The H1 Neuron Measures Change in Velocity Irrespective of Contrast Frequency, Mean Velocity or Velocity Modulation Frequency

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Phil. Trans. R. Soc. Lond. B 1991 **331**, 205-211
doi: 10.1098/rstb.1991.0009

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SUMMARY

The H1 neuron of the fly *Lucilia cuprina* is one of the wide-field motion-perception interneurons of the lobula plate. The response, measured as the mean spike rate over many repetitions of the same stimulus sequence, is initially large at the onset of a movement, quickly falling to a plateau and then continuing to adapt slowly when the stimulus is a steady motion of a pattern. Modulation of the velocity of the moving pattern (velocity contrast) causes a modulation of the mean spike rate, which adapts more slowly than the adaptation to the mean velocity. The modulation of the spike rate and the average maximum spike rate are both measures of the velocity modulation irrespective of the contrast frequency, mean velocity, or velocity modulation frequency up to 12 Hz. The responses are in phase with the sine-wave modulated stimulus velocity; suggesting that H1 measures $\Delta\omega/2\bar{\omega}$ not $\Delta\omega/\Delta t$. If the responses of the H1 neuron are representative of their properties, the unit motion detectors are specialized for high resolution, high gain, short latency, and transient detection of direction of velocity change. These features are those required in controlling errors in stability while flight is already in progress, and other aspects of insect vision presumably are carried in other neurons.

INTRODUCTION

Notwithstanding the obvious phasic properties of the H1 neuron, most investigations have been concerned with the steady-state responses to continuous motion, or to various mimics of motion with two modulated light sources or narrow bars. The H1 neuron detects small movements of localized contrasts towards the preferred direction anywhere in its large visual field. The optimum local displacement of a small target is about the same as the angle between visual axes, and the H1 neuron acts like a funnel which collects excitation from many directional unit motion detectors at the highest resolution available to the retina. The H1 neuron has been accepted as a representative of the numerous lobula plate neurons which reveal the properties of the unit motion detectors of the fly (Hausen & Egelhaaf 1989; Franceschini *et al.* 1989). The actual function of the H1 neuron in the processing circuitry is in doubt because it responds to horizontal motion forwards across the eye towards the anterior, and its axon connects the two optic lobes.

Adaptation takes two forms. First, the H1 neuron responds strongly to the onset of a forward horizontal movement across the eye, and the response quickly falls to a plateau then continues to fall more slowly while the motion is maintained at constant velocity. Over the short term, the fall in the response R is approximately exponential $R = r\ (1+e^{-at})$ where r is a low background spike rate, and a is a time constant. This form of adaptation suggests that the H1 neuron does not have a function related to steady-state motion. The second form of adaptation is a shortening of the time constant a when the frequency of passing contrasts is increased. This form of adaptation has the effect that the temporal resolution for the detection of changes in the motion of the stimulus, is improved by the motion itself. This increase in temporal resolution is controlled locally by the stimulus and does not depend on the impulse frequency of the H1 neuron. When we put together both types of adaptation, it suggests that local motion detectors adapt in response to local motion in much the same way that photoreceptors do to their own signal, light intensity (Maddess & Laughlin 1985). Light adaptation of photoreceptors and of the second-order neurons, the lamina ganglion cells, is also accompanied by an improvement in temporal resolution (Laughlin 1981). As a consequence of adapting to background intensity, photoreceptors provide a measure of $\Delta I/2\bar{I}$ where $\bar{I}$ is the mean intensity, the well known Weber relationship.

As a test of the effects of adaptation, Maddess and Laughlin demonstrated the following for the H1 neuron.

(*a*) An increase in the response to a small change in velocity when the adapting velocity was increased.

(*b*) Responses to a fixed increment or decrement of velocity are reasonably independent of the background adapting velocity.

In (*a*) there was only one change in the adapting velocity, and in (*b*) only one velocity increment was tested at five adapting velocities over the range from 3° s^{-1} to 100° s^{-1}. We have confirmed this work and extended it to a range of contrast, spatial frequency, background velocity, velocity modulation frequency, and background contrast frequency.

METHODS

Cultured female sheep blowflies of a standard wild strain of *Lucilia cuprina*, were kindly supplied by CSIRO, Division of Entomology, Blowfly Genetics Group, Canberra, ACT, Australia. They were kept in natural daylight in a cool place and fed on sugar solution.

Flies were waxed to a support on a ball joint without the use of carbon dioxide. The head and eye were then aligned with the screen of a cathode ray tube (type 609 with P31 phosphor) as described by Maddess & Laughlin (1985). For optimum stimulation of the H1 neuron the flies were oriented so that a point 30° lateral to the fly's midline on the equator of the eye pointed to the centre of the screen, which subtended 54° at the eye. The H1 neuron was recorded from the contralateral side, leaving untouched the side ipsilateral to the stimulus. As in previous work, recordings were discontinued if the H1 neuron showed irregular or regular bursting responses. The recording room was in darkness, with temperature controlled at 22 ± 2 °C. All flies were light-adapted to their position in front of the screen, and illuminated at an average brightness of 7 cd m^{-2} for at least 20 min before recording. Apart from the first few seconds while they rapidly became adapted to a steady rate, the responses to velocity-modulated moving patterns were all averaged over large numbers (usually 50 repetitions) of the modulation.

The patterns were generated by a computer (PDP 11/03) with a frame rate of 160 Hz and a frame of 1024 lines, similar to that used by Maddess (1986). Spikes were recorded by standard methods, collected by computer, and displayed as phase-locked histograms or average numbers of spikes in bins 6.5 ms wide, under the control of hybrid Assembler/Fortran/DAOS (data acquisition operating system) software.

The stimulus was a sine-wave striped pattern controlled in average intensity, contrast, spatial frequency, average velocity, velocity modulation (= velocity contrast) and in velocity modulation frequency. Most stimuli were maintained in a steady state for periods of more than an hour, and the corresponding records are of the steady-state responses, with recordings initiated many minutes after the onset of the stimulus. The recordings of the averaged spike frequencies were phased-locked to the modulation of the stimulus and printed as in figure 1.

DEFINITIONS

Bearing (ϕ). The angle on the eye. This is the direction of a stimulus with reference to the eye. The long axis of the insect is of the reference zero.

Contrast frequency (ω/λ). The temporal frequency (Hertz) of the flicker induced in an ommatidium by the movement of a contrasting striped pattern over it; see equation 1.

Contrast frequency contrast ($\Delta\omega/\lambda$) ($2\bar{\omega}/\lambda$). The change in contrast frequency relative to the average contrast frequency; see equation 2. In the present paper this contrast occurs in time, not space.

Intensity (I). The absolute intensity of the stimulus, measured in photons per second per facet, or photons per second per square centimetre at the eye.

Intensity contrast ($\Delta I/2\bar{I}$). The relative difference in intensity of the dark and light bands in the stimulus pattern.

Modulation of Intensity ($M(\lambda)$ $\Delta I/2\bar{I}$). The relative change in intensity at the receptors caused by the movement of a striped pattern across the eye. This is not the same as the intensity contrast in the stimulus ($\Delta I/2\bar{I}$) because it depends on the spatial frequency and on the optical modulation transfer function M as a function of spatial wavelength λ for the lens of the eye. When the spatial frequency is adjusted to keep the contrast frequency constant at a new velocity, the stimulus *contrast* must also be adjusted to bring the modulation of intensity back to the former constant level (Dvorak *et al.* 1980).

Pattern period (λ). The angle subtended at the eye by one period of a striped pattern.

Spatial frequency ($1/\lambda$). The reciprocal of the pattern period, measured in cycles per degree.

Velocity (ω). The angular velocity of a stimulus across the eye, measured in degrees per second.

Velocity contrast ($\Delta\omega/2\bar{\omega}$). The change in angular velocity of the stimulus relative to the average velocity; see equation 2. In the present paper the change occurs in time.

Velocity modulation frequency (Hertz). The temporal frequency of the velocity modulation.

RESULTS

The response of the H1 neuron (averaged over many repetitions of the stimulus sequence) to the onset of a striped pattern moving at a constant velocity is an initial peak that decays exponentially to a plateau. When the stimulus is maintained, the response is a slowly decreasing average spike frequency that initially depends on the contrast frequency and contrast but progressively drops to a background level that depends only on the time that has elapsed since the onset of the stimulus. In the long term, the H1 neuron does not give a measure of steady-state contrast frequency. When a sine-wave oscillation is added to the maintained drift of

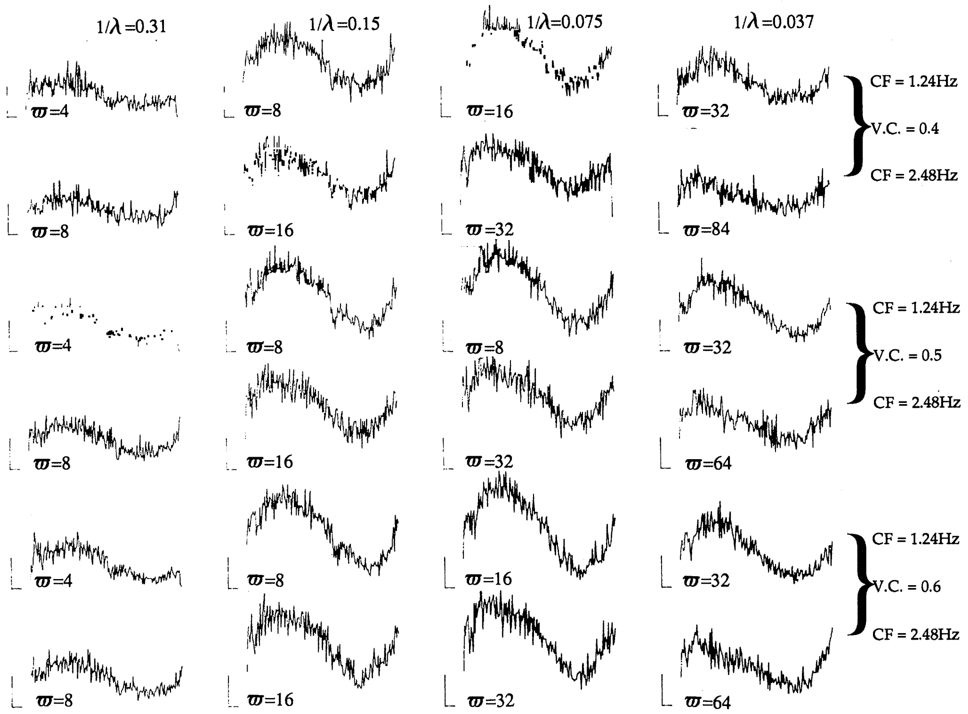

Figure 1. Records of responses. The vertical axis is the average spike frequency over 50 repetitions. The horizontal axis is phase-locked to the modulation of angular velocity of the stimulus, all at a velocity modulation frequency 1 Hz. Therefore each record is one second long. The four vertical columns are at four different spatial frequencies. Alternate lines of data are at contrast frequencies of 1.24 Hz and 2.48 Hz. In lines 1, 3 and 5 the contrast frequency was 1.24 Hz; in lines 2, 4 and 6 it was 2.48 Hz. The top two lines have velocity contrast 0.4 the middle two have velocity contrast 0.5 and the lower two have velocity contrast 0.6. This is some of the primary data plotted in figure 2.

the stimulus in one direction (i.e. when the velocity is modulated), the response of the neuron is also sine-wave modulated in phase with the modulation of the stimulus velocity. The response is in phase with the changes in velocity and not with the acceleration (figure 1).

The spike frequencies in response to changes in a number of parameters of the stimulus can now be tested, namely average intensity, intensity contrast, spatial frequency, mean velocity, velocity contrast, and velocity modulation frequency. We will concentrate upon the last two variables.

The responses are measured from the phase-locked histograms in two ways because we do not know the features of the H1 response that are significant for the next neurons down line. The first measure of the response is the average modulation in the H1 spike frequency, which is the maximum mean spike frequency minus the minimum mean spike frequency. This measure ignores the background spike frequency upon which the modulation is superimposed but it is aimed at measuring the response to the modulation. Alternatively the response is measured simply as the peak of the average spike frequency, a value which may have more significance to the next neurons down line but which depends on the mean background firing rate, which in turn depends on the time since the onset of the moving stimulus.

Examples of the response modulation to various levels of velocity modulation are shown as raw traces in figure 1, and more are plotted in figure 2. The upper set of curves (figure 2*a*) were measured at a mean contrast frequency of 2.48 Hz, which involved ad-

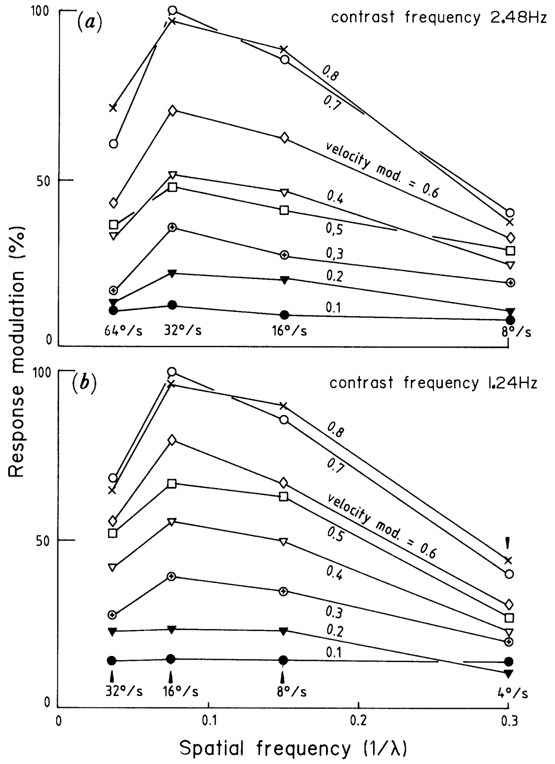

Figure 2. The response modulation as a function of spatial frequency for a range of velocity modulations, at two contrast frequencies (*a*) 2.48 Hz, and (*b*) 1.24 Hz. The four sets of measurements, made at spatial frequencies of 0.3, 0.15, 0.075 and 0.037 cycles per degree, were done at mean velocities of 8° s^{-1}, 16° s^{-1}, 32° s^{-1} and 64 s^{-1} in (*a*) and 4° s^{-1}, 8° s^{-1}, 16° s^{-1} and 32° s^{-1} in (*b*). This way of plotting the data shows that the response to velocity modulation is not changed by doubling the contrast frequency.

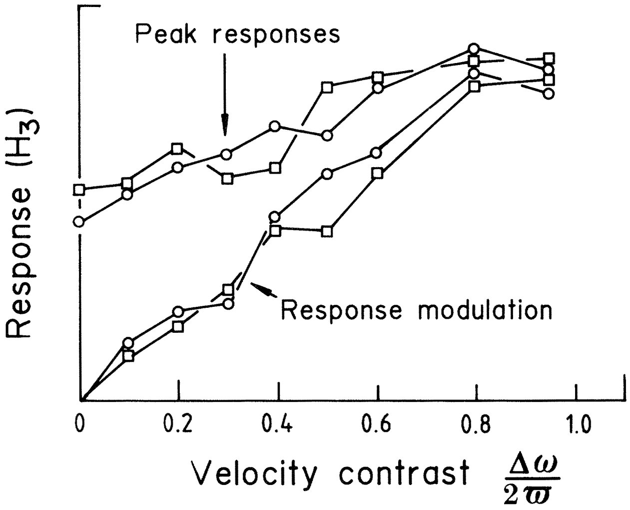

Figure 3. The response as a function of the depth of the velocity contrast ($\Delta\omega/2\bar{\omega}$) at two contrast frequencies, showing saturation at about $\Delta\omega/2\bar{\omega} = 0.8$. The peak responses are partly attributable to the background velocity and therefore do not fall to zero. The values plotted here are the totals summed for the four different spatial frequencies in figure 2. It is apparent from the spacing of curves in figure 2 that similar curves are obtained at each separate spatial frequency. (□, $\omega/\lambda = 2.48$ Hz; ○, $\omega/\lambda = 1.24$ Hz.)

justment of the mean velocity over the range 8° s^{-1} to 64° s^{-1} to compensate for changes of the spatial frequency from 0.31 to 0.37 cycles per degree. The lower set of curves (figure 2*b*) were measured at a mean contrast frequency of 1.24 Hz, near a previously determined optimum for the H1 neuron at 1.4 Hz (Eckert 1980).

Comparison of (*a*) and (*b*) in figure 2 shows that, when the responses are plotted against spatial frequency, the response modulation to velocity modulation is the same irrespective of the doubling of mean contrast frequency. Response modulation increases smoothly with velocity modulation, as seen by the progressively higher peaks in figure 2, and as plotted from the same data summed from all mean velocities (figure 3). This plot also shows the summed mean maximum responses for the same set of stimulus situations at mean contrast frequencies 1.24 and 2.48 Hz. Over the range tested, therefore, the responses of the neuron are a measure of the velocity modulation irrespective of mean contrast frequency, but depending in a particular way on spatial frequency. We observe that responses to velocity modulation do not depend on the mean velocity (figure 2), and in fact we already know that the response to the mean velocity progressively declines with adaptation whereas the response to velocity modulation adapts much less.

The curves in figure 2 show that the response to velocity modulation depends in an interesting way on spatial frequency, being maximum for stripes of period about 14°, falling off below 10° and above 20°. These differences are not attributable to the effect of stripe period on the modulation passed by the optics because for the smaller stripe periods, the contrast of the stimulus was increased to compensate for the loss of intensity modulation peripherally. This adjustment was made by calculation from the previously measured relation between contrast threshold and stripe period for the H1 neuron (Srinivisan & Dvorak 1980). Of course, with increasing spatial frequency, the intensity modulation in the receptors would ultimately disappear, but we did not approach this limit.

(*a*) *Effect of velocity modulation frequency*

With a controlled range of values of mean velocity, spatial frequency, contrast frequency and velocity modulation, the velocity modulation frequency was changed over the range 0–12 Hz and the response measured as before as the modulation of the spike rate and as the peak mean spike rate. The result is that these measures of the response are independent of velocity modulation frequency up to the highest frequency, 12 Hz, that could be achieved with the equipment (figure 4). The actual response values depend on other parameters such as the contrast and the spatial frequency, and of course on the amplitude of the velocity modulation.

That the H1 neuron responds to velocity contrast, not acceleration, is shown by the fact that the response is in phase with the sine-wave modulation of the velocity. The same is shown by the fact that the plot of response versus modulation frequency is flat (figure 4*a*). If the response depended upon angular acceleration ($\Delta\omega/\Delta t$), the response would increase linearly with velocity modulation frequency. It was shown by previous work that the H1 neuron responds to increments or decrements in velocity of a random grating pattern (Maddess & Laughlin 1985); we have now shown that it responds to $\Delta\omega/2\bar{\omega}$ rather than to $\Delta\omega/\Delta t$, for the range of velocity contrasts up to 12 Hz for regular sinusoidal gratings.

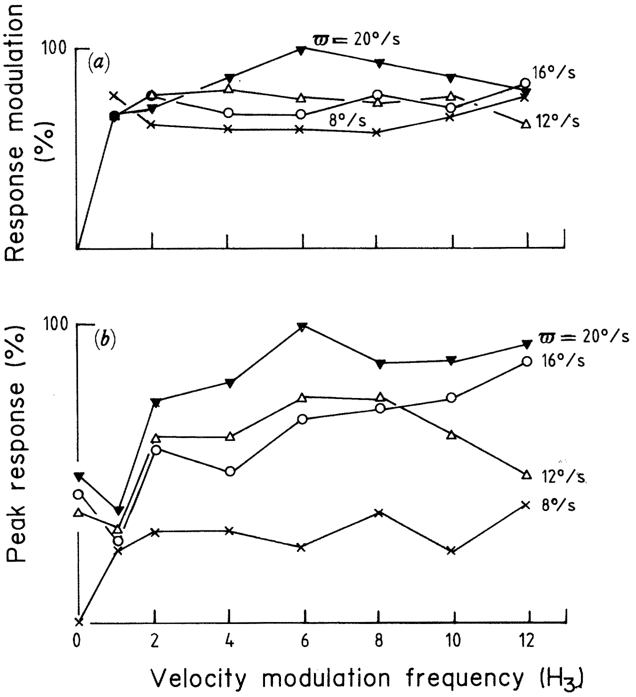

Figure 4. Response as a function of velocity modulation frequency at a velocity modulation of 0.5 (*a*) The response modulation at four different mean velocities. (*b*) Peak response at the same four mean velocities.

DISCUSSION

(*a*) *Contrast frequency, velocity and spatial frequency*

Over the past 30 years it has become clear that the optomotor behaviour and the responses of the associated neurons of the lobula plate of the fly to a moving regular striped pattern are a function of the contrast frequency rather than the velocity of the stimulus (Eckert & Hamdorf 1981). This applies also to the worker bee (Kunze 1961) and to directionally sensitive neurons of the butterfly medulla (G. A. Horridge & L. Marcelja, unpublished results). These features are shown for the fly H1 neuron in figure 5*a*, *b*. When average responses over a given period after onset of the stimulus are plotted against pattern velocity, a different bell-shaped curve is obtained for each spatial frequency (figure 5*a*), but when the responses are plotted against the contrast frequency generated by the same motion, the bell-shaped curves more or less coincide (figure 5*b*). When the stimulus is a regular striped pattern and the responses are summed, this result is to be expected from any system which responds to each edge passing the motion detectors. We are tempted to infer that a system with this dependence on pattern can form only a part of the visual processing mechanisms which depend upon motion of the input stimuli.

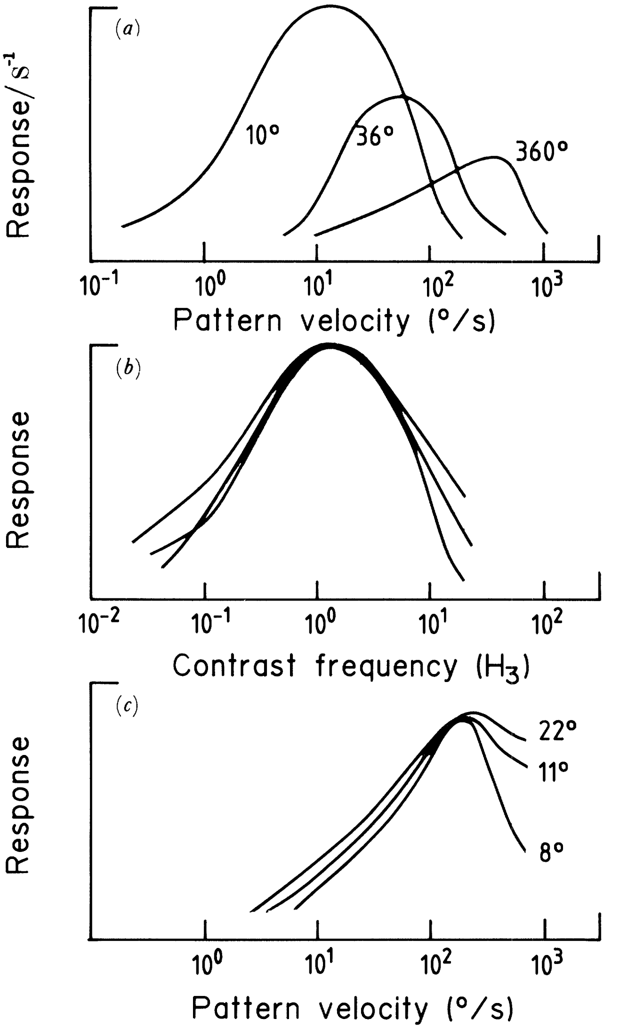

Figure 5. Stylized responses from previous work to illustrate the significance of contrast frequency. (*a*) Response (measured as spike frequency over a set time long after the onset of the stimulus) of the fly H1 neuron, plotted against pattern velocity at three different stripe periods, 10°, 36° and 360°. (*b*) The same responses normalized to 100% and plotted against the contrast frequency, (*c*) Responses of a dragonfly self-movement detector neuron plotted against pattern velocity for stripes 8°, 11° and 22° period. ((*a*) and (*b*) after Eckert 1980; (*c*) after Oldberg 1981).

Without explanation, other workers have found a different behaviour in some other insect directional motion-detectors. In wide-field motion detectors of the locust ventral cord (Kien 1975, figure 3), motion detectors of the dragonfly ventral cord (Oldberg 1981, figure 8) and in the control of flight speed by *Drosophila* (David 1982) the curves coincide when the responses to different spatial frequencies are plotted against velocity rather than against contrast frequency (figure 5*c*), showing that, at this level in the nervous system, the response to velocity is independent of pattern. More recently, the template model (Horridge 1991) suggests that the direction of a stimulus and its other attributes such as velocity can be processed in separate channels and provides a way of measuring velocity irrespective of temporal frequency.

Studies on the adaptation rate of the H1 neuron itself have even found opposite results with respect to contrast frequency and velocity. The control of the time constant *t* of adaptation to a transient directional stimulus was at first considered to be a function of the background velocity, irrespective of the spatial frequency (de Ruyter van Steveninck *et al.* 1986, figure 6), but is a function of contrast frequency according to Maddess & Laughlin (1985) and Borst & Egelhaff (1987). The disagreement was probably due to differences in the test stimuli used and especially in the ranges of the velocities tested. The intensity contrast should not be saturating and should be increased to compensate for loss of modulation at high spatial frequencies (Dvorak *et al.* 1980). Flicker without motion adapts H1 nearly as well as motion in either direction. Another consideration is that if the stimulus starts from a stationary state, memory effects must be reduced by use of random patterns (Maddess 1986), and the angular velocities in the test stimulus must be within the physiological range.

The velocity of the whole visual field, or of single objects moving steadily relative to the eye, cannot be measured from the responses of the H1 neuron for numerous reasons, some of them given above. Too many attributes of the stimulus besides background velocity influence the response, but the greatest impediment is adaptation, in that the response to any constant velocity stimulus continuously declines with time. Adaptation to a parameter of the stimulus must be interpreted as disinterest in the absolute value of that parameter by that neuron.

Motion perception of a flying insect must be performed against a background of steady forward flight, and the most outstanding feature of the H1 neuron is that it continuously adapts to the motion in the opposite direction, which is its preferred stimulus.

Many neurons, especially phasic sensory cells, adapt to a maintained stimulus in this way over a wide (but usually fixed) range of rates of adaptation. The general inference from the phenomenon of adaptation, summarized by the Weber–Fechner relation, is that as a result the neuron responds to a *change* in the stimulus over a wide range of the background stimulus without faithfully recording the maintained or background level. The H1 neuron has the further and surprising property that the temporal resolution to make the transient response is improved just when it is needed.

(*a*) *Velocity contrast is equivalent to contrast frequency contrast*

For a regular pattern, of spatial frequency $(1/\lambda)$:

contrast frequency = angular velocity × spatial frequency $= \omega/\lambda$, (1)
contrast frequency contrast = $(\omega_1/\lambda_1 - \omega_2/\lambda_2)/(\omega_1/\lambda_1 + \omega_2/\lambda_2)$, (2)
so, if λ is constant, $\lambda_1 = \lambda_2$, and
contrast frequency contrast = velocity contrast. (3)

The velocity contrast describes the motion of the stimulus: the contrast frequency contrast describes the resulting temporal modulation of the flicker at each receptor. For constant spatial frequency, velocity contrast is identical to contrast frequency contrast. Therefore the unit motion detectors could simply report the *directional* contrast frequency contrast, irrespective of mean contrast frequency.

(*b*) *The action of the H1 neuron*

We confirm by a different method the conclusion of Maddess & Laughlin (1985) that the H1 neuron, and by implication other large lobula plate neurons such as VI that behave similarly, detect changes in velocity of a moving pattern, report their direction and give a measure of their amplitude. The earlier work was restricted to an indication that sensitivity to increments and decrements of velocity increased with adaptation, that the response to a change in velocity is optimum around the adapting velocity and that the response to a constant velocity contrast is fairly independent of the adapting velocity. We have shown that responses increase with velocity modulation independently of background velocity, contrast frequency or velocity modulation frequency. We also found that at low intensity contrast the response to sinusoidal modulation of the velocity was also sinusoidal and in phase, at least up to 12 Hz. Therefore the response is to velocity modulation, not acceleration, and the background velocity is not of great interest to this neuron. Indeed, we can repeat that adaptation of H1 has the same effect on the response to motion as adaptation of the receptors has upon their response to light. Further, the adaptation is apparently a property of the unit motion detectors or directional templates because it is localized to the stimulated visual axes and not influenced by the actual spike rate of the H1 neuron. Therefore, by analogy with the photoreceptors, which report changes in photon flux, the unit motion detectors report changes in motion, and the responses of the directional motion templates, whatever they are, follow the Weber–Fechner relationship, like photoreceptors.

(*c*) *The mechanisms involved*

Electrophysiology has not yet uncovered the unit motion detectors, which have so far only been inferred from the spatial resolution of large field motion detection. Three different ideas about the mechanism have been aired. All agree with the observation that the steady-state response is independent of pattern when plotted against constant frequency, but this is true for any mechanism that gives a unit response to the passing of each edge, especially when the effect of increasing contrast saturates at a low contrast level. The autocorrelation theory of Reichardt (1961) is the most popular. It is a steady-state theory which has been extended to account for adaptation (Egelhaaf & Borst 1989). Essentially it is a way of manipulating the stimulus pattern to predict a single final output. By choice of parameters, the output is fitted to the input, with no assistance to those seeking neural mechanisms. The second idea is that pairs of neuron terminals from adjacent visual axes make an asymmetrical compound synapse upon a dendrite of the motion detector neuron and bring about directionally selective motion detection (Torre & Poggio 1978). Again, there are sufficient parameters to fit to the required output. These are minimal theories, the simplest to fit the results, and not mutually exclusive. A theory about neuronal functions is that there is a group of templates which are repeated on each visual axis at the level of the medulla, and that these templates respond to combinations of contrast states at adjacent pairs of visual axes at pairs of successive times (Horridge 1991). The templates could be neurons or parts of neurons. Their essential feature is that they respond phasically to their own preferred features passing them in the moving image, and the responses of the various templates are separately line-labelled so that they can later be counted, or ratios taken, in the same way as different photoreceptor responses lead to colour vision. This is a very general theory that accounts for much more than the optomotor response. We can add to this theory that adaptation is a significant property of the unit motion detectors or templates.

(*d*) *What use is velocity contrast?*

In the natural situation, with the moving animal in flight, there is a one-dimensional flow field expected at each point on the eye (except looking directly ahead). There are long-term mechanisms, such as overhead light acting via the compound eyes which keep the fly on an even keel (Hengstenberg 1989). Similar ocellar mechanisms have this function in some insects (Wilson 1978). The most obvious feature of the neural mechanisms are that they are phasic, high spatio-temporal resolution, very high gain, short-latency and directional, all of which can be accommodated by the template model. Errors in flight control must be corrected with the stiffest possible feed-back loop at maximum gain in the right direction. The urgent requirement is the sign of the additional phasic stimulus, and it may be incidental that anything is measured quantitatively. The relation between velocity contrast and response modulation may simply be an arbitrary consequence of having many templates in parallel all adapting to background motion but optimizing their ability to give an immediate response to a transient in their own preferred direction.

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Received 15 August 1990; accepted 5 December 1990