Abstract. Horseshoe crabs use vision to find mates. They can reliably detect objects resembling potential mates under a variety of lighting conditions. To understand how they achieve this remarkable performance, we constructed a cell-based realistic model of the lateral eye to compute the ensembles of optic nerve activity ("neural images") it transmits to the brain. The neural images reveal a robust encoding of mate-like objects that move underwater during the day. The neural images are much less clear at night, even though the eyes undergo large circadian increases of sensitivity that nearly compensate for the millionfold decrease in underwater lighting after sundown. At night the neural images are noisy, dominated by bursts of nerve impulses from random photon events that occur at low nighttime levels of illumination. Deciphering the eye’s input to the brain begins at the first synaptic level with lowpass temporal and spatial filtering. Both neural filtering mechanisms improve the signal-to-noise properties of the eye’s input, yielding clearer neural images of potential mates, especially at night. Insights about visual processing by the relatively simple visual system of Limulus may aid in the design of robotic sensors for the marine environment.

Introduction

The world is rich with sensory information, and animals are highly efficient at extracting what is essential for their survival. The retina begins the processing of visual information by transforming patterns of incident light intensity into trains of impulses in optic nerve fibers (Dowling, 1987). The retina encodes information it receives in a reliable and efficient manner (Rieke et al., 1997) but does not encode all of it. Rather, the retina extracts certain features in the visual scene at the expense of others (Lettvin et al., 1959). An important first step for exploring the neural code the eye transmits to the brain when an animal sees is to understand what an animal can see in its natural habitat. The next step is to examine the retinal coding of natural scenes in activity of optic nerve fibers. Recordings from single nerve fibers have indeed yielded useful insights about retinal function; however, it is difficult to infer from them the information transmitted by arrays of optic nerve fibers to the brain about the complex patterns of illumination animals encounter in their natural habitat. Techniques such as multi-electrode arrays (Meister et al., 1994) and voltage-sensitive dyes (Wong et al., 1995) can access patterns of activity generated by ensembles of retinal neurons, but they are not practical for recording from large numbers of optic nerve fibers in behaving animals.

A Computational Model of the Limulus Eye

An alternative approach is to construct a realistic computational model of the eye. The relative simplicity of the eyes of lower vertebrates and invertebrates offers the best opportunities (Werblin, 1991; Teeters et al., 1997). The lateral eye of the horseshoe crab Limulus polyphemus is a particularly attractive model system for the following reasons: first, its visually guided behavior is well known (Barlow et al., 1982; Powers et al., 1991; Herzog et al., 1996); second, it processes visual information with integrative mechanisms shared by more complex systems (Barlow, 1969; Ratliff, 1974); and third, its lateral eye contains the largest neural network (~1000 neurons) for which a quantitative cell-based model exists (Hartline and Ratliff, 1957, 1958; Barlow and Quarles, 1975; Barlow et al., 1993b).
Figure 1. A horseshoe crab, Limulus polyphemus, mounted with a video camera, “CrabCam,” for recording underwater movies and a microsuction electrode for recording responses from a single optic nerve fiber. A white Teflon cap (2.5 cm diameter) seals the recording chamber, which is attached to the carapace anterior to the right lateral eye. The barrel of the microsuction electrode protrudes from the recording chamber to the right. Tethers lead the video and optic nerve signals to recording electronics located on shore or in an overhead skiff as the animal moves about underwater at depths of 0.5 to 1 m. Experiments were carried out in an estuary near the Marine Biological Laboratory, Woods Hole, Massachusetts.

We have constructed a computational model of the lateral eye that predicts optic nerve responses with good accuracy (Passaglia et al., 1998). In brief, the model treats the retina as an array of neurons that samples visual space as the compound eye does, incorporates the known excitatory and inhibitory integrative mechanisms of the retina, and adapts to changes in ambient illumination.

Our strategy for examining the retinal code underlying behavior is to first videotape the lateral eye’s view of its underwater world with an animal-mounted camera (“CrabCam”) while simultaneously recording from a single optic nerve fiber of an ommatidium viewing the central region of the videotaped scene (Passaglia et al., 1997a). Figure 1 shows the CrabCam and the watertight recording chamber mounted on an animal before it enters the water and passes near submerged mate-like objects near the water’s edge in Woods Hole, Massachusetts. Back in the laboratory we digitize the CrabCam recordings and feed them to the cell-based model, which then computes the arrays of optic nerve activities in response to the underwater scenes. The computed arrays of activities are converted to a grey scale and mapped to their appropriate retinal location, generating “neural images” of the eye’s input to the brain (Fig. 2). Finally, we assess the accuracy of the model’s predictions by comparing the response recorded from a single optic nerve fiber to that computed by the model for the corresponding receptor. Correlation coefficients between recorded and com-
Computed responses are typically greater than 95% \((n = 5)\) under controlled laboratory conditions but lower for field experiments because of the difficulty of precisely determining the stimulus to the recorded ommatidium. Once satisfied with the accuracy of the model’s predictions, we analyze the neural images for information the eye sends to the brain when the animal sees.

**The Limulus Eye Functions as a Global Feature Detector**

The eye transmits to the brain robust “neural images” of objects having the size, contrast, and motion of potential mates (Passaglia et al., 1997a). Inspection of the neural images computed for the daytime state of the eye in Figure 2 shows that the eye is highly sensitive to images of crab-
size objects moving within the animal’s visual range at about the speed of a horseshoe crab (15 cm/s). Indeed, measurements of the spatial and temporal transfer functions of the eye using linear systems analysis show that it functions as a tuned spatiotemporal filter. These filtering properties can readily account for the animal’s ability to see high-contrast objects but not low-contrast ones. Natural fluctuations of underwater lighting enhance the visibility of low-contrast objects. Beams of light created by overhead waves strobe the underwater scene in a range of frequencies (~2-6 Hz) for which the temporal transfer function shows the eye is maximally sensitive. Such wave-induced flicker increases the visibility of low-contrast, crab-sized objects during the day, as observed in field studies (Passaglia et al., 1997b; Krutky et al., 2000). The high-contrast object is detectable in the computed neural image in Figure 2, but the low-contrast object is almost completely obscured by random photon events that characterize low nighttime levels of illumination (Hitt et al., 2000). The high-contrast object is detectable in the computed neural image in Figure 2, but the low-contrast object is hardly recognizable in the computed neural images (not shown).

A Circadian Clock Modulates Lateral Eye Sensitivity

The 

Limulus

eye operates in two distinct states: daytime and nighttime. It not only responds to changes in illumination; it anticipates them. At dusk a circadian oscillator in the brain transmits efferent optic-nerve signals to the lateral eye, influencing almost every physiological and anatomical property of the retina (Table 1).

The endogenous rhythms of the retina combine with mechanisms of light and dark adaptation to increase visual sensitivity by about 10\(^6\) at night, nearly compensating for the decrease in the intensity of illumination in the animal’s marine environment. In our initial theoretical analysis of retinal coding discussed above, we constructed a computational model to simulate the daytime state of the eye. To examine the retinal coding that underlies vision at night, we must modify our computational model so that it can account for the circadian changes in lateral eye function. We have developed a “nighttime” model that includes most of the circadian changes listed in Table 1.

Photon Noise Dominates Retinal Responses at Night

Neural images of mate-like objects are less clear at night. They are dominated by bursts of spikes triggered by random photon events that characterize low nighttime levels of illumination (Hitt et al., 2000). The high-contrast object is detectable in the computed neural image in Figure 2, but the low-contrast object is almost completely obscured by random photon events. Computations require the setting of
initial conditions, and an important initial condition is the mean light level of the visual scene. To simulate the nighttime state we reduce the mean light level by $10^6$ relative to daytime levels. At such low light levels the Poisson nature of photon absorption events produces substantial phototransduction noise that can obscure signals generated by visual stimuli.

The response of a single optic nerve fiber in Figure 3A recorded under nighttime light levels is indeed variable. It shows no clear sign that a high-contrast crab-sized object had moved across the visual field. This experiment was performed in the laboratory because the Crabcam is insensitive to the low light levels in the animal’s habitat at night. To overcome this problem we simulated nighttime conditions by aligning an animal in front of a monitor that played back CrabCam recordings made in the animal’s habitat. The output of the monitor was attenuated by $10^6$ with neutral density filters to approximate nighttime levels of illumination. The highly variable optic nerve response shown in Figure 3A is consistent with the noisy neural images in Figure 2 that were computed with the nighttime model of the eye.

**Brain Processing Enhances Retinal Signals**

How does the brain extract a reliable signal from such a noisy retinal input? Optic nerve fibers carrying the retinal signals synapse on neurons of the lamina of the brain. Single-cell recordings show that the laminar synapses integrate retinal signals with a time constant of about 400 ms (Passaglia et al., 1997a). To assess the effect of these “slow” synapses we added a stage of temporal integration to the computational models. Figure 2 shows that synaptic integration with such a long time constant suppresses the high-frequency fluctuations in optic nerve activity both day and night. The effect is especially striking in the neural images computed for the daytime state where temporal integration nearly recovers the visual stimulus. It is interesting that in another invertebrate visual system, that of the fly *Lucilia cuprina*, temporal integration reliably recovered the stimulus-induced response component from noisy neuronal signals in the motion pathway (Warzecha and Egelhaaf, 1997).

Returning to *Limulus*, temporal integration of the neural images generated by the retina in its nighttime state does not recover the visual stimulus. The burstiness evoked by random photon events (Fig. 2) remains prominent and obscures information about the visual stimulus.

Because horseshoe crabs can see potential mates nearly as well at night as during the day, the brain must possess additional neural mechanisms for processing the retinal input, although these mechanisms need not be located in the lamina. One such mechanism could be spatial integration within the receptive fields of laminar neurons (Hitt et al.,
detect potential mates, a critical task that it performs equally well day and night. The clock does so by modulating almost increases its sensitivity at night, enabling the animal to enough to be understood. Using a computational approach, has proven complex enough to be interesting, yet simple behavioral response? Analyzing a relatively simple nervous system may yield important insights about the functioning of more complex ones. Indeed the visual system of Limulus has proven complex enough to be interesting, yet simple enough to be understood. Using a computational approach, we unraveled its coding properties and determined the neural image it sends to the brain about behaviorally relevant stimuli during the day. The Limulus eye, however, turned out not to be so "simple" after all. A circadian clock increases its sensitivity at night, enabling the animal to detect potential mates, a critical task that it performs equally well day and night. The clock does so by modulating almost every property of the retina, from stabilizing rhodopsin to weakening lateral inhibition and increasing photoreceptor gain (see Table 1). The challenge addressed in this paper is to understand how the eye efficiently encodes information about potential mates under the photon-limited conditions of the animal's marine environment at night. The answer in part appears to be that coding mechanisms in the eye together with integrative mechanisms in the brain overcome environmental noise to enhance the neural images of behaviorally important visual stimuli.

The neural basis of visually guided behavior has been studied extensively in another invertebrate, the fly. Particular attention has been paid to understanding how the fly visual system adapts to, encodes, and processes natural stimuli (Review: Rieke et al., 1997). Adaptative mechanisms in the fly retina appear to enhance the efficiency of coding information about natural scenes (Review: Laughlin, 1994). In more central pathways, adaptive motion-sensitive mechanisms rescale the dynamic range of neural responses to match that of stimuli and thereby maximize information transmission (Brenner et al., 2000). Adaptation of the motion-sensitive mechanisms decreases contrast sensitivity while preventing saturation of neural responses and preserving receptive field response properties (Harris et al., 2000). Whether Limulus possesses such adaptive mechanisms is not known. However, as described above, retinal mechanisms endow the Limulus eye with high sensitivity to the motion of natural stimuli, and central mechanisms suppress noisy retinal signals to recover stimulus-induced responses.

This brings us to more complex systems such as the vertebrate retina. With tens of millions of cells, dendritic processes, and synaptic contacts, the task of deciphering its neural code is indeed daunting. Developing a cell-based, realistic computational model as we did for Limulus appears unrealistic. A different computational approach is needed; one that by necessity models ensembles of neurons. The danger is that such modeling may overlook essential details in the neural circuitry. As was the case for Limulus, important insights can come from understanding the function of a sensory organ and how it adapts to changing environmental conditions. Endogenous adaptation mechanisms, such as efferent inputs and circadian oscillators, can often reveal critical aspects of underlying neuronal mechanisms. Perhaps most important of all is first to understand the role of a sensory modality in an animal's life and then to investigate the underlying neural mechanisms.

**What Is the Neural Basis of Behavior?**

How does the intricate circuitry of a nervous system receive sensory information, process it, and generate a behavioral response? Analyzing a relatively simple nervous system may yield important insights about the functioning of more complex ones. Indeed the visual system of Limulus has proven complex enough to be interesting, yet simple enough to be understood. Using a computational approach, we unraveled its coding properties and determined the neural image it sends to the brain about behaviorally relevant stimuli during the day. The Limulus eye, however, turned out not to be so "simple" after all. A circadian clock increases its sensitivity at night, enabling the animal to detect potential mates, a critical task that it performs equally well day and night. The clock does so by modulating almost every property of the retina, from stabilizing rhodopsin to weakening lateral inhibition and increasing photoreceptor gain (see Table 1). The challenge addressed in this paper is to understand how the eye efficiently encodes information about potential mates under the photon-limited conditions of the animal's marine environment at night. The answer in part appears to be that coding mechanisms in the eye together with integrative mechanisms in the brain overcome environmental noise to enhance the neural images of behaviorally important visual stimuli.

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**Implications for Artificial Sensory Systems**

Sensory systems, especially those of invertebrates, often serve primary functions. They are highly efficient at extracting from the physical world specific information for behaviors essential for survival: mating, finding food, and avoiding predators. In some animals, subsections of a sensory system may serve singular functions. For example, the Limulus brain segregates the processing of visual information, devoting a major locus in the medulla to the region of the visual field that views potential mates. Horizontal strips of ommatidia serving this region form a precise map onto an expanded locus in the medulla (Chamberlain and Barlow, 1982), suggesting that the primary task of this region is mate detection (Dodge et al., 1999). Understanding the functions of such specialized regions of a sensory system and the underlying neural integrative mechanisms may aid in the design of artificial sensory systems useful for remote sensing and robotics.

Excitation and inhibition are universal mechanisms for processing the spatial and temporal features of sensory information. They "tune" sensory systems, selecting essential features from a world rich in information. Remarkably,
the integrative mechanisms of the *Limulus* eye make it highly sensitive to moving, mate-like objects. Mechanisms of adaptation enable the eye to operate over wide ranges of environmental conditions. In sum, the neural mechanisms of this so-called “primitive” eye encode and analyze visual information and send a highly processed neural image to the brain both day and night.

The implications for artificial sensory systems are (1) a relatively simple neural circuit can encode and process sensory information, and (2) the same neural circuit can operate over a wide range of environmental conditions. Can an artificial system be designed and constructed with these properties? We implemented a software-based computational model that incorporates these properties, but with current hardware it cannot function in real time. Computations are an order of magnitude slower than real time; that is, computing the eye’s response (neural images) to 6 s of visual input requires about 60 s. At this time a computational model appears unrealistic. An alternative approach is to construct a silicon retina having all the known properties of the *Limulus* eye. Such artificial retinas have been fabricated (Mahowald and Mead, 1991), but they are mostly hardwired and not readily adaptable to changing environmental conditions. However, techniques of microcircuitry are advancing at a rapid pace. Perhaps in the not-too-distant future it will be possible to fabricate a silicon retina with stimulus-dependent circuitry that can simulate an eye’s numerous adaptive mechanisms. Such a dynamic “softwired eye” would find many uses, from remote sensing in hazardous environments to the navigational control of robots. Because *Limulus* incorporates many of the integrative mechanisms found in more complex vertebrate eyes, it is conceivable that a *Limulus*-inspired “softwired eye” may also prove useful as the first stage of a prosthetic visual system for humans.

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**Literature Cited**


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