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pete effectively with gene regulatory proteins and polymerase to suppress transcription initiation? The tools needed to attack these questions are now in hand.

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NEUROSCIENCE

Temporal Coding in Neural Populations?

Eberhard E. Fetz

The waking brain continually performs a remarkable range of neural computations, processing its interactions with the environment as well as performing numerous internal operations. Consider the immediate example of your ability to quickly comprehend the spatial patterns on this page. Scanning successive words and decoding their meaning is a common miracle performed effortlessly by cerebral networks. If you pause to contemplate how neurons could perform these feats, your thoughts are also generated by a complex calculus of neural impulses. Realizing that your entire mental existence depends on neural operations, you can appreciate why neuroscientists would like to understand the underlying mechanisms.

To investigate how neurons process information, researchers typically relate the firing rate of single neurons (the rate at which neurons generate all-or-none action potentials) to a behavioral parameter, such as a sensory stimulus or motor response (1–3). Neural activity is quite variable, even with precise repetitions of the behavioral conditions, so mean firing rates have been obtained by averaging neural responses over many trials, thereby enhancing the rate-coding “signal.” The success of this approach has led to the belief that firing rates of neurons are the necessary and sufficient mechanism underlying information processing, and furthermore, that firing rates not only code peripheral sen-

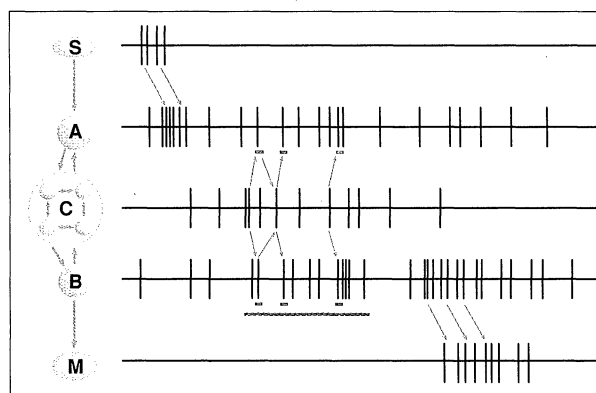
sory and motor events, but also mediate central cognitive processes.

But in fact, large populations of neurons are involved simultaneously in any behavior (4), and the temporal structure of spike activity in neural assemblies provides additional dimensions for coding information. Increasing numbers of researchers are now recording from many neurons simulta-

been proposed (5, 6), although such ideas are in dire need of compelling experimental support. In this regard, the report on page 1950 of this issue by Riehle *et al.* (7) provides new tools and supporting evidence. Using a simple algorithm for detecting real-time interactions in neural populations, the authors have found that neural activity became transiently synchronized during a purely internal cognitive process—when a monkey expected the presentation of a signal, in the absence of any sensory or motor events.

These findings relate to a current controversy concerning neural coding: whether neurons process information only by rate coding or whether the brain also exploits “temporal coding,” in which the relative timing of spikes can carry information (1, 7–10, 14). Temporal coding can employ the temporal structure of the firing pattern of single neurons (10) or, as considered here, the precise relation between firings in multiple neurons of a functional assembly (5, 9, 12, 14). If the relative timing of spikes in a neural population can represent information, as it surely does in the auditory system, the “bandwidth” for neural processing could be significantly expanded. As yet, there is no accepted standard for how this increased channel capacity would be used for high-definition neural computation. But a common feature of most temporal codes is the synchronization of spikes in neurons. The report by Riehle *et al.* shows that motor cortex neurons can become significantly more synchronized in relation to expected events, independently of any changes in firing rates.

The figure illustrates the different types of neural interactions. The two representative neurons (A and B) can fire in relation to peripheral events, like a sensory stimulus (S) or movement (M), and can also participate in internal cognitive events, symbolized by the central assembly (C). The proposed signature of the cells’ participation in assembly activity is increased synchronization, produced by common input from the assembly. Synchronous activity provides an effective propagating mechanism within the assembly, and can



Neural communication. Schematic representation of interactions of two cortical neurons (A and B). Sensory event S affects A and motor output M is affected by B; in both cases the neuronal firing rate codes a peripheral parameter. The central assembly (C) can also engage A and B in synchronous activity. This can be detected by the increased synchrony in the brief intervals (red) compared to that expected from activity in the longer interval (blue).

neously (3, 4). Indeed, the techniques for multiunit recording have outstripped the development of algorithms for analyzing the dynamics of neural populations. Some investigators have found ways to derive better fits between multiunit activity and behavioral parameters (3), but most population-coding schemes still employ functions of firing rates. The possibility that information processing may involve the instantaneous relations between members of neural assemblies has

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also change the efficacy of synaptic connections between the synchronized cells (9). Riehle *et al.* detected the increased synchrony by comparing the number of observed coincident spikes (red bars) with the number expected by chance, based on a running estimate of rates over a longer interval (blue bar). This running comparison can identify exceptional synchronizations whenever they occur. Interestingly, these occurred at times when the monkey expected a possible cue, as well as when he made a motor response. Thus, synchronization and rate coding can occur separately or together (8, 9, 12, 14, 15).

Several other approaches can detect coherent activity in neural populations at millisecond resolution. Standard cross-correlations between simultaneously recorded neurons commonly reveal synchronous activity, and time-dependent cross-correlation measures (11) have revealed that synchronous firing can be rapidly modulated with behavior, even without changes in firing rates (12). Other studies have found evidence for precisely timed patterns occurring among neural groups in a behavioral situation (5). Simulations have shown that such synchrony can be preserved in chains of neurons with realistic synaptic connections (13). Another form of synchronized activity in neural populations is the widespread periodic oscillations seen in visual cortex neurons, which has been suggested to subserve a binding function (9), a suggestion potentially applicable to coordination of motor responses (14, 15). Another approach uses the "gravity" method to identify groups of neurons that tend to fire in synchrony: If n neurons are located in n -dimensional space, and their spikes are endowed with a transient "charge," those cells that fire synchronously tend to be attracted and form identifiable clusters (6).

Although all of these algorithms can detect the existence of precise temporal structure in neural activity, this does not yet establish their function as a temporal code. What is needed first is some demonstration that synchronization occurs reliably under particular behavioral conditions. The accumulating evidence is suggestive (5–9, 12, 14) but still leaves the exact function unproven. Establishing the functional mechanism may not be a matter of finding tighter correlations with behavioral events; for example, holographic mechanisms code distributed information in terms of phase relations rather than literal representations (2). Skeptics can still argue that the temporal events revealed by these methods are epiphenomena or products of the statistical models, and that anything temporal coding can do, population rate coding can do as well (16). Moreover, there are open questions about how temporal codes are established

and how they interact with rate coding (8, 15). These issues can now be investigated with the tools at hand: Multiunit recordings can be analyzed with these algorithms, and the detected events can be related to behavior. Neural network simulations can also help to demonstrate how the putative coding mechanisms could actually work (2, 5, 13). This combination of approaches should crack the temporal code one way or the other.

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APPLIED PHYSICS

Longer Life for the Blue Laser

Gerhard Fasol

Less than 1 year after announcing the first continuous-output gallium nitride (GaN) blue light semiconductor laser at room temperature, Nakamura *et al.* at Nichia Chemical Industries Ltd. are now reporting such lasers with a demonstrated lifetime of 3000 hours and an estimated lifetime of over 10,000 hours (1). This now reaches the realm of commercial application, where lifetimes of 10,000 to 20,000 hours are required. Nichia estimates that commercial GaN laser diodes will be introduced in the fall of 1998.

Nakamura's recent development (2) of GaN-based violet, blue, and blue-green light-emitting diodes and laser diodes is certain to have a large impact on the world as we know it, and it has opened a new material system for scientific and commercial exploration. These devices have large ready-made commercial markets: displays, high-density data storage, laser printing, communications, and lighting, just to name a few. There may well be several other applications that have not yet been imagined.

Not surprisingly, therefore, researchers of many large corporations and universities are competing to develop GaN lasers. To my knowledge, six laboratories in addition to Nichia have now reproduced variations of Nakamura's pulsed room-temperature GaN laser: Cree Research (on SiC substrates), Fujitsu, Toshiba, the University of California at Santa Barbara, Xerox, and Sony. This means that Nakamura is about 2 years in advance of his competition. Under today's circumstances, this is astonishing. High-temperature superconductivity, the scanning tunneling microscope, and other recent breakthroughs were reproduced much more quickly in competing laboratories. And this despite incomparably higher competitive market pressures in the case of the GaN laser.

Nakamura's new laser diodes are similar to those of 1 year ago (Fig. 1), which had a lifetime of only 27 hours. There are two main advances in the recent work. First, for the present lasers, modulation-doped superlattices are used with 120 periods of 2.5-nm thick doped GaN separated by undoped 2.5 nm $\text{Al}_{0.14}\text{Ga}_{0.86}\text{N}$, instead of thick AlGaIn layers, which easily cracked. Second, the laser diodes are grown onto epitaxially laterally overgrown (ELOG) GaN substrates (Fig. 2).

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