to VCSEL-based optical interconnections inside these large telecommunication switches to move data between PC boards.

When VCSELs can be commercially made to emit in the 1300- to 1550-nm range, they will also be useful with the single-mode fiber installed in the "last-mile" bottleneck mentioned earlier. Thus, the simplification of optical links enabled by the VCSEL will be applied to the short-reach single-mode connections, further reducing costs as the optical network migrates closer to the home. Several companies have presented data on such long-wavelength VCSEL prototypes.

Speeding up electronic routers with optical backplanes is, however, only a temporary solution. Since the invention of the semiconductor chip, the number of circuits on a chip has doubled every 18 months, following Moore's law. This results in denser and denser printed circuit boards, and the communications channels that move the signals between components are becoming overloaded. Integrated circuits will soon generate so much input/output (I/O) traffic that they won't be able to communicate electronically. VCSELs can be applied at this level in a "photonics on CMOS" architecture that will enable Internet router throughput to continue to increase (*2*, *3*).

As these developments make access networks faster and faster, the I/O bus of the desktop computer becomes the Internet's choke point. Ever more powerful CPUs cannot move the content off the network and into the display subsystem fast enough because of this internal constraint. You can see a microcosm of this problem when you send a document to a locally attached printer and try to work on another document while it prints. There is plenty of processor power available, but your computer responds sluggishly because there is no room on the bus. Network servers have the same problem, and the computer industry is addressing it with Infiniband, a switched fabric I/O architecture that gets rid of the old shared-bus architecture (*4*). Think of it as an Internet inside a single computer. If VCSELs become cheap enough, these intracomputer networks can become optical, thus solving the I/O bottleneck on a single PC board.

Before this can happen, though, the optical industry must overcome some key challenges that are encountered when optical interfaces are placed directly on a microprocessor. First, there is the issue of heat. Integrated circuits run at a much higher temperature than VCSELs are designed to withstand, creating a materials problem. Second, there is a form-factor problem. The electrical-to-optical converter needs to be as small as two wire bond pads on an integrated circuit, or about 0.03 mm^2. Today, the equivalent function requires a 12 mm by 50 mm package that fills up a 600 mm^2 area on a mounting surface. The optical technology thus needs to shrink by four orders of magnitude. Third, the manufacturing yields of optical transceivers need to improve by about two orders of magnitude.

Optics has solved the communication bottlenecks for undersea and long-haul applications. Reduced cost of short-reach optical solutions is now bringing optics closer to the home to solve the last-mile bottleneck of today. VCSELs will be the enabling technology to solve the emerging bottlenecks inside computers and telecommunications equipment. Eventually, VCSELs will be needed to communicate across individual PC boards. As the demand for bandwidth increases and optical link technology evolves to produce lower cost solutions, optics is set to solve each bottleneck in our internet infrastructure.

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PERSPECTIVES: NEUROSCIENCE

Noise Makes Sense in Neuronal Computing

Maxim Volgushev and Ulf T. Eysel

Everyone agrees that a noisy telephone line does not improve the transmission of information. Yet, under certain circumstances, added noise can actually enhance rather than diminish the detection of weak signals. Neurons in the primary visual cortex, the part of the brain responsible for processing incoming visual signals, seem to have taken advantage of this effect, as Anderson *et al.* (*1*) show on page 1968 of this issue. They present new evidence that synaptic noise in primary visual cortex neurons enables these cells to maintain their encoding of the orientation of lines in an image at the same quality, regardless of whether the image is seen at high or low contrast (a phenomenon called contrast invariance of orientation tuning).

Nerve cells use action potentials (also called "discharges" or "spikes") to encode information that they transmit to other neurons. In the visual system, this information contains many different aspects of a viewed image including color, contrast, and orientation of lines and borders of the image. Generation of action potentials by a primary visual cortex neuron critically depends on parts of the visual image being orientated in the preferred range for that neuron. Visual stimulus orientations in the range preferred by that cell evoke action potentials, whereas other orientations do not (*2*). But these other orientations do elicit responses in other neurons. At the same time, the rate at which action potentials are produced increases in all neurons of the primary visual cortex when the contrast of the image is increased. Although the response strength does change as the stimulus contrast is varied, the tuning of a cell (that is, the dependence of the action potential frequency on the orientation of the stimulus) does not—a property called contrast invariance (*3*). This invariance allows independent encoding of the two different stimulus features, namely, contrast and orientation, by the same neuron.

Anderson *et al.* (*1*) report that contrast invariance of orientation tuning holds true not only for the action potentials generated, but also for the membrane potential responses, that is, at low contrast the signal is weak but the tuning width for stimulus orientation is preserved (see the figure). This result is in apparent conflict with a nerve cell's dependence on its membrane potential reaching a threshold before an action potential is generated. Classically, a neuron is considered to be an integrate-and-fire unit, with a simple relation between the depolarization of its membrane (due to a net influx of positively charged ions into the cell) and generation of the action potential. When the membrane depolarization reaches a certain threshold, action potentials are generated, and with a further increase in depolarization the rate of action potential generation increases (*4*). The necessity for the membrane potential to reach a threshold before being transformed into a train of action potentials accounts for sharpening of orientation tuning (*5*) through the "Iceberg effect" (see the figure, left). Like the tip of an iceberg, only part of the modulated membrane potential is visible above the threshold (red line in the figure); accordingly, action potential responses are

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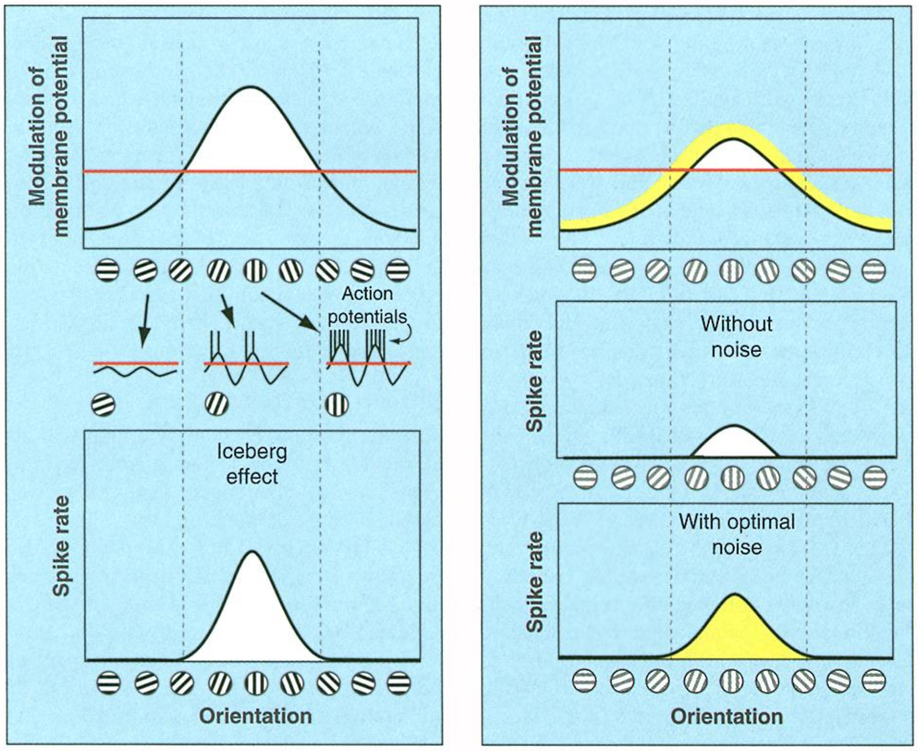
restricted to the corresponding range of stimulus orientations. Anderson *et al.* applied this integrate-and-fire model to the averaged membrane potential traces obtained from single visual cortical neurons at different stimulus contrasts. This resulted in a contrast dependence of orientation tuning—the model failed to predict the contrast invariance that they (*1*) and others (*3*) had found in visual cortical neurons in vivo. Anderson and colleagues suggest that the reason for this inconsistency is the noisiness of the membrane potential caused by the nonstop synaptic bombardment of neurons in vivo. They further demonstrate that the performance of the standard integrate-and-fire model can be rescued by the use of individual nonaveraged traces or by adding a certain degree of stochastic (random) noise to the averaged membrane potential curves (see the figure, right) (*6*).

Obviously, the comparison of the averaged membrane potential traces to the mean action potential rates does not help us to understand the intrinsic mechanisms of spike generation because, after averaging, the fine temporal structure and the high-frequency components of the signal are lost. Several lines of evidence indicate that it is exactly these high-frequency fluctuations that are of utmost importance for the generation of action potentials. Experiments in brain slices have shown that oscillatory modulation of the membrane potential leads to reliable generation of action potentials (*7*, *8*), and increasing the power of the modulation in the gamma-frequency range (25 to 70 Hz) improves the precision of spike timing (*7*, *9*). Stronger fluctuations in the membrane potential in the gamma-frequency range are associated with stronger spike responses to visual stimuli (*10*). Earlier qualitative observations (*11*) and recent quantitative analyses (*12*) show that the power of the gamma-frequency fluctuations in the membrane potential correlates with optimal stimulus orientation, that is, optimal stimulus orientation induces the highest "gamma-power." To make the story even more complicated, the threshold of action potential generation in vivo is not a fixed constant value, but fluctuates within a range of several millivolts (*10*, *12*), depending in part on the rate of membrane depolarization that precedes the action potential (*13*). Together, these data indicate that the fine temporal structure of the membrane potential itself carries important information, rather than just being noise.

The unique fine temporal pattern of fluctuations in a neuron's membrane potential is produced through a combination of the ongoing activity in the cortical neuronal network and the precise timing of sets of specific incoming sensory signals. This genuine property of the working brain is expressed in fluctuations of the membrane potential in the frequency range of 10 to 100 Hz. These fluctuations appear as "noise" but are often nonrandom, endowing nerve cells with several important capabilities. These capabilities include coordination of activity between assemblies of neurons that are responsive to coherent features of the image stimulus (*8*, *14*), the reliability and temporal precision of spike generation (*7*, *9*), and the detection of weak visual signals. This improvement in weak signal detection, a seemingly counterintuitive process, is closely related to "stochastic resonance" in nonlinear systems, a phenomenon in which the addition of a certain amount of noise enhances the detection of subthreshold signals. Stochastic resonance has been proposed to explain the periodic occurrence of Ice Ages, as well as certain properties of bistable lasers and living cells (*15, 16*). The Anderson *et al.* (*1*) analysis shows that the visual system may intelligently exploit this phenomenon to generate contrast invariance of orientation specificity during visual processing.



Watch out for the icebergs. The Iceberg effect in the selective response of neurons to the orientation of a visual image **(left)**, and its partial compensation by the addition of noise to the membrane potential **(right)**. (Left) Only high-amplitude modulations of the membrane potential of a primary visual cortex neuron, evoked by orientations of the visual stimulus in the preferred range, reach beyond the threshold (red line) and lead to the generation of action potentials (spikes). Stronger modulations of the membrane potential lead to higher spike rates. Membrane potential responses to visual stimuli in other orientations remain below the threshold and do not produce spikes. As a result, the tuning curve of spike responses (bottom) is narrower than the tuning curve of membrane potentials (top). (Right) Any orientation of the visual stimulus evokes smaller membrane potential modulations (top) because of the lower stimulus contrast (compared with the left panel). Without noise, the resulting tuning of spikes is very narrow and thus shows a strong contrast dependence (middle). The added noise (yellow area in the upper panel) lifts some of the weaker signals above threshold, and the resulting spike frequency tuning curve (bottom) becomes as wide as the one on the left. Anderson *et al.* (*1*) suggest that the addition of noise to the membrane potential can lead to orientation tuning that is independent of stimulus contrast in primary visual cortex neurons.

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