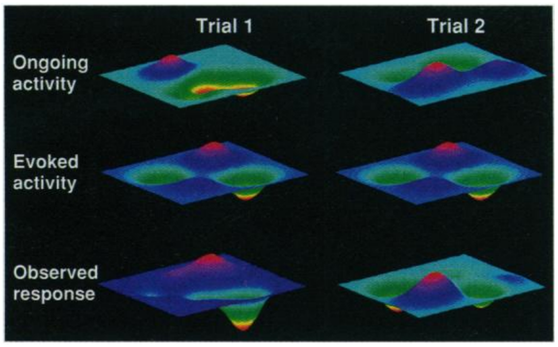
# Is Neural Noise Just a Nuisance?

David Ferster

Neurons are maddeningly noisy devices. The response of a neuron in the visual cortex to a repeated visual stimulus is never the same, either in amplitude or in timing (*1, 2*). Despite triggering the neuron with the correct stimulus—the one it responds to best—some trials yield no spikes at all, making the range of variability as large as the signal itself. For cortical physiologists who want to measure precisely the properties of cortical neurons, noise is merely a nuisance. Most simply sidestep the noise, repeatedly presenting the stimuli and reporting averaged responses. Variability is mentioned briefly, if at all. But the biophysical origins of this variability and its consequences for perception are of great interest to a small industry of physiologists and theorists (*2–6*). And new data presented in this issue by Arieli *et al.* (*7*) may change the way we think about neural noise.

Variability makes the response of a single neuron a poor indicator of the event that triggered it. A stimulus might have all the right properties to activate a neuron in the visual cortex, but if the brain were to rely on this neuron alone to report the presence of such a stimulus, then on those occasions when the cell by chance responded poorly, how would the brain "know" of the presence of the stimulus? The brain, of course, has more than one neuron reporting on any one stimulus. According to the standard theory, because of the random nature of noise, while one neuron is responding poorly others are responding well. The average response of all the relevant neurons will then contain precise information about the stimulus (*8*). In the same way that the averaged responses of one neuron to many stimulus trials can provide precise information about a stimulus, single responses of many neurons to one trial could do the same. The key to the success of population codes based on this principle, however, lies in the critical assumption that the noise in each neuron is more or less independent of the noise in its neighbors. If not, and noise is strongly correlated among a group of neurons, then the population response will be as noisy and unreliable as the individual responses (*9*).

Such disruptive strong correlations in the neuronal noise over large regions of cortex are just what Arieli *et al.* observed. Using a 144-element photodiode array, they made optical recordings from a 2 mm by 2 mm patch of cat visual cortex stained with a voltage-sensitive dye (*10*). Each photodiode can capture responses to single stimuli with a resolution of milliseconds, with the resulting signal reflecting the summed activity of thousands of neurons and their dendrites in a small region of cortex. Signal processing removes large artifacts resulting from respiratory and cardiovascular movements of the brain. The method provides an accurate, real-time view of neuronal activity spreading across several cortical hypercolumns as they respond to a stimulus.




**What makes up neural activity?** After a stimulus, the ongoing activity and evoked activity sum to produce the observed response.

Using this method, Arieli *et al.* observed waves of activity appearing and disappearing or traveling across the cortex in response to visual stimulation, with each crest or trough covering a significant fraction of the recording area [see figure 1 in (*7*)]. But just as in the responses of single neurons to repeated stimulation, the evoked spatiotemporal pattern of the optical activity varies tremendously from one trial to the next: A stable and precise response pattern emerges only when a large number of individual responses are averaged. The source of the variability is a randomly changing pattern of activity, which is ongoing both in the presence and the absence of stimulation and which seems to be superimposed on the underlying evoked response. The response during one stimulus trial, then, is the algebraic sum of the evoked activity (identical from trial to trial) and of the ongoing activity (different in every trial). Because this variable component may be nearly as large as the averaged evoked activity, the patterns recorded during two individual stimulus trials hardly resemble one another and rarely resemble the underlying averaged response (see figure). According to Arieli *et al.*, visually evoked activity of single neurons is highly correlated with optical signals from nearby cortex. Because the optically detected waves of activity spread across hundreds of micrometers of cortex, the response variability must be correlated among a large fraction of the underlying tens of thousands of neurons.

With the assumption of independent variability among neurons seriously undermined, one can no longer take it for granted that averaging among populations of neurons can be used by the brain to obtain low-noise signals. In the absence of effective averaging, then, an animal's ability to detect visual stimuli should be no better than the information contained in the responses of single neurons. Britten *et al.* have performed this exact comparison in awake behaving monkeys, measuring the responses of single neurons to the optimal stimuli while simultaneously measuring the animal's ability to detect the stimuli (*9*). The performance of the monkey was no better than the best of its neurons. Britten *et al.* concluded from simulations of their data that the noise among neurons with similar receptive field properties might be highly correlated. Arieli *et al.* now provide direct evidence for such correlations. So monkeys seem not to average the responses of their cortical neurons in the way that physiologists do.

Other questions now arise. Does the phenomenon occur in awake animals? (Arieli *et al.* mention preliminary evidence that it does.) What intracellular events underlie the waves of activity? And, more difficult questions: How is it that we obtain a stable percept of repeated visual stimuli when the neural response appears to be so different from trial to trial? And if random activity reduces the reliability of neuronal detection, what function does it serve? The answers may reveal something new and fundamental about how the brain works.

The author is in the Department of Neurobiology and Physiology, Northwestern University, Evanston, IL 60208, USA. E-mail: ferster@nwu.edu

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