
Responses of the H1 Neuron of the Fly to Contrast and Moving Bars

G. A. Horridge and Lyerka Marcelja

Phil. Trans. R. Soc. Lond. B 1990 **329**, 75-80
doi: 10.1098/rstb.1990.0151

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

Responses of the H1 neuron of the fly to contrast and moving bars

G. A. HORRIDGE AND LYERKA MARCELJA

Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, Box 475, P.O. Canberra ACT 2601, Australia

SUMMARY

The responses of the H1 neuron of the fly were measured as a function of contrast. The stimuli were either transient jumps of edges, bar and regular stripes, or smooth movements of these patterns. The directional motion-sensitive system saturates with respect to contrast at low contrast levels, showing that it is adapted to detecting small contrasts rather than measuring them over the whole range, and suggesting that linear calculations cannot be based on responses to sine-wave stimulation. Below saturation the response is not related to the square of the contrast, suggesting that multiplication of the stimulus intensity at neighbouring receptors is not a significant component of the motion processing mechanism. The short-term memory of the previous state, that is essential for motion detection, takes longer to build up at lower contrast and the effects of contrast are independent of pattern. The same conclusion is also suggested by the effect of the width of a smoothly moving bar upon the responses of the H1 neuron as a function of angular velocity. The results are interpreted in terms of the (as yet unknown) spatio-temporal fields of unit motion-detecting neurons, along the lines of the template model for transient stimuli (Horridge 1990) rather than in terms of correlation of the visual image with itself.

INTRODUCTION

In the previous paper (Horridge & Marcelja 1990) on the directional sensitivity of the H1 neuron of the fly, the aim was an analysis of transient responses to small transient movements of edges and bars. We inferred that black–white and white–black edges are processed separately, and therefore confirmed for scenes what Franceschini *et al.* (1986, 1989) have already shown for stimulation of single photoreceptors. We concluded that the transient visual processing mechanism does not involve the algebraic multiplication of signs that was a part of the original Reichardt (1961) model for directional motion perception in the fly.

Although some aspects of the steady-state perception of motion agree with the correlation of the signal with itself as seen in an adjacent receptor, there are three basic objections to this idea. The first is that vision is essentially a transient phenomenon; transient motion of a contrast in the visual field must be detected as it occurs, and therefore mechanisms that do this will be selected rather than those that require averaging over time or selection of the best correlation. In natural visual systems the latency of the visual processing neurons is minimized when each neuron field responds or not to its own specific ‘primitives’ as the visual field passes over it. Secondly, in natural visual processing systems, the spatio-temporal pattern of the signal is convolved with the spatio-temporal fields of the neurons, which is not the same as supposing that the stimulus is multiplied by itself. It is an interesting possibility that with certain non-linearities the response

may be proportional to the product of the contrast contours in the pattern and the corresponding sensitivity contours in the field, so that a response proportional to $(\text{contrast})^2$ could result. Thirdly, the little electrophysiology that we have reveals severe non-linearities in the medulla neuron responses, and shows that directionality involves facilitation in the preferred direction and inhibition in the null direction.

The autocorrelation theory of motion perception in its original form was based upon the idea that the signal at a receptor was correlated with itself as seen in an adjacent receptor. Correlation is a process of multiplication, so that the response to a moving pattern is proportional to $(\text{contrast})^2$ if the output depends on correlation. In its classic form the theory referred to the steady-state response to a regularly repeated pattern. Of the numerous algorithms that have been used for the analysis of the visual image, the common ones differ strongly in their treatment of contrast. The autocorrelation of the image with itself at a later time (Reichardt 1961) gives the direction of motion as a response proportional to $(\text{contrast})^2$. Saturation and adaptation effects modify strongly this dependence on contrast. In an alternative theory, simple veto of the pathway from one receptor to the path from an adjacent receptor (Barlow & Levick 1965), does not specify the dependence upon contrast. A third form of interaction, lateral inhibition, whereby each excited region inhibits neighbouring regions according to the rule that emphasizes edges, results in the loss of absolute measures of contrast, and contrast interacts with form. A fourth algorithm (called the gradient

model) divides each local rate of change of intensity with time by the local rate of change of intensity in space on the retina to give the local velocity of the image relative to the eye, and the result is theoretically independent of contrast down to the limitation due to photon noise (Limb & Murphy 1975; Fennema & Thompson 1979). These algorithms have all been used in models of visual systems, which is itself sufficient reason for testing the effect of contrast on any available visual-processing neuron.

The effects of contrast can be measured with a sine-wave grating, or regular square-wave stripes, or with bars or a single edge, all of which can be either in continuous motion or make a single jump. The bar or edge can be black or white with controlled contrast against a grey background. We have tested all these stimulus situations in the context of the development of the template theory (Horridge 1990; Sobey & Horridge 1990), which itself leaves open the prediction of the effects of contrast upon the response. The quantitative treatment of the template theory, still to be done, will also require a measure of the threshold of the templates, a measure of their time constant for the build-up of local short-term memory, and a time constant for the corresponding local short-term forgetting. The effects of these time constants are shown here by moving an edge at different speeds across the eye, followed at a controlled time by a second edge at the same speed. These two edges, of course, form a moving bar of controlled speed and width. The width of a single moving bar has a strong effect on the response of the H1 neuron as a function of velocity, and it should be possible to relate this effect of velocity to the temporal properties of the templates as measured from transient stimuli. Taken together, the measurements in this paper are a prelude to the fuller quantitative treatment that leads towards the direct measurement of the small fields in the local motion-detection neurons that lie somewhere between the retina and the H1 neuron.

METHODS

During the work on the H1 neuron we found that the visual system of cultured wild-type *Lucilia cuprina* (Wied.) from the fly stocks at the CSIRO Division of Entomology, Black Mountain, Canberra, often differed from those caught locally in the wild. The most obvious relevant difference is that the dynamic range over which contrast has an effect is greater in the wild flies than in flies reared for many generations in cages without competition. The responses to contrast have a narrower dynamic range in cultured flies.

The experiments were conducted as described previously from this laboratory (Maddess & Laughlin 1985; Horridge & Marcelja 1990). The brightness of the screen, and from it the contrast, was measured with a calibrating equipment (International Light Inc. SEE 400 photo detector). The maximum brightness (100% contrast) yielded a flux of 1.0×10^{11} photons $\text{cm}^{-2} \text{s}^{-1}$ at the eye when measured through an interference filter with a peak at 492 nm and width 30 nm at 10% pass.

The stimulus pattern was generated by an Innisfree CRT image synthesizer controlled by an IBM-AT computer, which also recorded the neuron spikes and organized them into histograms and drew the graphs directly from the stored data. To overcome the high flicker fusion frequency of the visual system, the image refresh rate on the screen was 200 Hz. Most of the long experiments on the H1 neuron were done with extracellular recording, and other neurons were excluded by stimulation of the contralateral eye. When the stimulus was a pattern of regular stripes (figure 3), it was replaced by a grey screen at 50% intensity during the periods when not moving, and spikes were recorded over 2 s periods of pattern motion to avoid adaptation and memory effects (Maddess 1986). The measure of the response is always arbitrary. When the stimulus was a jump, the measure of the response was the total number of spikes in response to the jump. When the stimulus was steady motion the spikes were counted over the initial 2 s period after stimulus onset, including the initial transient response.

Each point on a graph can require 20 or more repeats of the stimulus, from which it is clear that an experiment such as that in figure 1 required about 2000 stimulus presentations. For success in such experiments it is essential to give the preparation sufficient resting time between stimuli, to feed sugar solution to the fly, and occasionally to test with a standard stimulus where the sensitivity of the preparation changes.

RESULTS

(a) *The effect of contrast at a single edge*

With a jump of a single edge in the preferred direction, the total number of spikes generated by the jump is independent of contrast when contrast is high but as the contrast is reduced below about 30% the response falls off. The response was in fact measured as the total number of spikes during a 0.5 s period, which covers the total response to the jump of a single edge. The log (number of spikes) was plotted against log (contrast) for a large number of different types of stimulus. For a given contrast the responses are much greater with a black advancing edge (curve 8 in figure 1) than with a white one (curve 5). When the pattern is repeatedly replaced by a bright screen at intervals of 2 s, the 'off' response also falls off at low contrasts, as before, in approximately the same contrast range. The slope for the advancing black edge was sometimes steeper than for the advancing white edge in the same preparation, but there was no indication that responses to 'off' or to motion vary as the square of the contrast.

(b) *Contrast effects with spots and bars*

For a given preparation that is tested with a variety of simple stimuli, we found no significant effect of the location, pattern or size of the stimulus on the slope of the contrast-response curve in logarithmic coordinates. With a white or black spot that jumps at various positions in the field, the whole curve is moved to the right in the less sensitive regions of the field of the H1

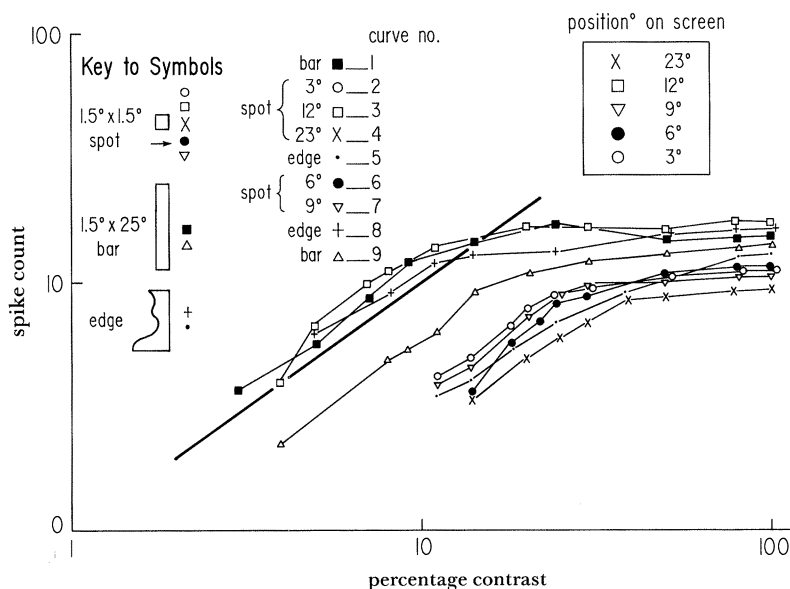


Figure 1. Responses of an H1 neuron to jumped edges, bars and spots as a function of contrast, plotted in logarithmic coordinates. The thick straight line has a slope of 1. The shape of the responses curve is independent of pattern, and has slope 1 in the dynamic range for contrast. For a spot stimulus the response amplitude depends strongly on the position in the visual field of the neuron.

neuron (figure 1, curves 2, 3, 4, 6, 7, 0), but the slope is the same as for a single edge (curves 5, 8) or for a bar (curves 1, 9). This constancy of the effect of contrast suggests that contrast at an edge is processed irrespective of location, pattern or size. The curves in figure 1, however, are not identical, and in the amplitude of the plateau response we find effects of bar width, bar length, and especially of the position of the stimulus in the neuron field. These effects show that there is summation over larger parts of the field for larger stimuli and suggest that the contrast sensitivity curve, and in particular its saturation, are properties of the motion-detecting system rather than more peripheral processing.

The bar and spot stimuli occupy a small fraction of the screen; the slope of the curves in figure 1 are similar for white or black stimuli on a grey background, and the stimulus is a sudden small jump. For these reasons it is unlikely that there are significant widespread effects of adaptation contributing to the transient responses although the individual receptors looking at the stimulus are each adapted to their own fields.

(c) The effect of contrast with regular stripes

With the screen at maximum luminance the response to an optimum moving striped pattern saturates at 10–40% contrast, depending on the fly. Contrast is more easily saturated in the range 10–20% in cultured flies, but freshly caught wild flies saturate between 30–40% contrast. As the contrast is reduced at constant average intensity, the response falls off, at first slowly, then more quickly at the lowest levels (figure 2), but on a log–log plot the slope is usually in the range of 1 to 1.3 and rarely reaches 2 in wild flies.

With the same range of contrasts, but with a neutral density filter between the screen and the eye, the middle part of the curve is shifted to the right along the

contrast axis, the curve becomes less steep and responses now saturate at a higher contrast (figure 2). The lower the average intensity of the screen, the less steep the curve in figure 2. Therefore, it is not possible to explain the smaller slopes on the right side of figure 1 as caused by stronger stimulation or larger responses. Reducing intensity to remove effects of adaptation reduces the response, but does not increase the slope of the curve, suggesting that there are increasing contributions of photon noise at the lower intensities. These curves show, foremost, that the slope of the contrast–response curve depends on the illuminance of the pattern, which makes it harder to infer mechanisms of motion perception from the slope of the curve at an arbitrary intensity. At other spatial frequencies and at other speeds of movement we found similar effects of placing an neutral density (ND) filter in front of the screen.

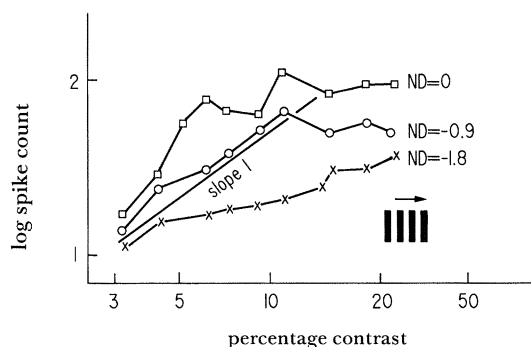


Figure 2. The log of the number of spikes plotted against the log of the contrast for an optimum square wave pattern moving in the preferred direction, measured at three intensities over a period of 2 s. With no filter (ND = 0) the responses are greatest, and remain near saturation until below 10% contrast. With the strongest grey filter (ND = -1.8) in front of the eye there is a shallow slope over a wider range of contrast. Animal used: cultured *Lucilia*.

When the stimulus is a square wave pattern moving in the preferred direction and the response is plotted as a function of the drift frequency, the responses cannot follow high drift frequencies at low contrast (figure 3), suggesting that the temporal properties of the synaptic interactions limit the responses at low contrast. The peak response is at a higher drift frequency for greater contrasts, up to the saturation level of the contrast. Apart from this saturation effect, increasing the contrast increases the response at all drift frequencies and extends the range to higher frequencies. These curves also show that at low drift frequencies the response is approximately proportional to the drift frequency, suggesting that each edge evokes a component of the response as it passes each visual axis, so that the total response is simply the sum of the number of passing edges as an artefact of summation in the recording process. Another way of expressing this, for constant contrast and illumination, the response per passing edge is constant until at high temporal frequencies the response progressively falls off. The temporal frequency at which this fall-off becomes significant determines the contrast frequency at peak response, and the time constants of the H1 response are clearly influenced by contrast and intensity. In the study of templates in the early visual processing, it will be necessary to measure the response per passing edge as a function of the frequency, contrast and intensity. The literature on fly vision, e.g. Maddess & Laughlin (1985), shows that responses depend on drift frequency when the stimulus is repeated as it moves across the facets and suggests that the control of the time constants is also controlled by the motion of each contrast through the field.

(d) *The effect of the width of a moving bar*

The properties of templates that respond to motion cannot be restricted to the responses to an extreme transient stimulus such as the jump of an edge, spot, or pattern. In fact, we find that the H1 neuron responses (measured as total number of spikes in a 2 s period) are larger at the initiation of a steady movement than to a jump over the same small angle, for the same stimulus pattern. They give the impression that the best stimulus is the progressive decrease of intensity at a receptor while there is an increase of intensity at the neighbouring receptor. It is also evident from any model that time is required for the build-up of an image, so that a subsequent change can be detected as motion in one direction or the other. Therefore we can expect that the period over which a contrast remains stationary on a receptor will influence the size of the response when a movement eventually occurs.

To this test, we measured responses to bars of three different widths moving at various angular velocities over the whole range that elicits a response, from 3° s^{-1} to 250° s^{-1} (figure 4). Responses are small for the low and the high end of the dynamic range, and rise to a peak at an angular velocity that depends on the width of the bar. For a thin bar subtending 0.75° the peak is near 30° s^{-1} ; for a 6° bar the peak is near 60° s^{-1} . Responses to wide bars are always greater than to

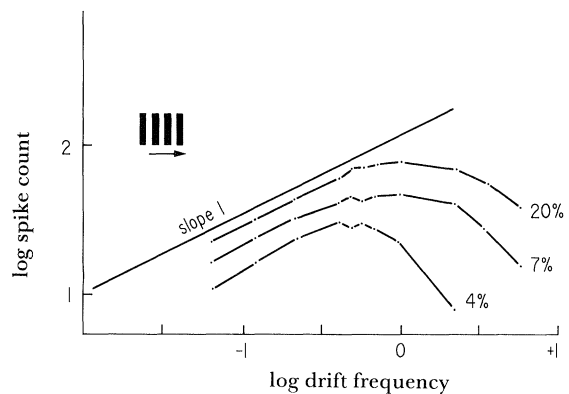


Figure 3. Responses as a function of drift frequency for square wave patterns at three different contrast levels. At low contrast the system cannot follow the high frequencies. At low drift frequencies the response is approximately proportional to frequency, suggesting that it is driven by the passing of each edge.

narrower ones for the same angular velocity, and responses to wide bars extend to higher velocities than to narrow bars (figure 4). The differences are not entirely attributable to receptor field width and modulation because they extend to wider bars. The optimum drift frequency for stimulation of the H1 neuron is also dependent on contrast, being reduced at lower contrasts. Again, we interpret this effect as resulting from the longer time that is needed for building up the short-term memory effect necessary for motion perception.

These results can be interpreted as arising from the build-up of a memory-like effect during the time that the middle part of the bar is passing the unit motion detectors so that they see only constant illumination. Some part of the result, however, is attributable to adaptation, as well as to the impulse response of the receptors and the smaller modulation of intensity caused by the thinner bar in the fields of the receptors. All three effects would contribute to the results in figure 4. In addition, we might look for other limiting factors that lie in the visual processing mechanism at the level of the motion detection.

Over its typical small dynamic range, a change in the contrast of the bar has a similar effect to a change of the bar width: lower contrast bars are less well seen and the response cuts off at a lower angular velocity. These effects are difficult to interpret because the time constants of the receptors are probably matched to those of the templates that detect motion, which are in turn matched to the time constants of the H1 neuron, so that it becomes impossible to separate the properties of the unit motion detectors without recording from the interactive elements at every level.

The lowest velocity at which a bar can be seen is lower for a wide bar than for a narrow one. This threshold has an effect on the range at which an object comes into view. A black bar 8 cm wide subtending 1.3° in the flight path at 10° from straight ahead reaches threshold (inferred from H1 neuron responses) when it is about 3.4 m distant, and similar calculations can be made for other bar widths, bar contrasts and relative velocities from the data given in the figures.

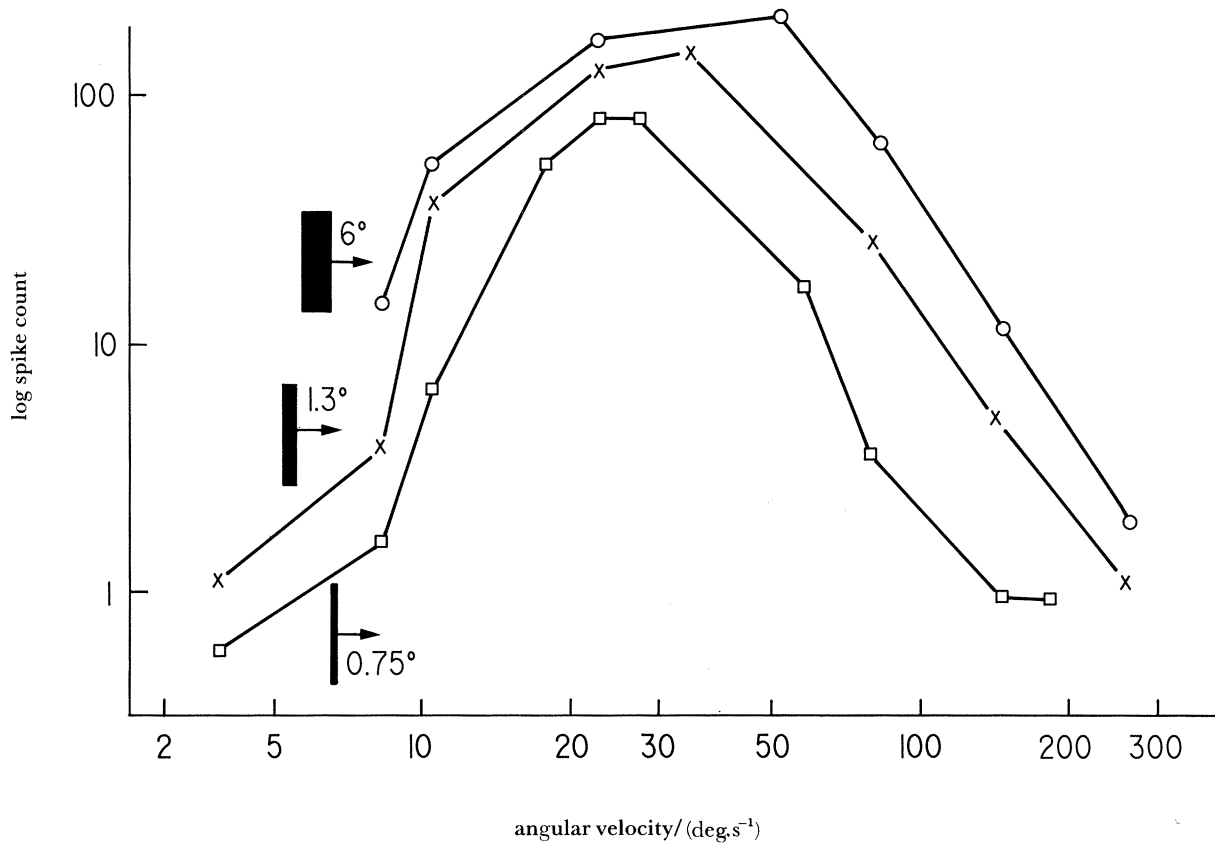


Figure 4. The effect of the width of a black bar on the responses of H1 to the angular velocity of the bar. Wider bars give responses up to higher velocities than the narrower bars, and the peak response is also at a higher velocity. The lower velocity threshold is less affected than the upper limit by bar width.

DISCUSSION

The first issue of general significance is the ease of saturation to contrast, which implies that it is more important for the fly motion-perception system to detect a small contrast than it is to discriminate contrast over a wide range, or even over the whole range of natural contrasts. Laughlin (1982, 1983) made the point that the responses of lamina ganglion cells L1 and L2 appear to be matched to the distribution of contrasts in normal scenes, in which information from very low and from very high contrasts is unreliable, and that these lamina cells optimize the transmission of the middle range of contrasts. The motion perception system behaves differently: it reveals that weak contrasts are disproportionately amplified, as if there is a strong selective advantage in seeing anything at all that may be an obstacle in the flight path. It is important not to miss a weak signal, but evidently not so important for motion perception to see the difference between 25% and 75% contrast. Of course, the lamina ganglion cells may indeed be tuned to the range of normal contrasts as Laughlin suggested, while the motion perception system saturates easily, because they could be independent pathways (Coombe *et al.* 1989). On the other hand, Sobey & Horridge (1990) have shown that change in contrast in adjacent receptors is an adequate input for directional motion perception. In insects with a variety of receptor colour types, motion perception is already

known to be colour blind and object vision is associated with colour vision, showing that there are other separate pathways in early visual processing. In fact the whole topic of the independent discrimination of contrast, colour pattern and velocity is an open question in insect vision, and it is probable that parallel channels for contrast exist beside the motion detection pathway, particularly in the context of colour discrimination.

If the visual system is interested mainly in the direction and range of edges as seen by motion in the three dimensional world, then, in addition to being colour-blind, the contrast is readily saturated by a high gain amplifier that simplifies the visual processing by effectively making contrast all-or-nothing. Contrast gradients are then sharpened into edges which become the only features of importance in subsequent directional responses. The principles have been built into an artificial seeing system (Sobey & Horridge 1990).

REFERENCES

- Barlow, H. B. & Levick, W. R. 1965 The mechanism of directionally selective units in rabbit's retina *J. Physiol., Lond.* **178**, 477–504.
- Coombe, P. E., Srinivasan, M. & Guy, R. G. 1989 Are the large monopolar cells of the insect lamina on the optomotor pathway? *J. comp. Physiol. A* **166**, 23–35.
- Fennema, C. I. & Thompson, W. B. 1979 Velocity determination in scenes containing several moving objects. *Computer Graphics and Image Processing* **9**, 301–305.

- Franceschini, N., Riehle, A. & Le Nestour, A. 1986 Properties of the integrated circuit mediating directional selectivity in a movement-sensitive neuron. *Soc. Neurosci. Abstr.* **12**, 859.
- Franceschini, N., Riehle, A. & Le Nestour, A. 1989 Directionally-selective motion detection by insect neurons. In *Facets of vision* (ed. D. Stavenga & R. Hardie), pp. 360–390. Berlin: Springer Verlag.
- Hausen, K. 1981 Monocular and binocular computation of motion in the lobula plate of the fly. *Verh. Dtsch. Zool. Ges.* **1981** 49–70.
- Horridge, G. A. 1990 A template theory to relate visual processing to digital circuitry. *Proc. R. Soc. Lond. B* **239**, 17–33.
- Horridge, G. A. & Marcelja, L. 1990 Responses of the H1 neuron of the fly to jumped edges. *Phil. Trans. R. Soc. Lond. B* **329**, 65–73. (Previous paper.)
- Laughlin, S. B. 1982 A simple coding procedure enhances a neuron's information capacity. *Z. Naturforsch.* **36c**, 910–912.
- Laughlin, S. B. 1983 Matching coding to scenes to enhance efficiency. In *Physical and biological processing of images* (ed. O. J. Braddick & A. Sleight), pp. 42–52. Berlin: Springer Verlag.
- Limb, J. O. & Murphy, J. A. 1975 Estimating the velocity of moving images in television signals. *Computer Graphics and Image Processing.* **43**, 311–327.
- Maddess, T. 1986 Afterimage-like effects in the motion-sensitive neuron H1. *Proc. R. Soc. Lond. B* **228**, 433–459.
- Maddess, T. & Laughlin, S. B. 1985 Adaptation of the motion-sensitive neuron H1 is generated locally and governed by contrast frequency. *Proc. R. Soc. Lond. B* **225**, 251–275.
- Reichardt, W. 1961 Autocorrelation: a principle for evaluation of sensory information by the central nervous system. In *Principles of sensory communication* (ed. W. A. Rosenblith), pp. 303–317. New York: John Wiley & Son.
- Sobey, P. J. & Horridge, G. A. 1990 Implementation of the template model of vision. *Proc. R. Soc. Lond. B* **240**, 211–229.

(Received 13 March 1990; Accepted 9 May 1990)