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ADAPTIVE PROCESSES AFFECTING THE RESPONSE
OF THE MOTION SENSITIVE NEURON H1

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Abstract- Recent findings on two processes which effect the response of the fly motion sensitive neuron "H1" are discussed. One of these is an gain control mechanism with properties like light adaptation in photoreceptors. The second process is similar to afterimage formation in humans in that it can mask the visibility of objects to H1. New results are presented showing that the second process operates at velocities creating temporal modulation of up to 4 Hz, and so must be considered along with the gain control in any description of H1's behaviour.

Introduction

The word adaptation has been applied to a range of Neural and psychophysical phenomena. The topics presented here are two processes which separate bodies of literature describe as adaptation. Both of the effects manifest themselves in a single fly optic lobe neuron known as H1 which is one of a collection of directionally selective optic lobe neurons coding all degrees of freedom of optical flow field motion: H1 is sensitive to horizontal side-slip and yaw movements counter to the usual flow field direction [1]. The first form of adaptation is a gain control procedure governing the accuracy with which the motion signal is represented [2]. The second form is like an afterimage [3]. Both processes appear to be computed over **localised eye** regions by neural elements presynaptic to H1, which sums these signals over virtually the whole eye. The gain control procedure clearly acts over a wide range of flow field velocities, and data will be presented here to show that the afterimage like effect persists up to angular velocities of 40 °/s, and so will strongly affect H1's response over a large part of its operating range.

Methods

The methods have been described previously [2][3], however a brief overview will be given here. Visual stimuli were generated on a Tektronics 604 display monitor under the control of a Digital Electronics Company LSI 11-03 computer and a home built display buffer. The frame refresh time was 6.5 ms. Patterns used included sine and square wave gratings, thin lines, and spatially bandlimited aperiodic gratings. **The latter** have been described previously [2] and are designed to mimic the natural distribution of contrasts and spatial frequencies.

Sheep blowflies, *Lucilia cuprina*, were each fixed with insect wax to a stand and subsequently oriented to the monitor so that their right eye viewed the screen. Extracellular recordings of H1's spike activity were monitored by the computer controlling the stimulus.

In the afterimage experiments the procedure was modified from that described earlier [3]. In those experiments a stationary adapting stimulus was briefly presented to the eye. Following this, a scene at the mean luminance, and featureless but for a single vertical line, replaced the adapting stimulus. This line swept the monitor face coming to

rest at its starting position. When the line completed its traverse it too disappeared and the mean luminance scene then remained on for a time more than sufficient for the afterimage to disappear. The moving line serves as a probe for changes in sensitivity to moving objects, these changes showing up as response fluctuations in H1. This sequence was repeated many times with one variation: the starting position of the probing line and the adapting stimulus changed, with the effect of averaging out, over the many trials, the spatial weighting function of H1. The resulting response histograms thus describe the average decay in time of the afterimage. Previous experiments [3] show the effects of altering the contrast, duration, spatial frequency, and other aspects of the adapting stimulus, as well as the effect of dark and light probing lines. In the new experiments described here the adapting stimuli were moved at 7 octaves of angular velocity from 1.46 to 93.54 °/s, to test afterimage persistence at these speeds.

Gain Control

All neurons are extremely limited in their information capacity, or the number of just discriminable "bits" of information the cell can transmit per unit time. Neurons are largely divisible into two widely recognised classes generally described as "spiking" and "non-spiking" neurons. The former have their signaling ability limited by their low maximum spike rates (<1000Hz) and the stochastic processes underlying spike generation [4]. "Non-spiking" cells are limited by the noise accompanying sensory transduction and

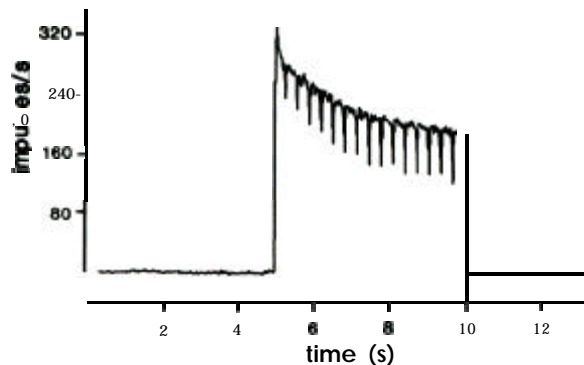


Figure 1 A demonstration of the increase in relative sensitivity of H1 to brief decreases in the velocity of an otherwise constant adapting velocity. The figure is a histogram of the spike counts generated by H1. The elevated response between about 5 and 10 seconds corresponds to the period when the grating moved at a constant velocity of 58 °/s except for 16 equally spaced 39 ms test periods, when the grating slowed by 23.4 °/s. Accompanying the decline in the response to the brief test stimuli, indicating a gain reduction which releases H1 from saturation.

synaptic transmission [5]. Both neuronal classes are restricted by integration times which are very sluggish by electrical engineering standards (>10ms). Thus, neurons can generally be thought of as being constrained to signalling their messages with an absolute upper limit of a few hundred "bits" per second.

In the face of these restrictions it is not surprising that cells should adopt some form of gain control. The best known of these is light adaptation in photoreceptors. This system allows humans to code up to 10 decades of light intensity without significant signal loss through saturation of the photoreceptors' response, or through insufficient amplification. The result of this strategy is that, over a wide range of intensities, the encoded parameter is the photometric contrast [6][7], defined as the local intensity divided by the mean. The property of maintaining this strategy over a range of absolute intensities is termed "contrast constancy". The utility of this procedure is that contrast describes the relative reflectivity of objects, which is invariant under absolute illumination, discounting for the moment self luminous objects. Obviously such a strategy could be utilised for any possible neural signal, in particular for those signals where the relative or "contrast" signal has concrete physical meaning.

Recent work has shown that H1 shows some adaptive character. In particular H1's temporal resolution of gratings displaced in discrete jumps, increases with increasing jump frequency [8]. More recently it has also been shown that the adaptive behaviour extends to yield a gain control mechanism similar to that of photoreceptors, but where the signal is motion related [2]. The words "motion related" or "motion signal" are used because the basic unadapted response is proportional to the average flicker rate induced by the spatial frequencies making up the optical flow field, rather than being a true velocity measure [9]. H1's motion detection ability is well described [10] by the "correlation model" of motion detection, and as such is phase blind. Interestingly, the correlation model has also recently been shown to describe human motion sensitivity [12].

One property of the gain control described is that cells will reduce their gain to save the system from saturation, and so enhance their relative sensitivity to changes in strong stimuli. Figure 1 shows the response of H1 when an aperiodic grating, described in Methods, begins moving at velocity which initially saturates the cell. Slower test velocities are briefly superimposed on the continuous (adapting) velocity. After a few seconds H1's response to the adapting velocity has declined and its responses to the test velocity grow appreciably, indicating a gain in relative sensitivity.

The origins of this sensitivity change are best shown in experiments like those summarised in figure 2. Here an H1 cell has been tested with briefly presented test velocities in two adaptation states. The stimulus is the same aperiodic grating used in figure 1. The upper curve represents H1's unadapted velocity/response relation. The lower curve shows responsiveness after steady states are achieved in response to movement at the same adapting velocity used in figure 1. The aperiodic grating serves to average out the effects of the afterimage-like process which can be severe when periodic gratings are used (see figure 4). Notice that the slope of the adapted (lower) curve is steeper than the

unadapted curve (upper) in the region of the adapting velocity (arrow). Thus, as indicated by the qualitative experiment of figure 1, the adapted cell is better able to respond to signal fluctuations about the new mean signal.

In introducing this section the concept of contrast constancy was described. Since contrast can be defined for any signal S (i.e. $\Delta S/S$), contrast constancy in the velocity domain was looked for in H1. Figure 3 shows the result for one method used [2]. Responses to equal "velocity contrasts", were determined in twelve cells over a range of adapting

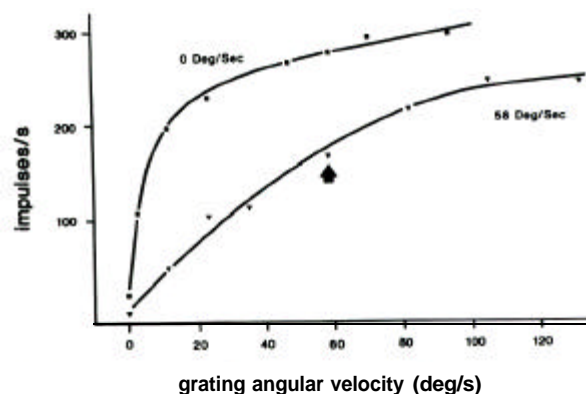


Figure 2 Quantitative determination of the gain change indicated by figure 1. The cell's response was determined under two adaptation states. The points in both curves are the average peak spike-rate obtained over 40 repetitions of 104 ms long test velocities, presented once every 1.7 s. For the lower curve the aperiodic grating moved continuously at 58 $^{\circ}/s$, except for the 104 ms test periods. For the points in the upper curve the grating was stationary, except for the test periods.

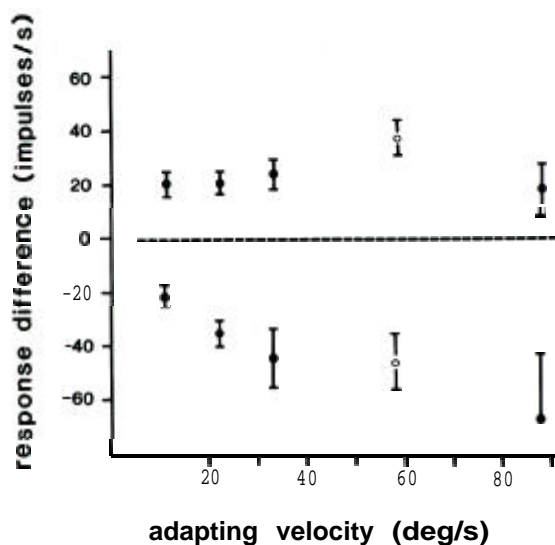


Figure 3 Response of H1 to velocity contrasts of +0.3 at several adapting velocities. The solid circles are averaged data from 6 cells, and the open circles from 6 other cells, for which complete velocity response curves like those of figure 2 were obtained. Error bars are one standard deviation. Responses are defined as the difference between the steady state response and the response to the test velocity contrast. If exact contrast "constancy" occurred the points would lie along two horizontal lines.

velocities, where velocity contrast (C_v) is defined as:

$$C_v = \Delta V / \bar{V}$$

V is a test velocity, and \bar{V} is the adapting velocity. Both negative and positive velocity contrasts of amplitude 0.3 were tested. If contrast constancy holds, responses to equal contrast will be equal irrespective of absolute velocity. This condition is met reasonably well (figure 3). but responses to positive and negative contrasts are somewhat asymmetric. In particular sensitivity to negative velocity contrasts seems to increase slightly with adapting velocity. This is opposite to what would be expected if the neuron did not adapt. The asymmetry is reduced at lower velocity contrasts owing to the shape of the response curve (figure 2). Nevertheless, a near constant response is given to either polarity, even at the highest adapting velocity, which is itself saturating in the unadapted case, e.g. upper curve figure 2.

Afterimage-like Effects

The afterimage-like effect described in this section bears some resemblance to the reverse contrast afterimages seen by humans after brief exposure to low contrast stationary adapting stimuli. In this section the word contrast will always mean photometric contrast. In psychophysical experiments involving moving sinusoidal gratings moved across optically stabilized retinas, the grating afterimages appear to persist at temporal frequencies of up to 0.5 hz, and have been implicated in the spatiotemporal tuning mechanisms of human vision [13].

In previous work [3] the effect found in flies has been shown to be not due to photoreceptor light adaptation, but instead a product of a system occurring before motion computation which integrates its input over a few hundred milliseconds, and decays away exponentially with a time constant of about 0.5 to 0.9 s. In response to sinusoidal intensity gratings presented for 0.8 s once every 13 s. the afterimage is saturated by contrasts of 0.4, and at this contrast afterimages from adapting stimuli presented for as little as 200 ms can persist for a few seconds. Whole field illumination and moderately low spatial frequencies are not as effective as higher spatial frequencies. In response to adapting stimuli consisting of a single bar, both dark and light bars yield response depression. In the case of dark bars, a portion of the response depression continues to grow for up to 1 s after the adapting stimulus is removed, even at contrasts as low as 0.1. The response to moving bright objects is more affected than are dark ones. Finally, there is also a short-lived loss of directional selectivity accompanying the adaptation.

Figure 4 demonstrates this last effect, as well as some other salient features. The three traces in figure 4 contain an H1's neuron's response to a contrast 0.15 sinusoidal grating, of spatial frequency 0.21, moving at 46.8 °/s. The grating moved for 1.7 s (the period labelled "motion time course") within a repeated period of 5.8 s. The responses of figure 4a resulted from the grating moving in H1's preferred direction, while the grating moved in the opposite direction for figure 4b. The strongly modulated response of figure 4a (thin line) resulted when, during the 3.1 s inter-stimulus period, the eye was adapted to a stationary grating of the same wavelength as the test grating but with

contrast 0.8. In addition to the effect of the high contrast, the modulation depth is enhanced because the periodic grating effectively sets up a periodic sensitivity mask across the eye. Thus, the modulation is increased in proportion to the number of synchronously interacting grating cycles, and adapted eye regions.

In the case of the darker, less modulated curve, in figure 4a, the eye was shown only a featureless field at the mean luminance between motion tests. As will be shown, the weak modulations result from an afterimage set up by the moving test grating itself, which persists between the short inter-test time (3.1s). Previously reported experiments [3] show that these weaker modulations disappear with longer inter-test intervals. Like the strongly modulated (thin line) response in figure 4a, the response in figure 4b was obtained with prior adaptation to the high contrast stationary grating. However, in figure 4b the test grating moved in H1's non-preferred direction. Normally the inhibition generated for reverse motion is sufficient to completely silence H1. In the presence of stimuli which produce a strong afterimage, H1 seems to temporarily lose its directional selectivity. Apparently, the site saturated by the afterimage also blocks the mechanism of directional selectivity.

Clearly these effects are quite powerful and need to be taken into account when the eye has been viewing stationary objects for even a short time. However, the method used to obtain the results of

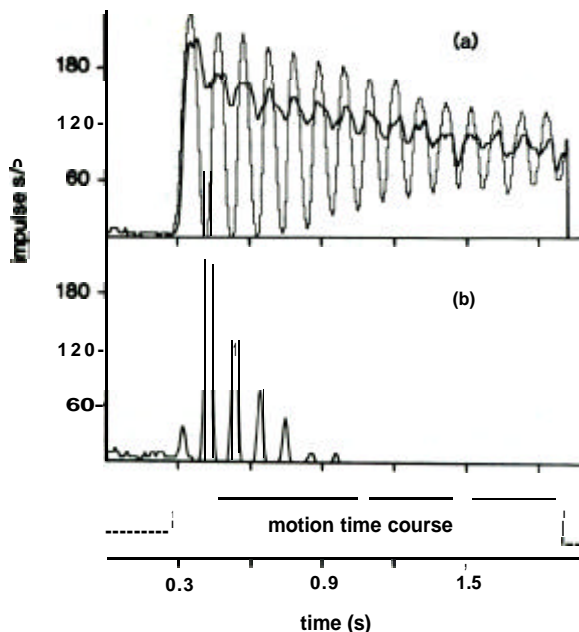


Figure 4 Afterimage effects for stimuli moving in H1's preferred (a), and non-preferred (b) directions. (a) The effect of prior adaptation with (thin line), and without (thick line), a high contrast stationary adapting grating presented between motion trials. The dashed line indicates the period when the test grating was in motion, much of the remaining 3.1s stationary phase is not in the picture. The 180° phase shift of (b) is consistent with the earlier finding [3] that brighter-than-average moving objects are most affected. All traces are the average of 32 trials, and the points in the smooth histograms were interpolated with straight lines.

figure 4 is unsatisfactory for further investigation for two reasons. Firstly, the gain control system mentioned in the first section complicates matters by modifying the envelope of the response profile. Secondly, the dependence on the number of cycles of grating seen by the eye is further complicated by the asymmetric weighting that H1's receptive field imposes on the visual stimulus. The procedure using a narrow moving line, outlined in Methods, solves these problems by spatially averaging and infrequent stimulation of any one eye region. The resultant histograms indicate the space-averaged temporal decay of the afterimage process.

This averaging procedure was modified to determine the relative strength of the afterimages for slowly moving adapting gratings. Afterimages were found to remain until about $40^\circ/\text{s}$, or temporal frequencies of 4Hz. Figure 5 shows some representative decay data for two adapting conditions. Notice that the amplitude of the response modulation is greater when the adapting grating is not moved (figure 5a), and that the phase of the modulation produced by the more quickly moving grating (figure 5b) leads that of figure 5a. The speed of the grating used in figure 5b was such that the grating moved by half a wavelength over the adaptation period. However, the afterimage has shifted by very close to a quarter wavelength. If the adaptation process can be described by a linear integrator then this phase shift suggests that the

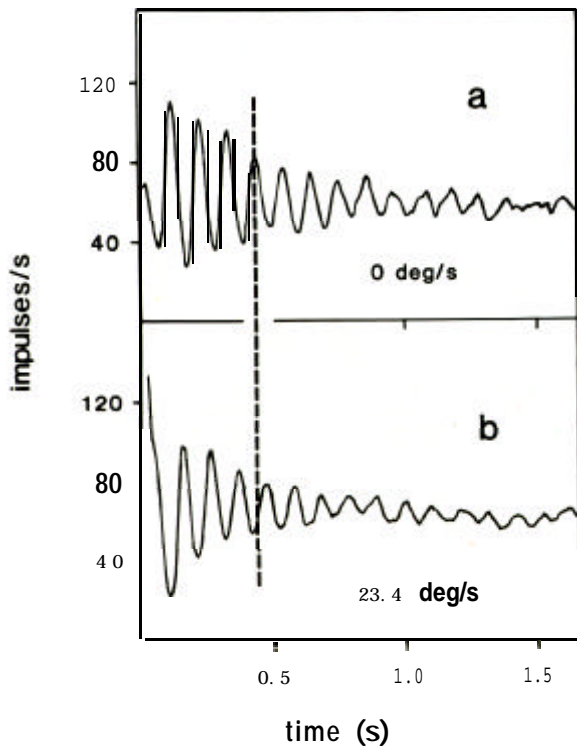


Figure 5 The temporal decay of the afterimage averaged over 32 eye positions. Both traces are the average of 224 determinations in 5 cells. Both curves were smoothed by two three-point running means, and points were interpolated by straight lines. The adapting grating speeds are indicated and adapting stimuli were shown for only 208ms out of every 13 seconds. This ensured that the response to the moving line used to probe afterimage strength was little disturbed by the response gain control outlined in the previous section. The dashed vertical line demonstrates the relative phase lead of (b).

integration time is close to the time the adapting grating was presented, since the afterimage lies between the initial and final positions of the grating. The phase shifts introduced by other adapting speeds are commensurate with this idea.

The amplitudes of the response modulation were determined in two ways, and the results are summarised in figure 6. The first method is described previously [3] and involves measuring the amplitudes of the response modulations in a decay trace and fitting these to an exponential function. Responses are then taken as a hypothetical amplitude at a fixed time after the removal of the adapting grating (figure 6, triangles). Fits obtained in this way accounted for 95% or more of the response variance, and allowed determination of the time constant of decay. This method could not be performed on all the data collected here since there were few response modulations at high speeds. Instead, the average height of the second, third, and fourth cycles was used as an index of afterimage strength (closed and open circles). Results obtained using both methods are shown in figure 6, and results from both methods are in good agreement. Experiments were also performed at some velocities (figure 6, squares) using square gratings. Results for these could not be distinguished from those obtained using

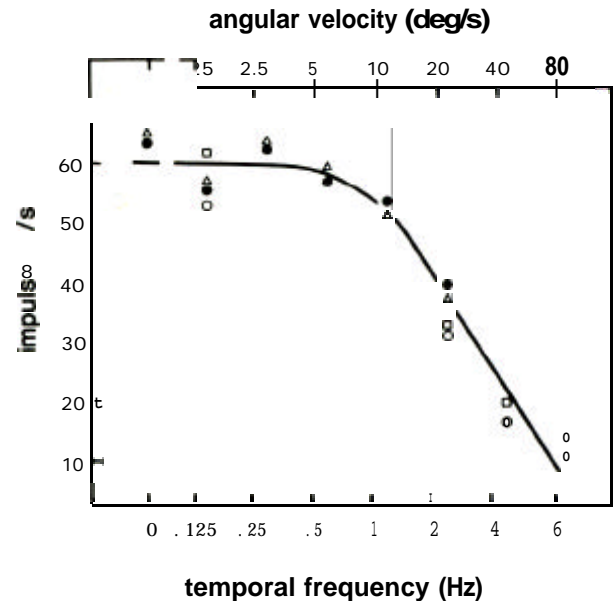


Figure 6 The afterimage strength, expressed as the amplitude of the response modulation in spikes per second. Square symbols are data obtained using a contrast 0.4 square wave intensity grating of 9.73° , all other data was gathered using a sinusoidal grating of the same contrast and wavelength. This spatial wavelength is about optimal for H1 [14]. Solid circles are each the result of a total of 224 determinations in 4 cells. Open circles are derived from 160 determinations in 2 other cells, and squares from 96 determinations in 2 final cells. Samples were taken in blocks of 32 averages, and samples for different conditions were interleaved in a randomized sequence. Triangles are scaled amplitudes derived from fits to the modulation amplitudes in the traces used to obtain the solid circle data. The fitted function was $A \exp(t/T)$. Data points other than triangles were determined by the summing method described in the text. Grating contrast was defined as $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min})$; I = radiance.

sine wave patterns.

Discussion

On the gain control

The gain control described has some further interesting points. Firstly, stimuli containing flicker, but not motion, alter the gain far less effectively. Secondly, the time over which more adapted states are obtained for moving sinusoidal gratings is not controlled by the level of excitation of H1, but instead by the temporal frequency created [2]. The simplest explanation for this is probably that, the temporal frequency signal is more indicative of changes in velocity than are changes in other parameters such as environmental contrast or orientation, which can equally well increase H1's spike rate. Thus, the gain control seems to be governed by the parameter available to H1's inputs which most reflects velocity change. The studies revealing this property [2] have avoided most of the low velocity range where, as shown here, afterimages play a role in H1's sensitivity, so it is not yet known how the two interact.

On the afterimage

One factor limits interpretation of the effect of the afterimage on the fly's percept of the world. This concerns the integration time of the neurons postsynaptic to H1. Faster neurons will reliably conduct the oscillations induced by the afterimage, while slower ones will not. As in figure 4a (thin line) afterimage modulated responses may overshoot the normal level of excitation. A fast cell, or a differentiating one, downstream from H1 would sense this overshoot, while a slower cell which integrated over several hundred ms would receive much less excitation than in the absence of an afterimage. Obviously the spatial frequency tuning of H1 may be affected by the afterimage, but this remains undetermined. One interesting feature of figure 6 is that the low frequency role off of the unadapted temporal frequency response of H1 [2] overlaps with the high frequency tail of the afterimage persistence. It is not known if these response properties are related. However, stimuli which produce afterimages appear to slow H1's temporal resolution of small displacements of a grating [3].

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