Adaptive Processes of the *Limulus* Lateral Eye*

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**Abstract**— Our ability to see spatiotemporal fluctuations in contrast over widespread levels of illumination is due to retinal gain controls that constantly modulate the properties of cellular and synaptic mechanisms in our eyes. At present two general forms of gain control have been described in the vertebrate retina, one of which adapts to mean luminance and the other to luminance variance (contrast). We sought to test for both processes of adaptation in an invertebrate retina by recording the spike trains of individual optic nerve cells in the horseshoe crab to white noise stimuli of different luminance and contrast. The stimuli were also input to conceptual models of the retina with linear-nonlinear elements in assorted configurations and to a cell-based computer model that accurately simulates the retinal response to underwater movies. We find that the crab eye shows both luminance and contrast adaptation. Only the former was reproduced by the cell-based model but the latter could be mimicked by linear-nonlinear cascade model, which suggests the two adaptive processes are related or a heretofore unknown mechanism underlies contrast adaptation. That such a simple eye can produce seemingly complex behaviors like luminance and contrast adaptation makes the finding of broad importance to vision research.

I. INTRODUCTION

Determining how neural systems represent information is a longstanding goal of neuroscientists and neuroengineers. The goal remains a challenging research problem because neural representations are not static. They are continually reshaped by a variety of biophysical mechanisms of adaptation at each stage of system processing. The inherently nonlinear property of these mechanisms and their embedding within networks of highly interconnected neurons makes their contributions to neural coding tricky to unravel. In the visual nervous system, two types of adaptive processes have been identified in the vertebrate eye, which adjust the gain and dynamics of retinal cell responses based on the mean luminance and contrast of the visual scene [1-3]. In so doing these processes are thought to maintain the pattern sensitivity of the retina across a wide range of lighting conditions. Since such a role for retinal gain controls would be conceptually appealing to all animals, we hypothesized that the invertebrate eye should therefore also show luminance and contrast adaptation. To test the idea we investigated the compound lateral eye of the horseshoe crab, *Limulus polyphemus.*

The *Limulus* lateral eye provides an excellent testbed for evaluating retinal adaptation models because of its small size and simple structure. The eye consists of approximately 1000 ommatidial units, each of which has a lens that collects light from a 6°-12° region of space and focuses it onto the rhabdom of 10-12 photoreceptor cells. The photoreceptor cells convert the light signal into an electrical signal that passively spreads through gap junctions to a single optic nerve cell. The optic nerve cell then sums the photoreceptor signal with inhibitory signals from neighboring ommatidial units and encodes the result with a train of action potentials that are transmitted to the brain and across the lateral inhibitory plexus of the retina. Moreover, after over a century of research the inner workings of the eye are understood to the point that computer models can accurately predict its response to underwater objects of visual interest to the animal [4,5]. Since luminance adaptation is the only known gain control process operating in the retina, the expectation is that the horseshoe crab eye would not show contrast gain control but this has not been directly evaluated.

II. METHODS

A horseshoe crab was secured to a wooden platform and submerged to the gills in saltwater. A hole was opened in the carapace adjacent to the lateral eye. The exposed optic nerve was cleaned of tissue and inserted into a chamber mounted over the hole to the animal. A single nerve fiber was then dissected free, cut, and guided into a microsuction electrode attached to the chamber. Details of the recording technique have been reported elsewhere [6]. A 70µm optical fiber was aligned on the visual axis of the recorded cell and randomly modulated in time with white noise sequences of different mean luminance and contrast while the rest of the eye was kept in darkness. Fig. 1 shows the experimental setup. The presence and strength of adaptive processes in the eye was investigated by estimating linear-nonlinear (LN) models via white noise analysis of evoked spike trains. This was done by calculating the average stimulus waveform that preceded all spikes (L), convolving the waveform with the input, and mapping the result against measured response rates (N) [7].

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III. RESULTS

Fig. 2 presents representative results of LN analysis of crab optic nerve spike trains for white noise sequences of different mean luminance and contrast. The linear temporal filter (i.e., spike-triggered average stimulus) became shorter in duration at higher luminance levels (2A,left) and the nonlinear (input-output) mapping function shifted rightward (2A,right), which indicates a reduction in baseline sensitivity. Such behavior is consistent with prior research on light adaptation in the eye. More interestingly, the linear filter became less biphasic at higher contrast levels (2B, left) and the slope of input-output nonlinearity decreased (2B, right). The reduction in response gain for stimuli having the same mean but different variance is considered the hallmark of contrast adaptation in studies of the vertebrate retina.

![Image](image_url)

Figure 2. Linear filter (L, left) and nonlinear function (N, right) estimated by LN analysis of crab spike trains for noise sequences of different mean luminance (A) and contrast (B). Luminance data are for 100%-contrast noise at 0.6 cd/m² (black) and 6.0 cd/m² (red). The contrast data are from another cell for 25% (black) and 100% (red) contrast noise at 6.0 cd/m².

To identify a possible origin of the contrast adaptive effect, the white noise sequences were input to a realistic computer model of the crab eye [5] and to simple conceptual models. Model spike trains were then processed by LN analysis. The crab eye model did not show contrast adaptation, but Fig. 3 shows that a model consisting of two LN elements in series could reproduce the contrast-dependent gain change observed experimentally.

IV. DISCUSSION

According to white noise analysis of recorded optic nerve spike trains, the Limulus lateral eye exhibits light and contrast adaptive effects much like those of the vertebrate eye. The measured effects included changes in both response gain and dynamics. These effects were mimicked by an existing cell-based model of the eye only for conditions that evoke light adaptation, which is not surprising as contrast adaptation was not incorporated into the model. Conceptual models with LN elements in various arrangements were thereby explored, and it was found that an LNLN system can produce gain changes for conditions that often ascribed to contrast adaptation. This model does have a contrast gain control mechanism, which means that the phenomenological effects seen in Fig. 2 could derive from the same underlying process. If that is not the case, a heretofore unknown mechanism of contrast adaptation must operate in the horseshoe crab retina.

![Image](image_url)

Figure 3. An LNLN model shows contrast-dependent behavior according to white noise analysis. A. Model schematic. L₁ and L₂ were two linear filters of different duration resembling the estimated filter in B. N₁ and N₂ were rectifying functions that respectively scaled positive inputs linearly and quadratically. B. Linear filter (left) and nonlinear function (right) that were estimated from the LNLN model output in response to a white noise input of 25% (black) and 100% (red) contrast. The slope of the nonlinear function decreases at high contrast, which is often interpreted as evidence for contrast gain control but an LNLN model has no such mechanism.

V. CONCLUSION

In general, adaptive processes act to reduce the sensitivity of a system when stimulus strength is high to avoid response saturation and to elevate sensitivity when stimulus strength is low to improve signal-to-noise ratio. To implement these processes the vertebrate eye employs complex multicellular circuits that separately sense luminance and contrast [1,2]. Yet, the Limulus eye can achieve comparable results without even a single excitatory synapse. How the eye accomplishes these feats is therefore of broad relevance and interest. The biophysical mechanisms of luminance adaptation are known to reside largely within the phototransduction cascade of photoreceptor cells. The physiological origin of the contrast adaptive effects described here is unclear, and the possible candidate sites are very few. Intracellular studies using white noise analysis are required to help pinpoint a pre- or post-receptorial locus.

REFERENCES