

# Optimality and adaptation in motion estimation by the blowfly visual system.

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## Abstract

This study reports experimental results on the visual system of the blowfly *Calliphora vicina*, in which we record analog signals from photoreceptors and action potentials from wide-field movement-sensitive cells. The photoreceptor data allow us to quantify how much information is present at the input to the visual brain. A mathematical analysis of the problem of movement detection with noisy inputs shows that it is very beneficial to adapt the computation to the statistics of the incoming signals<sup>1</sup>. The experimental results suggest that the fly indeed adapts its computational strategy to a variety of statistical parameters of the input in ways predicted by the theory. Some examples of optimal processing and adaptation are presented.

## INTRODUCTION

An important task of the visual system, in fly as well as man, is to provide information for use in navigating through a highly complex and variable environment. Visual information processing begins in the retina, where an array of photoreceptors encodes a mapping of light intensities in the environment onto electrical signals. This process has several physical limitations: Diffraction by the optics, and waveguide coupling cut out high spatial frequencies<sup>2</sup>, while photon shot noise limits intensity resolution. Due to the combination of these two effects, visual resolution is limited in both space and time. This must be especially relevant in situations where fast and spatially precise judgments are called for, movement detection being a case in point. Here we show that, in a simple case, a fly movement sensitive neuron operates with a reliability close to the photon shot noise limit at behaviorally relevant light intensities. To estimate movement in a least-squares optimal sense, given that the inputs are contaminated by noise, the visual system should tune its computational strategies to the statistical parameters of its environment<sup>1</sup>. The values of these parameters may show huge variations, but if these changes are slow compared to behavioral decision times, it will be to the animal's advantage to keep track of their value and adapt its information processing strategies accordingly. Here we propose that adaptation extends beyond the well known light adaptation effects at the photoreceptor level, and into more "algorithmic" levels that have to do with the type of computation the brain performs to make the best of imperfect input data. We observe several forms of adaptation in the response of movement sensitive cells and these observations are consistent with an interpretation in terms of optimal adaptive velocity estimation.

## METHODS

Both intracellular recordings from photoreceptors, and extracellular recordings from the H1 wide-field movement-

sensitive cell in the blowfly visual system were made using standard electrophysiological methods. Stimulus patterns were generated electronically and displayed on a monitor (either HP 1311A (radiance 32.5 mW/(sr.m<sup>2</sup>)), or Tektronix 608 (radiance 165 mW/(sr.m<sup>2</sup>)), with light intensities in the range of daytime indoor levels). The estimated rate of photoconversion for the two displays is about  $9 \cdot 10^3$  resp.  $4 \cdot 10^4$  s<sup>-1</sup> per photoreceptor<sup>3</sup>.

## RESULTS

Figure 1 illustrates what happens to the encoding of a movement stimulus when the input signal to noise ratio is switched from high to low. The fly watched a wide-field pattern that moved rigidly according to a computer-generated pseudorandom trajectory while the response of H1 was recorded. Velocity information is encoded in the neural signal much more accurately when contrast is high, than when it is low, as expected if the movement computation is noise-limited. To give this interpretation a more quantitative backing we show (fig. 2) the performance of H1 in a discrimination task for which it is relatively easy to compute the theoretical limit to performance based on the photoreceptor signal to noise ratio<sup>4</sup>. The data plotted in the figure represent the performance of H1 in discriminating two small step sizes (0.24° and 0.36° of visual angle (these sizes are within the hyperacuity

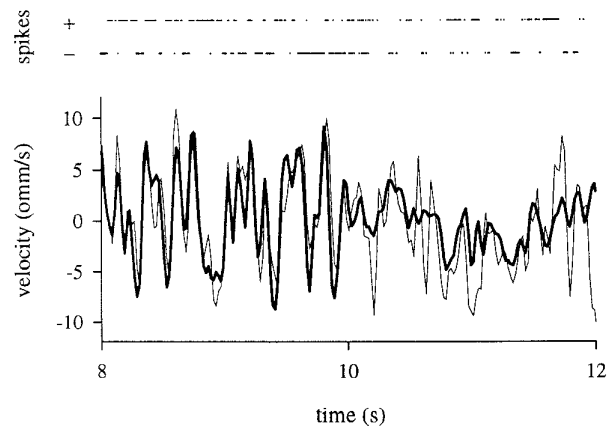


Fig. 1: Response traces on top are from the same neuron, but stimulated with velocity waveforms of opposite sign. This is done because H1 is directionally selective, being silent for movement in the null direction. From these two response traces, we compute a linear reconstruction<sup>5</sup> (heavy line) of the stimulus (thin line) that induced the responses. The stimulus was a random rigid motion of a random contrast pattern. At time  $t=10$  s, the average pattern contrast changed suddenly from 50% rms to 2.5% rms. The reconstructed velocity waveform is clearly much closer to the stimulus velocity waveform at high than at low contrast.

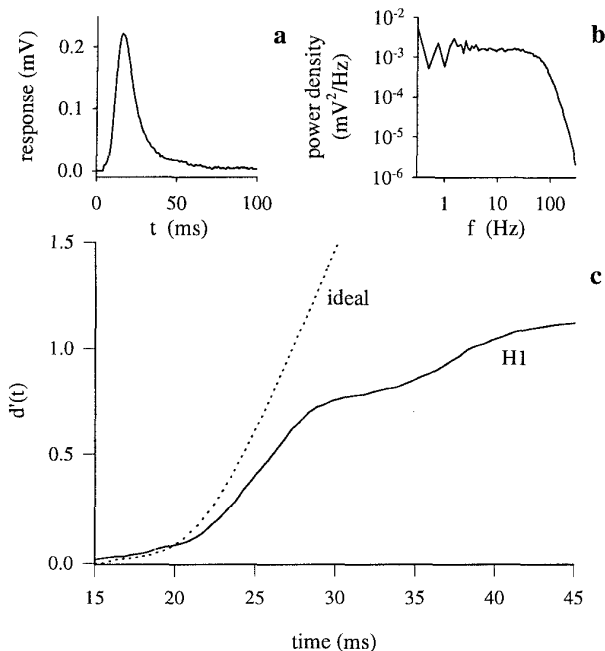


Fig. 2. *a,b*: Photoreceptor impulse response and noise spectrum. The low-frequency noise power is within 20% of the photon shot noise limit<sup>4</sup>. *c*: Reliability, expressed as the discriminability  $d'(t)$  between two small displacements ( $0.12^\circ$  difference). Solid line: H1 performance, based on the timing statistics of the first and second spike following stimulus presentation at  $t=0$ . Broken line: performance of an ideal movement sensor operating on photoreceptor signals typical for those in the H1 experiment.

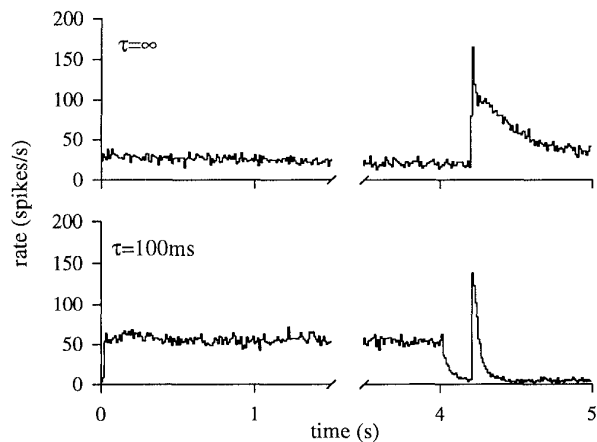


Fig. 3 The fly saw a stationary pattern in which each bar stayed constant (top) or flickered in luminance with a correlation time of 100 ms (bottom). After 4 seconds the flicker was switched off, and at 4.2 seconds the pattern made a single step displacement. The time course of H1's response to these test steps depends strongly on the dynamics of the preceding adaptation stimulus.

range for fly vision). We analyze the time-dependent statistics of spike arrival of the first two spikes generated after each of the movement steps. From this we get  $d'(t)$ , the discriminability performance of H1. From the photoreceptor data we compute the performance of a noiseless Reichardt correlator model that uses realistic, i.e. noisy, input signals. Over the behaviorally relevant time scale (about  $30 \text{ ms}^6$ ), H1's performance is within a factor of two from ideal. The fact that the fly behaves close to optimal in just these conditions is probably not an accident, but most likely due to adaptation of the fly's brain to the experimental conditions. It is known for some time for example, that H1 adapts its gain to contrast and mean luminance<sup>3</sup> and its dynamics<sup>7</sup> to temporal stimulus characteristics. Figure 3 has an example of the latter, showing that the response decay time depends upon the spectral width of random intensity modulations. Such effects can be understood from the nonlinearity of movement detection: If the input signals contain noise, it is a good strategy to filter out those frequencies in the input which are known to have a low signal to noise ratio, so as to minimize the spectral range where noise-noise cross-interactions produce low-frequency intermodulations<sup>7,3</sup>.

## DISCUSSION

The results presented here, and other observations, demonstrate that H1's response depends strongly on what the fly has seen in the recent past. Most of this adaptation is not present in the sense cells, but instead must be the result of the neural net adapting its properties. The way in which these properties adapt to the stimulus is qualitatively in accord with a view in which the system chooses its settings so as to make the best least-squares velocity estimate, given the input statistics. For example, it can be shown that at low contrast the optimal movement sensor should behave as a classical Reichardt correlator, whereas at high contrast it should approach the gradient model of movement detection<sup>1</sup>. This may resolve a long standing dispute among several authors working on movement detection<sup>8</sup>.

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