

steps of 10 and 100 μM hydroxyproline (Fig. 1A). The receptor cells were allowed to recover for at least 90 s between each stimulus series. Cell responses were quantified by the total number of spikes and by the maximum number of spikes in any 100-ms time period within a response.

Fifteen receptor cells survived the entire stimulus protocol and were used for data analysis. Cells responded to 10 and 100 μM test pulses with brief bursts of 12.4 ± 7.3 and 16.6 ± 6.6 spikes, respectively. Responses to the adapting pulse were phasic and terminated even when the odor was still present, indicating that the receptor cells completely adapted to the stimulus. After a 1 s recovery time, only 30% of the receptor cells responded to the probe pulse. When given a longer recovery time, individual receptor cells regained their sensitivity at different rates. After 30 s, all receptor cells recovered 90% of their original response: the magnitude of the probe pulse responses was not significantly different from the test pulse response magnitude ($P < 0.05$, paired t -test) for both stimulus concentrations used.

To assess the time course of recovery of the cell population, we compared the mean response values of the 15 cells for test

and probe pulses (Fig. 1B). Responses fully recovered within 25 to 30 s; beyond 30 s, responses did not significantly increase. Surprisingly, the time course of recovery was the same for both stimulus concentrations.

Although full recovery took 30 s, cells regained 50% of their sensitivity within 9 s. Hydroxyproline-sensitive cells can follow 2 Hz pulse trains (3). It is the time course of recovery from adaptation that integrates odor events and sets the high frequency limit of the system for detection of the spectrum of odor concentration fluctuations that occurs in an odor plume.

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Visual Responses in the Brain of *Limulus*

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The lateral eye of the horseshoe crab *Limulus polyphemus* is one of the best understood visual structures in the animal kingdom. Studies of the lateral eye have provided us with the concepts of adapting quantal bumps in response to the absorption of a single photon (1, 2), lateral inhibition as a mechanism of edge enhancement (3), and circadian modulation of retinal function (4) as a component of visually guided behaviors (5). We know relatively little, however, about how the brain processes retinal input for the animal to see (6, 7).

Here we report on the first intracellular recordings from the lamina, the first level of synaptic processing of retinal signals in the brain. Glass micropipettes (3.0 M KCl, 40–80 M Ω) filled with 5% Neurobiotin in 1.0 M KCl (+0.5 nA for 5 min) (8) were advanced vertically into the surgically exposed brain *in situ*. Signals from the microelectrodes were fed to a bridge amplifier and monitored with a digital oscilloscope. Light stimuli were delivered to individual receptor units (ommatidia) in the retina with a 70- μm light pipe and to large regions of the eye with a fiber optic bundle.

We frequently impale as yet unidentified cellular compartments in the lamina that receive synaptic inputs from many optic nerve fibers and action potentials from a single optic nerve fiber. Illumination of a single ommatidium in the retina generally evokes slow depolarizing potentials (0–5 mV) in association with a single train of action potentials (20–60 mV) in the compartment, whereas illumination of the entire retina elicits slow hyperpolarizing potentials (5–15 mV) and a spike train of reduced

rate (Fig. 1A). Resting potentials are in the range of –45 to –60 mV. Both discharge patterns resemble those of single optic nerve fibers (9), except that the spike size can change during a response and the spike duration can be up to four times longer (not shown).

Injections of Neurobiotin into the compartment have consistently labeled more than one fiber in the optic nerve (typically

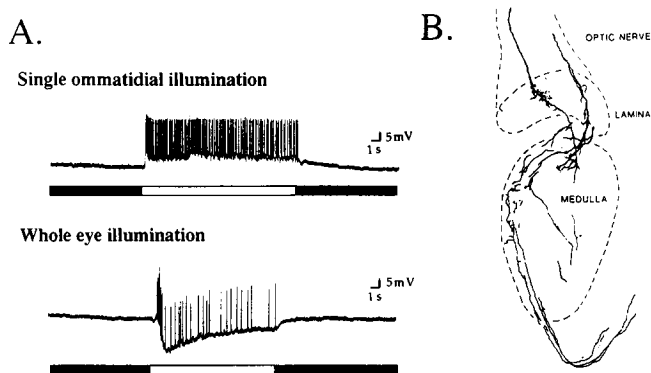


Figure 1. (A) Recordings from a cell in the first synaptic layer of the brain (lamina). The compartment receives excitatory input from a single retinal cell and inhibitory inputs from many cells. The spike amplitude has been attenuated by the chart recorder during reproduction. (B) Camera lucida reconstruction of cell after Neurobiotin injection. Note retrograde labeling of more than one optic nerve fiber.

three), as well as processes in the lamina and medulla ($n = 10$, Fig. 1B). Previous anatomical studies with cobalt chloride showed that a single nerve fiber gives off a puff of processes in the lamina as it continues on into the medulla and other optic nuclei (10).

What is the cellular compartment we are recording from? The spike discharge and Neurobiotin staining patterns strongly suggest the axons of optic nerve fibers. However, such large slow potentials would not be expected in this compartment because the soma is located 4–5 cm away in the retina. Moreover, it is unclear why the spike size would change, spike duration would differ, and multiple axons would stain if this were the case. Hence, it appears that we are recording from synaptic compartments, presumably in the branches of optic nerve fibers, that receive action potentials from the main axon and slow potentials from other nerve fibers or cells in the brain. The differences in discharge patterns to single ommatidial and whole eye stimulation result from lateral inhibition in the retina, whereas the differences in slow potentials are a consequence of synaptic interactions in the lamina.

Neural processing in the lateral eye of the horseshoe crab is hidden from microelectrodes in the tangled web of the lateral plexus that interconnects neighboring ommatidia to mediate lateral inhibition. Neural processing in the lamina appears to use the same integrative mechanisms as the retina and may be more accessible to electrode studies. If so, we may gain an un-

derstanding of the synaptic interactions that occur across a parallel array of optic nerve fibers and their influence on the information sent to other regions of the brain.

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Noise Components in *Limulus* Vision

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As a horseshoe crab moves along the bottom of a shallow bay, its lateral eye continuously transmits a picture of its environment back to his brain. This "video picture" contains only about 40×25 pixels, is blurred by the wide acceptance angle of the ommatidium, and is distorted by the way the eye samples visual space nonuniformly. Within the eye, two neural inhibitory processes enhance contrast, but the net result of all the steps in neural encoding is often a very noisy image. In spite of the rather poor image quality, neural circuits in the *Limulus* brain can extract visual information to guide the animal's movements.

Unattached males during the mating season provide a particularly straightforward example of visually guided behavior; they generally turn and approach any object that is about the size of a mate. As first reported here last year (1), we can record the neural signals that the brain receives as the eye scans the same targets used in the behavioral experiments. Analysis of several such experiments has revealed that targets at a distance beyond that of the behavioral threshold elicit a perceptible modulation of spike rate (2). This result is fully consistent with theoretical computations of the expected responses (3). If the behavioral threshold cannot be explained by the sensitivity of the photoreceptors, perhaps our experimental paradigms have consistently

underestimated the noise that the animal must contend with under natural conditions. We have therefore started to study how the statistical properties of the random fluctuations in spike rate depend on differing visual environments.

Two sources of noise that are intrinsic to the eye have been fully characterized; namely, the shot noise triggered by photon adsorption that is the excitatory input to the spike generator, and the summed inhibitory potential triggered by spikes in many neighbors. Because the unitary IPSP is longer than 0.5 s, it smooths nearly all fluctuations in its input and, in fact, makes only a minor contribution to the noise. The phototransduction noise can be quite large under dim ambient illumination, but decreases greatly as the eye adapts to higher illuminations. The power spectrum of this noise shows a relatively broad pass-band matching the dynamic transfer-function for sinusoidally modulated light (4). Phototransduction noise at illumination levels equivalent to the daylight field experiments (plus inhibitory synaptic noise) causes spike-rate fluctuations with a coefficient of variation (CV) of 7% or less.

As we move from the laboratory to the field experiments, we would expect to observe more noise caused by random fluctuations in light intensity. Some of the environmental noise is