocular visual field. In contrast, rabbits maximize their chances of survival by devoting a large portion of their visual cortex to a horizontal retinal line that help them detect distant predators, while using the rest of their visual cortex to nearly cover a complete visual-field-sphere surrounding their heads. Just as the differences in spatial mapping are closely related to visual function, future research may reveal the functional implications of specific topographic relations that remained hidden by our coarse technical tools.

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# Neuronal Mechanisms and Transformations Encoding Time-Varying Signals

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**Sensation in natural environments requires the analysis of time-varying signals. While previous work has uncovered how a signal's temporal rate is represented by neurons in sensory cortex, in this issue of *Neuron*, new evidence from Gao et al. (2016) provides insights on the underlying mechanisms.**

The song of the cricket and repetitive drumming of a woodpecker are examples of natural time-varying signals created by the periodic repetition of transient acoustic events (Figure 1A). Perceptually, we hear each woodpecker's peck as a discrete event, while the repetitive leg-wing rubbing that produces the cricket song is perceptually fused into a single continuous sound (compare Audio S1 and S2, available online). Why we perceive slowly repeated sounds as discrete events (flutter perception) and quickly repeated sounds as a continuous acoustic signal (fusion perception) is thought to be a direct result of how these signals are represented by sensory cortical neurons.

The temporal rate of a sensory signal is initially represented in the sensory periphery by a stimulus-locked temporal firing pattern. However, as signals ascend the auditory, somatosensory, or visual processing pathways, neurons progressively worsen in their temporal fidelity. In the auditory system, for example, although auditory nerve fibers can synchronize their responses to temporal rates above 1 kHz, this upper cut-off of stimulus synchronization decreases at hierarchically higher auditory areas, falling to around only 30–50 Hz in primary auditory cortex (Joris et al., 2004; Wang, 2007). Moreover,

in the somatosensory cortex, stimulus-locked neural activity evoked by flutter vibration seems to be all but lost downstream of primary somatosensory cortex (Romo and Salinas, 2003).

Without the ability to faithfully represent the temporal pattern of the signal with their spike timing, neurons transform the incoming stimulus-synchronized temporal code (Sync) into a neural code no longer reliant on spike timing, referred to as non-synchronizing (nSync). Non-synchronizing neurons that vary their firing rate with the temporal repetition rate of the sensory stimulus are able to encode temporal information with only their firing rate. In somatosensory cortex, both Sync and nSync response can be observed, with nSync neurons increasing their firing rate with stimulus frequency. Interestingly, in monkeys conducting a frequency discrimination task, S1 neurons have been observed that encode the temporal rate of the stimulus using temporal and rate codes. Although temporal coding is generally more precise than rate coding in these neurons, comparisons of neurometric and psychometric functions suggest that firing rate responses more closely match the monkeys' behavior than temporal response patterns (Romo and Salinas, 2003). Thus, rate coding rather than temporal coding may ultimately be the "language" used by sensory cortex to represent perceptual information.

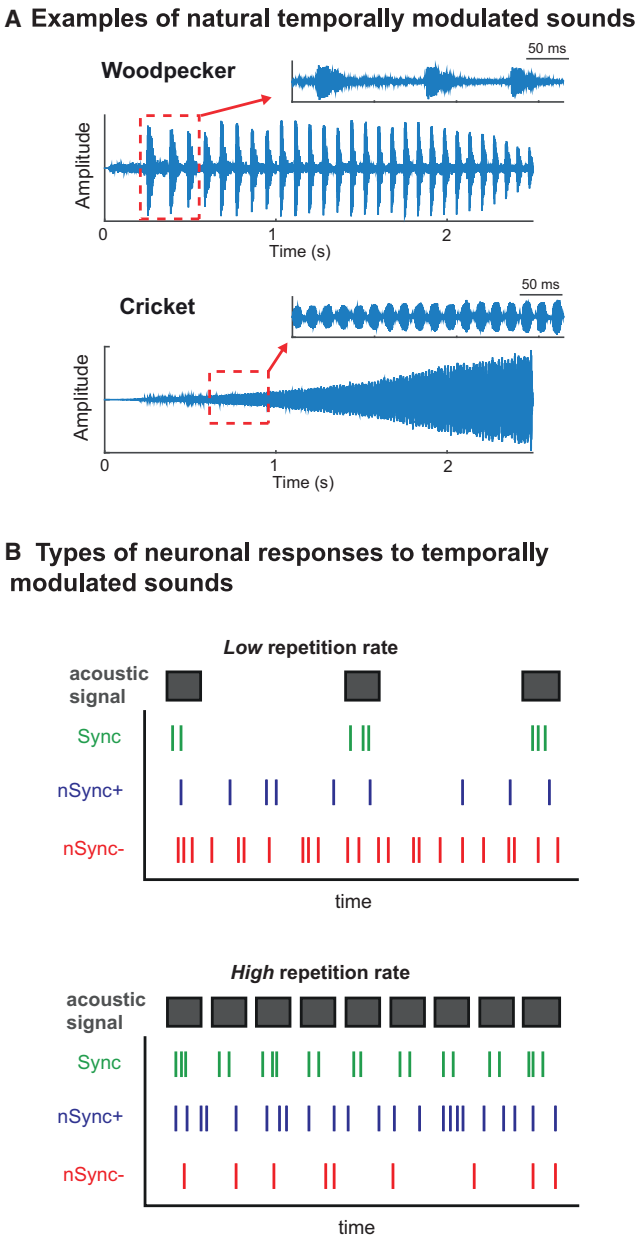


**Figure 1. Natural Variation in Sound Rate and Neural Coding Principles**

(A) Example sounds with different time-varying features and percepts are the drumming of the woodpecker and the cricket's song; see text and listen to Audio S1 and S2.

(B) Responses of Sync (green), nSync+ (blue), and nSync− (red) neurons to a sequence of acoustic events, repeated at a low repetition rate (top) or a high repetition rate (bottom).

However, neurons typically need to encode multiple features of the sensory stimulus with their firing rate, which creates the following dilemma. Imagine a neuron increases its firing rate with two distinct acoustic features. If the first acoustic variable has a low value, causing the neuron's firing rate to decrease, this will also decrease the dynamic range available for encoding the second acoustic feature. The problem is solved if an acoustic parameter is always encoded with a complementary rate code—one set of neurons increasing their firing rate and one set of neurons decreasing their firing rate—as the acoustic parameter changes. Thus, the neural coding dynamic range is maintained over the entire parameter range, with the relative difference in firing rate between the two populations (rather than absolute firing rate) encoding the acoustic parameter. A complementary rate coding strategy has been observed in both the auditory cortex (Bendor and Wang, 2007) and the secondary somatosensory cortex (Romo et al., 2002) of monkeys. In auditory cortex, this complementary rate code is generated by non-synchronized neurons that increase their firing rate with an increase in stimulus repetition rate (nSync+), and a separate population of neurons that do the opposite by decreasing their firing rate with an increase in stimulus repetition rate (nSync−). Similar neural rate coding strategies have also been reported for spatial localization (Stecker et al., 2005), and thus, opponent coding may be a general property in the brain for rate coding of certain sensory features.

How does auditory cortex transform stimulus-locked thalamic inputs into the variety of response types (Sync, nSync+, nSync−, mixed) that are observed (Figure 1B)? While the existence of these different classes of neuronal responses was first identified by single-unit extracellular recordings in awake marmoset monkeys, this approach could not reveal the underlying mechanisms. In particular, how do nSync neurons "lose" their temporal fidelity? Is this a by-product of competing excitatory and inhibitory dendritic inputs, or the passive biophysical properties of a neuron's membrane potential transforming

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