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Responses of the H1 neuron of the fly to jumped edges

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SUMMARY

Directional motion detection was measured as the response of the H1 neuron of the fly. The stimulus was the jump of a single black–white edge or a single bar through an angle of 1.5°, which is similar to the angle between adjacent receptor axes. An edge that advances by one receptor causes the same change in that receptor whichever way it moves, but the response is to one direction only. Therefore the steady state of the receptors before the stimulus jump is available to the directional motion perception mechanism no matter how long the stimulus has been at rest. This short-term memory of the previous state of the receptors persists even though the bar disappears briefly during its jump. Similarly, the response to a bar is directional although a black bar that jumps one way causes the same changes in a photoreceptor pair as a white bar that jumps the other way. Responses to 'off' are distinguished from directional responses to motion. If the contrast of the bar is reversed at the jump, the directionality is lost, showing that algebraic multiplication does not occur when the stimulus is a narrow bar. Motion is inferred by interaction of the nearest edge with the former position of an edge having the same orientation. Black–white edges therefore do not interact with white–black edges to produce a directional response. The results are discussed in terms of the template model, which is a Boolean representation of spatio-temporal fields of expectant neurons in parallel behind each visual axis.

INTRODUCTION

Vision is fundamentally an on-line detection of transients, and for a flying insect the urgency of detecting motion as soon as possible must always minimize the time available for improving the signal by averaging over time. The urgency implies the detection of the direction of the minimum angular motion on the retina, which in turn implies the detection of the direction of the smallest shift of intensity from a receptor to its neighbour, leaving no time for measurement of angular velocity, which requires measurement of a time interval or of the distance moved, or both. The alternative is to have a range of preset templates that respond without delay to the appropriate combinations of receptor responses (Horridge 1990; Sobey & Horridge 1990).

The elementary motion detectors of the fly visual system behave as if governed by these considerations. The transient response to a stimulus is rapid and larger than the steady state response. One single interaction between one pair of adjacent receptors is sufficient to elicit a directional response (Franceschini *et al.* 1989). The directional motion detection mechanism responds rapidly to the onset of a movement, but in the steady state the summed response is sensitive to the temporal frequency at which edges pass, and angular velocity is not measured independent of pattern. The adaptation to a repeated stimulus improves the response to transients (Maddess & Laughlin 1985), suggesting that the system is optimized for transients.

An appropriate stimulus for analysis is therefore a transient test of directional motion. For that, we might turn to the well known phi-phenomenon, which is the apparent motion caused by a small jump of a point source of light to a neighbouring position. A moving point source, however, has a leading edge and a trailing edge in any real visual system, because receptors have fields of finite size, and therefore a simpler stimulus is a single edge that jumps. An edge has the advantage that we can look for effects of polarity because a black–white edge is clearly not the same as a white–black edge moving in the same direction. A sudden small jump by either polarity of edge is a powerful stimulus that conveys directional motion for both man and insect, and it also permits the accurate measurement of the latency of the response so that it provides us with a way of tracing the sequence of activity from neuron to neuron.

The H1 neuron (named by Hausen 1976) is a large spiking directional motion-sensitive neuron with widely ramifying arborizations in the lobula plate of both optic lobes, and used for numerous studies of motion sensitivity in the fly (reviewed by Franceschini *et al.* (1989)). The neuron is excited by motion from the back towards the front of the eye in the horizontal direction. The response, measured as the number of nerve impulses to the onset or a short period of steady state motion, increases with velocity to a peak at a velocity that depends on the pattern. With regular patterns, however, the response depends on the contrast frequency (drift frequency) independently of the spatial frequency, as if there is a summed response to each edge that passes the eye.

By stimulating single photoreceptors R_1 and R_6 of adjacent visual axes behind a single facet, while recording from the H1 neuron, Franceschini *et al.* (1986) showed that: (*a*) a single 'on' or a single 'off' has no effect unless it is followed after an appropriate time by a similar stimulus at the adjacent receptor in the preferred direction, corresponding to the passage of either a self-luminous object or a black object in that direction across the retina. In the opposite direction there is inhibition of the background discharge; (*b*) when the stimulus mimics the passage of a single edge, the response occurs to the second 'off' for an advancing black edge and to the second 'on' for an advancing white edge, but 'the first contrast change is able to facilitate the response to the second contrast change only if it has the same polarity' (Franceschini *et al.* 1989, p. 381). Besides the requirements of direction and temporal delay, an 'on' facilitates only an 'on' and an 'off' facilitates only an 'off' when the stimuli are applied to single receptors in the fly. Therefore directional motion detection for 'on' is separate from that for 'off', and algebraic multiplication as proposed in the original model (Hassenstein 1951, 1958, 1959; Reichardt 1961) is clearly excluded. By stimulation with transient movements of edges and bars, and recording from the H1 neuron, we now make the same tests for fly motion detection for normal vision of patterns.

METHODS

Flies, *Calliphora stygia*, were reared in a warm glass house and used fresh. The head and wings were waxed to a block and a small hole made in the back of the head for the electrode to penetrate. The stimulus was applied to the contralateral eye, to ease the isolation and identification of the H1 neuron.

The stimulus was generated by an Innisfree Image Synthesizer controlled by an IBM-AT computer operating Data Acquisition On-line System (DAOS), Ausonics Pty, which also collected the responses, made post-stimulus histograms and plotted data. The stimulus was a square-wave or sine-wave grating of variable spatial and drift frequency, or a single black or white bar which appeared on a grey screen. The frame rate was 200 Hz. The edges of the stimulus were always vertical with reference to the normal posture of the fly. The screen subtended 25° by 25° at the eye and was moved around the visual field of the contralateral eye until it was in the centre of the field of the H1 neuron. With the single edge in the centre of the screen the photon flux at the eye was 3.7×10^{10} photons $cm^{-2}\ s^{-1}$ when measured through an interference filter with peak at 545 nm, and width 30 nm at 50% pass.

Recording was by a glass microelectrode of resistance 200 MΩ filled with potassium acetate or Lucifer yellow solution, placed in the lobula plate. After the H1 neuron had been located and penetrated, recordings lasted about an hour to give sufficient records. In some cases the neuron was filled with dye for anatomical confirmation of its identity. Some of the recordings were extracellular, with standard precautions about isolation of the single H1 neuron.

RESULTS

(*a*) *Edge stimulus*

The insect was mounted in its normal posture in front of the screen, on which a vertical black–white edge instantaneously (between frames at 200 Hz) jumped horizontally through an angle of 1.5°, which is similar to the interommatidial angle. There are four possible stimulus situations if the jump is instantaneous. The black can advance following white (called 'black edge') or the white can advance following black (called 'white edge'), in either case in the preferred (forward) or the anti-preferred (backward) direction (figure 1*a–d*).

Let us represent the array of receptors by a single row. In the most elementary cases the edge moves by one receptor with black edge advancing to the right (*a*) or to the left (*b*), the receptor marked (−) is suddenly darkened. With the white edge advancing to the right (*c*) or to the left (*d*), the receptor marked (+) is suddenly lit up. Adjacent receptors are not affected. If the inputs see only the change in intensity as represented in figure 1, or if the system after the jump has no memory of the previous state, a directional

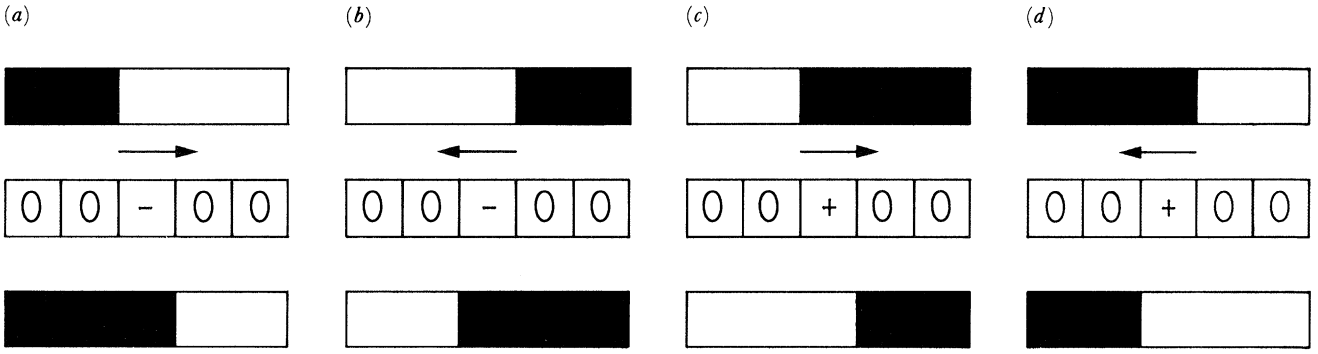

Figure 1. The jump of a single edge by one inter-receptor axis. The top line represents the situation before the jump, the second line is a row of receptors, the third line is the situation after the jump. In each case only one receptor sees a change in the intensity, lighter when the white edge advances, darker when the black edge advances, either to the left or to the right. Because the response is sensitive to direction, the motion-detectors must therefore take the initial situation into account, however long the edge has been stationary.

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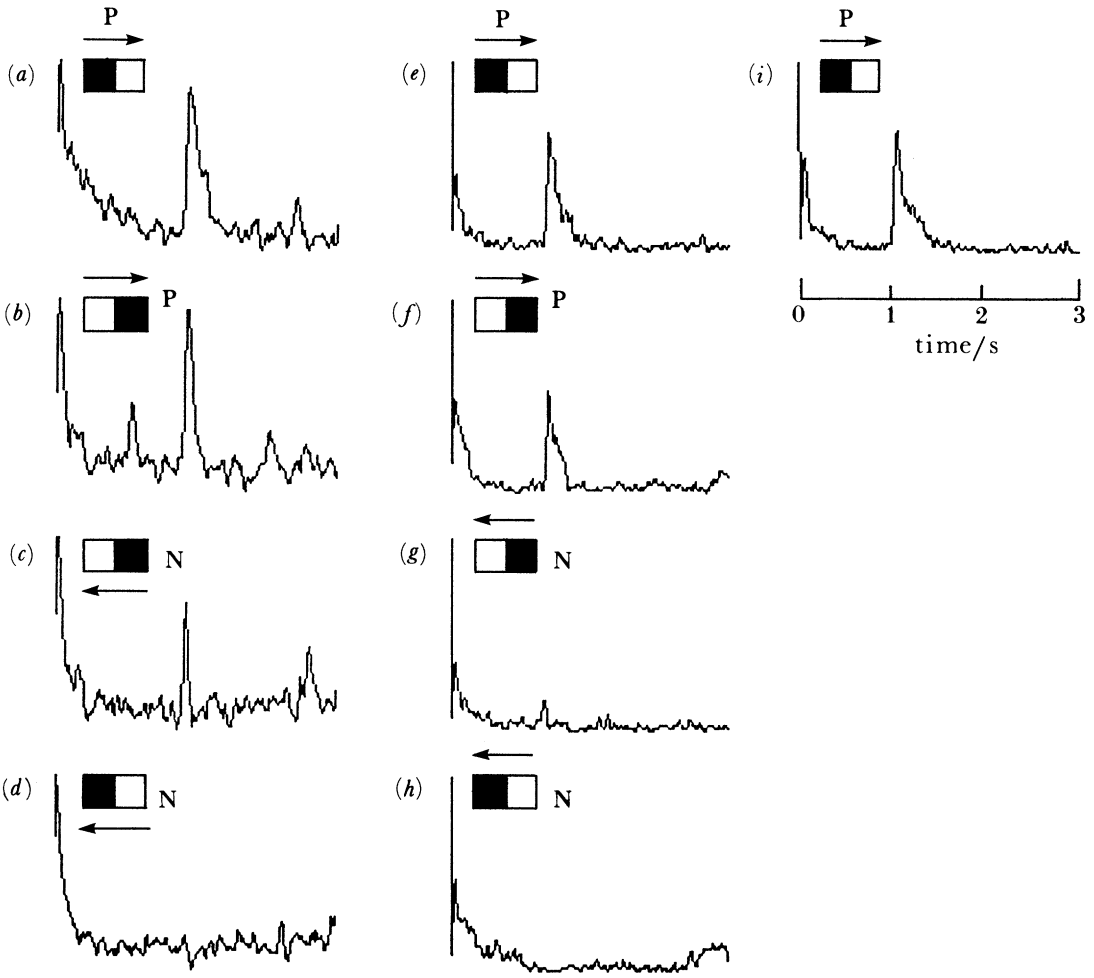

Figure 2. Responses to the jump of a single edge of either polarity. At the beginning of each trace the edge appears in the middle of the screen, which was previously grey. The response to this change rapidly falls to the spontaneous level. At the centre of the trace is the response to the jump by 1.5° in the direction indicated for each.

response is impossible. This stimulus is therefore a critical test, for some models, of directional motion detection.

Tests on the H1 neuron show the directional response to the jump of a single edge, and also that the advancing black edge gives a stronger response than does the advancing white edge (figure 2). In some animals there was a negligible response to an advancing white edge in the forward direction in some parts of the field of the H1 neuron, whereas the response to the advancing black edge is everywhere consistent, suggesting that there are some regional differences in the balance between the processing mechanisms for the advancing black edge and the advancing white edge.

With the jump of a single edge, we sometimes see a response to the black but not to the white edge advancing in the anti-preferred direction (figure 2*c*), but this 'off' response is consistently of shorter duration than when the motion is in the preferred direction. The directionality shows that the mechanism that detects the sudden jump of a single edge takes into account the previous stationary distribution of the pattern, and therefore the steady state illumination of the receptors before the jump.

There is always an initial transient response when the screen changes from 50% grey to any black–white pattern, as shown on the extreme left of each of the traces in figure 2. The fact that there is negligible response to a jump in the anti-preferred direction suggests that a continuously effective inhibition has spread laterally in the anti-preferred direction from the edge of the stationary image on the retina. This inhibitory spread takes place in one direction whichever side of the edge is black, therefore there must be a separate mechanism for edges of each orientation, ready to anticipate a move in either direction. Similarly there must be a continuously effective facilitation spreading continuously in the preferred direction from each polarity of edge.

Instead of an instantaneous jump, we now make a pause of 2 s between the disappearance of the edge at its first location and its appearance at the second location. During the intervening period the screen is uniformly grey at 50% brightness. The sequence on the screen is therefore (*a*) uniform grey at 50%, (*b*) appearance of an edge between black and 100% brightness, (*c*) after 2 s this edge is replaced by the 50% grey screen, (*d*) after 2 s the edge reappears with a shift of 1.5° (figure 3). The responses show that the directional mechanism still functions although the large change in brightness when the edge disappears causes a constant large first response. With the black

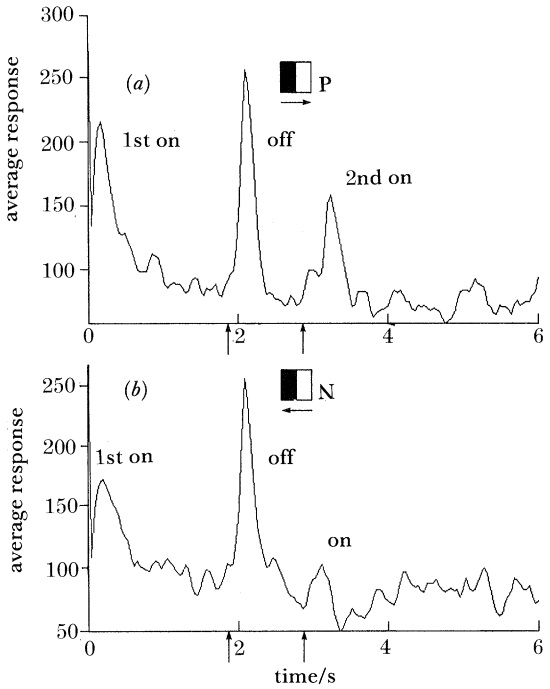

Figure 3. As in figure 2, but the edge is replaced by a plain grey screen for 1 s before it reappears 1.5° away. On the left is the response to the first appearance of the pattern. At time 2 s there is a sharp response to the disappearance of the edge. When the edge reappears (*a*) in the preferred direction at time 3 s, there is a facilitated response, but (*b*) in the anti-preferred direction the response is small and is followed by inhibition of the spontaneous level. Lateral effects therefore persist in the absence of the stimulus.

edge advancing in the anti-preferred direction there is a second small response to the second 'on', superimposed on an inhibition of the background, whereas in the preferred direction there is a positive response at the second 'on' (figure 3*b*). Therefore the lateral excitatory effect and the lateral inhibitory effects mentioned above persist for a short time in the absence of the stimulus.

Reversal of contrast with a jumping single-edge causes such large responses to the intensity changes that the directional effect of the small displacement of the edge is lost. The jump of a normal edge is surprisingly not the best stimulus to the H1 neuron. The human eye sees the jump clearly but the fly response is more effective to the onset of a steady movement of the edge.

(*b*) *Single bar stimulus*

The jump of a black bar 1 receptor-interval wide to the right by an angle of 1 receptor interval on the retina can be represented as in figure 4*a*, and we see immediately that the change caused at the receptors is exactly the same as if a white bar jumps to the left (figure 4*e*). Similarly, as seen by the stimulated eye, the change caused by a white bar jumping to the right is the same as that caused by a black bar jumping to the left (figure 4*b*,*f*).

The jump of a bar with simultaneous contrast reversal also leads to ambiguity if only single changes are observed. A jump of a black bar on a grey background to the right with contrast reversal is the

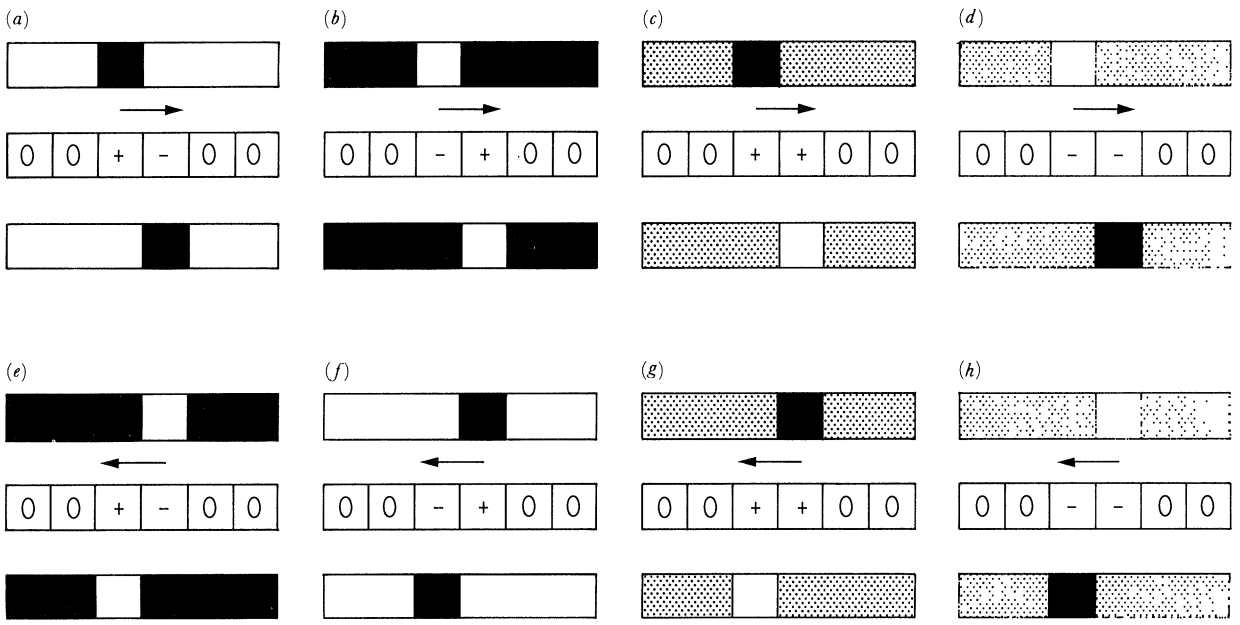

Figure 4. Representation of the jump of a stationary bar by one receptor width. The upper line shows the initial position, the second line the array of units, presumed to be photoreceptors, and the third line shows the stimulus position after the jump. The H1 neuron gives the directional response to (*a*) a black bar and (*b*) a white bar, although the sign of the change on the retina of one is the reverse of the other. It gives no response to a jump in the opposite direction, although the change in (*e*) is the same as in (*a*) and the change in (*f*) is the same as in (*b*). No directional response is obtained in either direction when the contrast is reversed (*g*) from black to white on a grey background (*h*) from white to black. Therefore the previous state at the receptors is taken into account in directional perception of motion.

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same as for a black bar to the left (figure 4*c*, *g*) and similarly for the white bar with contrast reversal (figure 4*d*, *h*). This stimulus is therefore appropriate to test for algebraic multiplication as incorporated into the original multiplicative model (Reichardt 1961).

Bar stimulus A

The bar appears briefly then disappears and it reappears a short time later at an adjacent position (figure 5). The actual sequence is as follows: a blank 50% grey screen with recording of background spikes for 1 s, then the 1.5° bar appears for 200 ms, then blank grey screen for 200 ms, then the bar reappears for 200 ms, then the bar disappears again and the record continues with blank 50% grey screen until a total of 3 s have elapsed; there is then a pause of 3 s until the sequence starts again. The bar can be either black or white on the grey background. The contrast of the background was adjusted to 50% in all experiments. The responses are completed during the middle one of the 3 s of the recording. The number of stimulus sequences that were summed was controlled up to 50, but usually 10 or 20 repeats were sufficient. The records show only the summed spiked occurrences although some of the recordings were intracellular.

Experiments were not necessarily done with the same order of stimulus presentation. In one example, a black bar was jumped to the left, then a white bar in the same direction (figure 5 *a*, *b*). Then the same stimulus was repeated with reversal of contrast at the jump (figure 5 *c*, *d*). Then the same was repeated in the opposite direction with the bars in the same locations as before (figure 5 *e*–*h*). Finally a number of controls were added, in which the bar reappears at the same place or changes in contrast with no motion, (figure 5 *i*–*l*) and finally a repeat of the first stimulus (figure 5 *m*). The appearance of a black bar for 20 ms on a 50% grey background causes a greater response than the appearance of a white bar of the same size at the same place. When the jump of a black bar is in the preferred direction there is always a stronger response to its second appearance, about double that to the first appearance. The jump of a white bar, all other parameters being equal, gives a weaker response than the jump of a black bar.

Bar stimulus B

In this stimulus sequence a black or white vertical bar is stationary for a time on a grey screen and then jumps instantaneously to a new position (figure 6). The recording of spikes begins when the bar appears, and continues with the bar stationary for 2 s. After the bar jumps, it stays for 2 s in its new position then disappears, while the recording of the response con-

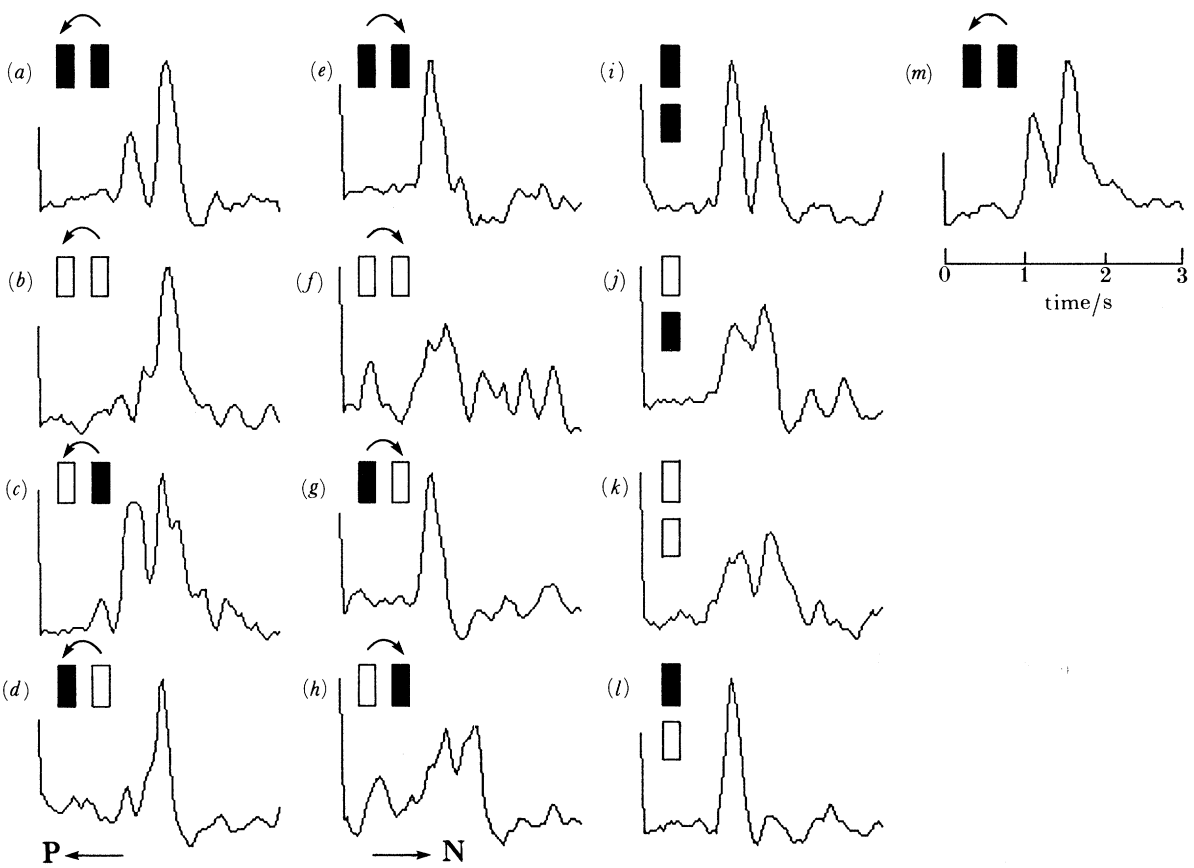

Figure 5. The bar 1.5° wide jumps by 1.5° on a grey background. The direction and contrast are shown for each record. The initial appearance of the bar at time 1 s causes a larger response for a black than for a white bar. The second appearance of the same bar at time 1.4 s in the preferred direction (*a*, *b*) causes a second and usually greater response. At any time the appearance of the black bar can cause a large response except in (*e*) and directionality is not reversed when the contrast is reversed (*c*, *d*, and *g*, *h*). A variety of responses are found when the bar does not move (*i*–*l*). The final repeat of (*a*) at (*m*) shows that the properties of the neuron do not change during the experiment.

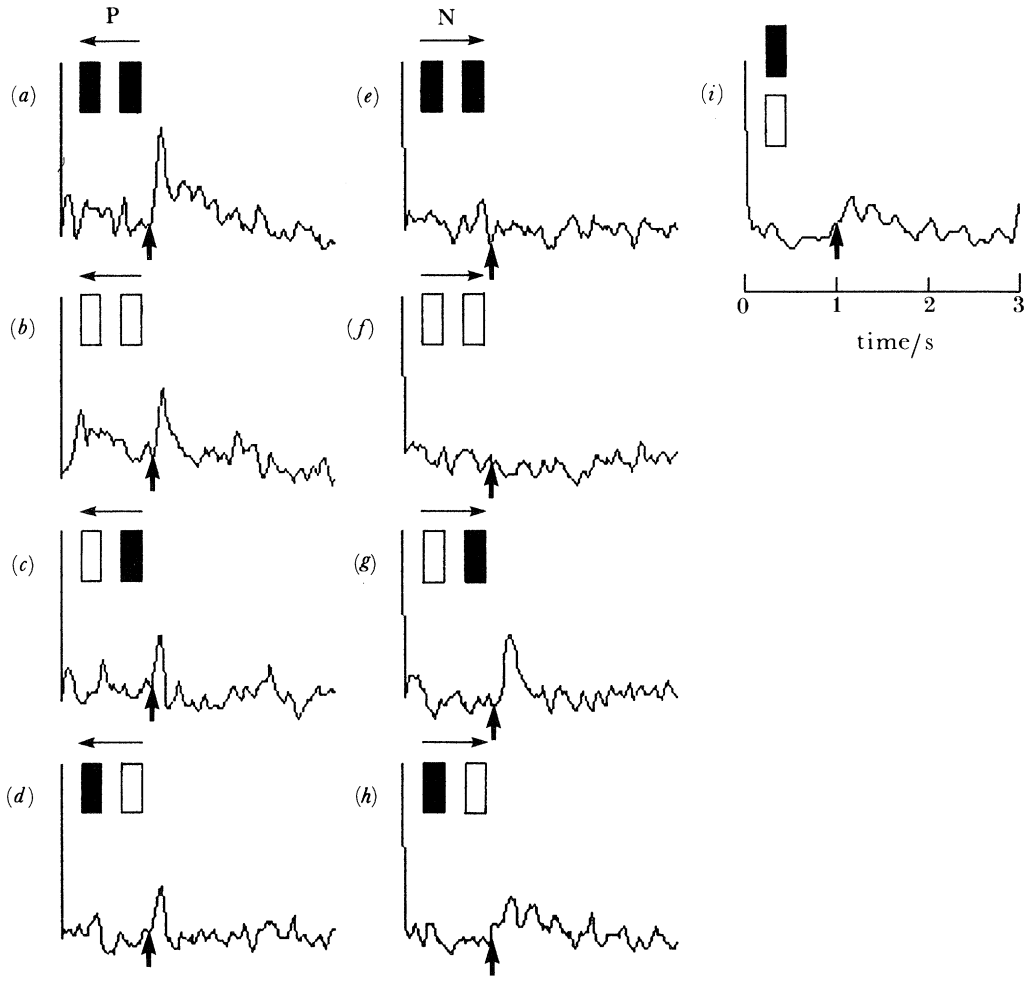

Figure 6. At the left side of each record the bar appears on the screen, where it rests for 2 s before it jumps by 1.5° (*a*) black and (*b*) white bar in preferred direction, (*c*) and (*d*) reversing contrast, preferred direction (*e*) black and (*f*) white bar in anti-preferred direction, (*g*) and (*h*) reversing contrast, anti-preferred direction, (*i*) reversing contrast without a jump.

tinues, to make a total record of duration 6 s. Then there is a wait of 3 s before the bar reappears in its first position and the sequence begins again. The bar subtended 5° by 1.5° at the eye, and jumped at right angles to its long axis in a horizontal direction with reference to the normal posture of the eye. The bar jumped through an angle of 1.5°, normally with an instantaneous movement. To the human eye this stimulus gives a strong impression of motion. The bar could be changed from light to dark, retaining the 50% contrast against the grey background.

The experiments with bars that jump show that there is usually a response to the darkening or 'off' when a dark bar appears but there is rarely a response to the simple arrival of a white bar. However, we find preparations which give anomalous results (figure 6) when the black or white bar jumps by 1.5° the response is large if the jump is in the preferred direction (figure 6*a*, *b*), but is zero or negative in the opposite direction (figure 6*e*, *f*). Black bars produce stronger responses, and stronger inhibition of background spike frequency, than do white bars. When contrast is reversed at the jump there is no reversal of the directionality: instead, an appearing black bar usually causes the off response irrespective of the direction in which it has just jumped. There are, however, exceptions (figure 6*g*, *h*). When there is no lateral motion, but the bar reappears in the same place as before, there is usually a response to both appearances of the bar, especially when a black bar appears. The same results are obtained if the bar disappears briefly before it reappears at the new place, whether or not the contrast is reversed. In brief, to generate the directional response to motion, the bar must not reverse contrast. The directional response is at full strength even if the bar has rested for a long time in its initial position. The directional response is decreased if the bar rests for too short a period in the first position, and also if it disappears for too long a period at the jump. These facts will eventually allow us to investigate the build-up and decay of the latent image of the bar in its first position.

DISCUSSION

Visual systems, especially of animals that use their eyes to detect predators or prey, or to stabilize themselves in flight, are superbly adapted for the rapid and sensitive detection of transients. The method of analysis must take this into account, because neurons tend not to respond to inappropriate stimuli. In

addition, the method of analysis must be appropriate for the further elucidation of neural pathways and discovering the functions of neurons in a system where every subsystem is reduplicated many times in parallel. It is also essential to have a stimulus that allows the measurement of latencies, the temporal and spatial properties at synapses and which facilitates the study of adaptation as a property of every element in the visual system. From this it follows that a mathematical theory that starts from the steady state responses is a hindrance to the analysis.

The experiments reported here confirm for visual scenes what Franceschini *et al.* (1986, 1989) have already shown by careful stimulation of two adjacent receptors in the fly, that the sudden motion of white–black and black–white edges is processed in separate pathways. Furthermore, the observation that transient motion of a thin bar fails to give the directional facilitation if the contrast is reversed at the jump, suggests that transient motion perception is not done by algebraic multiplication of signs. Apart from this and the work of Kien (1974, 1975) in Canberra on the locust, the algebraic nature of the multiplication in motion perception has not been questioned since the original experiments on the beetle *Chlorophanus* (Hassenstein 1951). We might ask how a motion in one direction coupled with reversal of contrast, could be mistaken for a motion in the opposite direction. There is no difficulty with a regular striped pattern because after a phase shift and a phase reversal the best autocorrelation of a regular pattern lies in the opposite direction. With a bar stimulus it is possible that one edge could, after contrast reversal, be correlated best for the other edge. In psychophysical tests on man (Anstis 1970; Anstis & Roberts 1975) and with tests on cat cortical visual cells (Emerson *et al.* 1987) it has been observed that the reversal of contrast causes the reversal of apparent motion. However, the autocorrelation model is not shown by these experiments for two reasons: (*a*) because vision involves the best fit of the stimulus pattern with the neuron fields, not the correlation of the stimulus with itself, and (*b*) because other models exist, which can equally well account for the data about contrast reversal (see also Thorson (1966, p. 65)).

In a real retina the receptors have fields of finite angular width, and therefore the sharp edge in the stimulus is degraded to a gradient on the retina. An interesting consequence of the separate processing of spatial gradients, which slope in opposite ways is that the jump of a point source or of a black spot is not the simplest stimulus for testing motion perception. To a real eye consisting of a retina of receptors, a spot must have two edges, one that leads and one that trails in a movement. Despite many statements that the simplest stimulus is a point source, the ϕ-phenomenon is more complex than the jump of a single edge, as is also clear from a study of the template model (see below).

For the past 30 years, the interpretation of data on insect motion perception in terms of algebraic multiplication, however successful, has not ruled out alternative models, and it has not stimulated critical tests of the mechanism of directional motion detection itself. The conclusion of Thorson (1966), that any of several possible models could explain his data, has been ignored. When Kien (1974) used single edges to elicit optomotor responses of the locust, she inferred that the detection of motion from light 'on' is in a separate system from that detecting motion from 'off', and concluded that 'this would not allow extrapolation from one system to another' (p. 421); that is, algebraic multiplication of changes having opposite signs was excluded. When Mimura (1975, p. 428) stimulated the retina with two spots of light in succession, and recorded from directional motion-sensitive neurons (presumably lobula neurons) he found 'an excitatory process in the preferred direction and an inhibitory one towards the null side'. Directionally selective cells with medium-sized fields in the locust medulla also show excitation towards the preferred side and inhibition towards the anti-preferred side (as in figure 3), with responses to a very wide range of velocities from $2° \text{ min}^{-1}$ to $100° \text{ s}^{-1}$ with peak response with a separation of flashes near 2° and responses down to contrasts of 0.01 (Osorio 1986). Therefore, when Maddess & Laughlin (1985) showed the strong effects of adaptation in the directional motion-detecting pathway of the fly, and then Maddess (1986) showed an after-image that is taken from a stationary image and stored in the visual system, we set about the re-examination of the detection of motion at a single edge. We avoided regular striped patterns, placed less emphasis on the steady-state models, and with an eye to the saturation of neuron responses at low contrast, formulated the template model (Horridge 1990; Sobey & Horridge 1990).

The template model for the sorting of sensory input in parallel differs from the autocorrelation theory of motion perception in that the latter involves the correlation of the stimulus with itself displaced in angle and time, whereas in the template model the input pattern is fitted to a selection of predetermined templates, which are digitized simplified neuron fields. The template model is more general than correlation, and it is a crude mimic of a natural system of diverse neurons with different fields all looking at the stimulus concurrently.

In the first template model based on intensity we take the state at a pair of adjacent receptors at two successive times (figure 7), and treat black as 0 and white as 1. This shorthand gives 16 sets of 4 spatio-temporal Boolean symbols, which have meanings in terms of the motion of edges in the visual field (figure 8). The performance of the templates depends on their threshold and two time constants, and they can also be constructed as analogue devices to respond to gradations of contrast or angular velocity. If the template has three of one symbol and one of the other, i.e. symmetrical about a diagonal, it responds directionally to motion of an edge. The template for directional motion detection is a very simple digitized version of mammalian cortical neurons, which respond to moving edges (Emerson *et al.* 1987). Any occurrence of 01 means that a black–white edge is involved, and similarly 10 means a white–black edge. This model can be extended to triplets of receptors, which are sufficient

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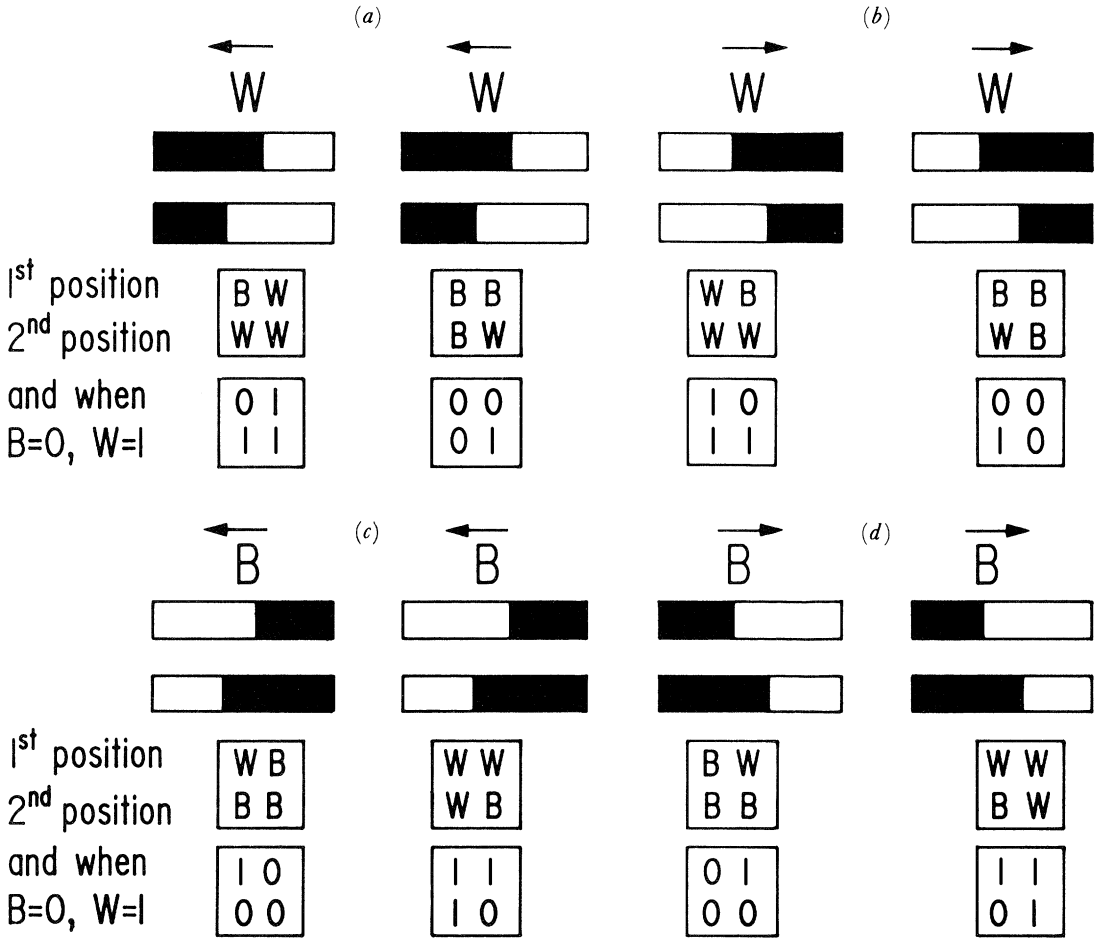

Figure 7. A single edge that jumps by the distance (angle) between adjacent receptors gives an impression of motion. Each part of this figure, (*a*)–(*d*) shows two ways of representing what pairs of receptors see before and after the jump. Four templates represent the motion in each direction. All possible templates are shown in figure 8.

for the detection of edges of objects moving against background (parallax) and convergence or divergence in the flow field. A full account of the template model is given by Horridge (1990), and an improved version for continuous motion in natural scenes (Sobey & Horridge 1990) uses templates based on contrast change rather than intensity.

This template model is intended to serve in several ways. First, it is a model that shows how the jump of a sharp edge by one receptor spacing may be detected. It shows the ultimate in parallel processing in that a look-up table of templates is placed behind each receptor axis. The model shows how combinations of visual primitives are relevant for simple behaviour, and points out the required line of development of new hardware for building visual systems that avoid numerical computation. It does not require analysis of flow fields and it replaces convolution by fitting the digitized image to one of a set of alternatives. This model also shows clearly that neurons are likely to

1st \ 2nd	00	01	11	10
00	⊙	W ←	X	W →
01	B →	⊙	W ←	X
11	X	B →	⊙	B ←
10	B ←	X	W →	⊙

Figure 8. A Boolean function or look-up table behind every receptor axis for first and second states of a pair of adjacent receptors, for horizontal motion. On the left are the first states of two adjacent receptors and along the top are the second states, as in figure 7. The table is filled by 16 representations of primitives in the visual world that correspond to the 16 possible spatio-temporal groups of zeros and ones. This Boolean function behind each receptor axis refers only to horizontal motion. (W, white advancing; B, black advancing; ⊙, no change; ×, change or flicker, but no motion; ⇄, directional motion.)

operate in specific combinations and that the responses of single neurons do not necessarily have unambiguous reference to the elements in the visual scene. The 4×4 look-up table in figure 8 provides plenty of versatility in signalling. The additional ability of neurons to act in combinations of different types behind each visual axis goes a long way to avoid the combinatorial explosion. As said above, the model is more general than earlier models; it depends on the previous illuminated state of the receptors as well as on changes in illumination, and it differs from autocorrelation in that the neurons of the visual system have fields that respond to predetermined specific combinations of the present and previous states. The template model based on intensity also shows exactly how neurons that record 'no change' are as significant as their active partners in parallel with them, because it is the whole ensemble that carries the total signal. The model based on contrast can detect directional motion without a 'no change' input. We can also imagine an evolution of visual systems by addition of templates as they become relevant to the response to the visual scene. The template model is also applicable to other sensory modalities; it gives meaning to the large numbers of neurons in columns as in the insect visual medulla or the vertebrate sensory cortex. Also, the template model, with its vast parallel processing and combinatorial possibilities, means that experimental analysis of the mechanisms must be based on latencies, must take into account the neurons recording 'no change', and must include the responses of the next neurons down the line because they alone have the correct connections to detect the relevant combinations that feed into them.

We thank Mark Snowball for writing the DAOS software, which generates the patterns on call from the keyboard, and which records the data as post-stimulus histograms, with graphs of spike numbers as a function of contrast, drift frequency etc., counted over any desirable interval. We thank Dr Srinivasan, Dr D. Osorio, Z. Aleksic, and A. James for stimulating discussions over a long period as this work progressed, and Elizabeth Watson for numerous drafts of the manuscript.

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