

ing the saccade<sup>5</sup>? One must be cautious in phrasing these matters, because the duration compression does not occur with auditory clicks—only with flashes. Therefore, it is not subjective time in general that is compressed; instead, only duration judgments about visual stimuli are modulated.

What might explain this duration compression? A good deal of excitement has been generated in the last decade about neurons found in lateral intraparietal area (LIP), superior colliculus and extrastriate cortex that dynamically remap their receptive fields around the time of a saccade<sup>11</sup>. Some of these neurons show a receptive field shift that is anticipatory, as though they are predictively forming a view of the scene where the eyes are about to land. It has been suggested that this remapping may be directly related to perisaccadic spatial distortions<sup>12</sup>. Following in that spirit, Morrone *et al.* suggest that the duration compressions, too, may result from the actions of dynamically remapping receptive fields, especially since LIP neurons participate in duration judgments<sup>13</sup>. Future neurophysiology experiments might be able to examine duration encoding during saccades to directly address this hypothesis.

Although the story of receptive field remapping starts off simply, it quickly becomes thorny. The remapping of LIP neurons is spread widely in time around a saccade: about one-third of the neurons change their coding predictively, while the remainder remap during or after the

saccade, with a spectrum of timings in between. This presses the question of how the remapping is temporally coordinated. It is unclear how such temporally spread signals could be related to an increase in precision found by Morrone *et al.* These considerations again remind us that the representation of time is as least as perplexing as the representation of space.

In addition to duration compressions, Morrone *et al.* report a second finding about time judgments during saccades, although its relationship to the first finding is currently unclear. Instead of duration judgments, they next asked subjects to make temporal order judgments: which of two targets appeared first? Within a small window before the saccade (−70 to −30 ms), they discovered a temporal inversion: two targets appearing within ~50 ms of each other were systematically perceived in the wrong order<sup>5</sup> (Fig. 1). Subjects were not simply worse at making judgments in this range: the order judgments were actually reversed. As the authors acknowledge, a clean explanation is still missing for this result.

The Morrone *et al.* study may introduce more questions than answers. For example, although some evidence implicates LIP neurons in duration judgments<sup>13</sup>, no evidence yet implicates them in temporal order judgments. It may be that temporal order judgments are constructed retrospectively from differentially distorted duration judgments, but this assumption cannot be taken for granted and,

moreover, would not clarify the different time windows of the two effects (Fig. 1).

Time will be critical in the emerging story of vision as an active construction of the world around us. Previous suggestions that the brain constructs its evolving picture of the world by optimal integration across saccades<sup>14</sup> will need to be revisited with these new timing discoveries in hand. Whatever the outcome, the new Morrone *et al.* findings bode well for a future in which neuroscience—like physics before it—attends to the relationship between time and space.

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## Auditory cortex cheers the overture and listens through the finale

John C Middlebrooks

**Although we hear sounds throughout their duration, studies on anesthetized animals have suggested that auditory cortex neurons primarily detect changes in sound. New evidence in a report in *Nature* from awake animals is forcing us to reconsider this view.**

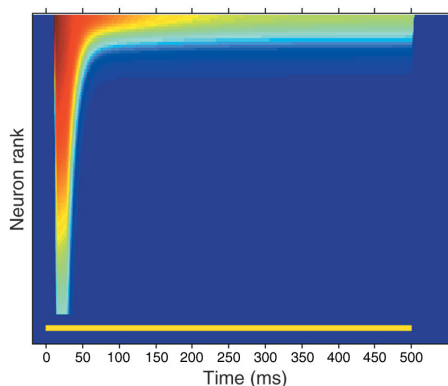
In the visual system, some neurons habituate rapidly to a featureless blue sky but readily detect the appearance of a bird passing overhead. Likewise, many studies have reported that neurons in auditory cortex of anesthetized animals demonstrate brief bursts of spikes (called ‘phasic responses’) to acoustic onsets or transients, but show little or no

tonic activity during the remainder of the sound. It would seem to be a reasonable strategy on the part of the brain to devote more resources to marking changes in the sensory world than to monitoring the steady state: “Ho hum, there’s nothing new over here.” However, one must ask how it is that a viewer knows that the sky continues to be blue and featureless or that a listener knows that a tone continues to play. If auditory perception were derived solely from phasic responses, one would expect the perception of an unmodulated tone to fade to silence within milliseconds. In contrast, we know

that auditory percepts persist throughout sounds lasting seconds or even minutes.

A report from Wang and colleagues<sup>1</sup> in a recent issue of *Nature* seems to resolve this conundrum. The report contains three key observations. First, unlike the situation in anesthetized animals, many neurons in the auditory cortex of awake marmosets responded throughout the duration of sounds, even for pure-tone stimuli that typically produce highly phasic responses under anesthesia. This observation provides a possible explanation for the persistence of auditory percepts. Second, the tonic responses were more selective for par-

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**Figure 1** The distribution of activity among auditory cortical neurons in response to a sound burst. Vertical axis: (virtual) ranking of neurons according to their preference for a particular stimulus. The red-to-green-to-blue color gradient represents increasing spike probability. Yellow bar: duration of a 500-ms sound. Most neurons show a brief, phasic response to the onset of the sound, but only those particularly tuned to the sound maintain their response until the end of the sound.

particular stimuli than were the onset responses, adding an insight to our understanding of stimulus coding in the cortex. Finally, also pertinent to stimulus coding, spike counts elicited in the cortex of awake animals were distributed with Poisson statistics, contrary to the conclusion of a recent study that auditory cortical responses are strictly binary<sup>2</sup>.

The vast majority of research on brain mechanisms of hearing has been conducted under conditions in which the experimental subject does not appear to hear anything at all—that is, in anesthetized animals. Surprisingly, the auditory cortex can be very responsive to sounds under such conditions. These studies have revealed much about the foundations of central auditory processing, including the basics of cortical sensitivity to the frequency, intensity, location and duration of sounds. However, it seems unlikely that anesthetized preparations will provide the last word on mechanisms of perception. Increasingly, investigators are turning to chronic recordings from awake animals. Such recordings, particularly from primates<sup>1,3,4</sup> and carnivores<sup>5,6</sup>, demonstrate a rich variety of temporal response patterns, including phasic responses, tonic responses persisting throughout the duration of the stimulus, responses at stimulus offset, responses consisting of inhibition of spontaneous activity and many combinations thereof. In many cases, parameters of the stimulus determine whether a cortical neuron responds phasically or tonically or whether it is excited or inhibited.

The new study by Wang and colleagues<sup>1</sup> involved recording from the primary auditory cortex (area A1) and lateral belt (LB) areas of awake marmosets. Single neurons responded to a broad range of sounds with phasic (onset) responses, but a limited set of 'optimal' sounds

elicited robust tonic responses lasting throughout the sound duration. That suggests a view of the auditory cortex (Fig. 1) in which acoustic transients elicit phasic responses across widespread neuronal populations. During the later part of the sound, responses persist only among the much smaller population of neurons (represented at the top of the figure) that are most selective to the particular spectral and temporal properties of the sound.

In the Wang study, most neurons in A1 and LB responded optimally to tones or noise that were amplitude modulated at a particular best modulation frequency. Again, neurons tended to respond tonically to sounds at their best modulation frequency and phasically to non-optimal modulation frequencies. The finding of tonic responses to modulated sounds is not entirely without precedent, even in anesthetized animals<sup>7</sup>. In previous studies, however, the tonic responses were usually the result of neurons firing in cycle-by-cycle synchrony with the modulating waveform, as if the modulated waveform acted as a sequence of onsets and elicited a sequence of phasic neuronal responses. In contrast, a previous report from the Wang laboratory<sup>8</sup> described a population of neurons that fire throughout the duration of a modulated sound, varying their firing rate according to the modulation frequency. Unlike the previously described phase-locked neurons, however, spikes from these 'non-synchronized' neurons showed no particular temporal relationship to the modulator. The non-synchronized neurons represent an instance in which a temporal parameter of a stimulus (modulation frequency) has been recoded as a non-temporal rate code.

Phasic onset responses have so dominated the picture in auditory cortex that it has even been argued that neurons code information in

a predominantly binary fashion. One example is a study<sup>2</sup> in which an attached-cell procedure was used to record from single neurons in anesthetized rats. Neurons fired one or zero spikes at the onset of each tone burst, never more. The authors hypothesized that stimulus-related information is coded by the probability of a spike. In other studies in anesthetized animals, including work from my laboratory, it has been argued that more stimulus-related information is transmitted by the latency from the stimulus onset to the first spike<sup>9</sup> (or by the relative latency among neurons<sup>10</sup>) than by the spike count. A strict binary-response hypothesis (as in ref. 2) is not supported, however, by the present results from Wang and colleagues<sup>1</sup>. They found that neurons responded with a Poisson-distributed range of spike counts averaging, in the published example, two spikes per trial for a 50-ms tone. Variations in mean spike count could potentially signal differences in stimulus efficacy. The first-spike latency hypothesis<sup>9,10</sup> has merit in terms of efficiency and speed of decoding<sup>11</sup>, but the present results<sup>1</sup> and results from my laboratory<sup>5</sup> indicate that additional stimulus-related information could be transmitted by spike counts. The jury remains out on whether sound stimuli are represented in the auditory cortex strictly by response magnitude (a spike-count code), by first-spike latency (a temporal code) or by some combination of the two.

The use of general anesthesia in auditory cortical research enables research that would be impossible in unanesthetized animals, including studies that require extensive mapping of cortical areas or the use of exhaustive stimulus sets. Nevertheless, it is becoming clear from recent results that there are impressive differences between temporal firing patterns in awake and anesthetized animals and that an awake, or even a behaving, subject is preferable whenever feasible. One anticipates that an even richer story will emerge from experiments in which the animal must listen actively to the sounds.

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