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# A test for multiplication in insect directional motion detectors

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## SUMMARY

The H1 neuron is a directionally sensitive motion-detector neuron with a large field that is fed by many high-resolution motion detectors in the fly optic lobe. As a stimulus pattern for it we used a random pattern of 50% bright and 50% dark squares on an oscilloscope screen. When this pattern is jumped by a small increment the H1 neuron gives a directional response. When the jump is greater than one pixel on the screen the response falls and becomes non-directional because jump direction can no longer be inferred. When the contrast is reversed at the jump, the response is the same for both directions, and is the same as when the contrast is reversed without motion. For the motion receptors this represents a non-directional 'on' or 'off' response. The result is discussed with reference to theories of motion perception.

## INTRODUCTION

Notwithstanding the lack of new positive evidence for a multiplication-like process, for the past 30 years the prevailing explanation of directional motion perception by insects has been the autocorrelation theory of Reichardt (1957, 1961, 1987) based on an analysis of visual behaviour of the beetle *Chlorophanus* by Hassenstein (1951, 1958, 1959). The earliest experiments were done with regular black/white stripe patterns moved in a drum and the response was measured as ratios of decisions to turn left or right at a Y-junction. After the initial experiments, attention switched to the fly and the measured response was usually the torque generated by the flying but fixed fly, with fixed head, as it attempted to follow the horizontal motion of the pattern. The preferred stimulus was a sinusoidally modulated regular striped pattern in motion. Similar stimuli were used as inputs for electrophysiology of single neurons, mainly with the neuron H1 of the fly which can be readily isolated and held for long periods in good condition. The stimulus always contained an equal number of edges of opposite polarity. A great volume of work along these lines has been published (Franceschini *et al*. 1989; Bult *et al*. 1989; Schuling *et al*. 1989; Borst & Egelhaaf 1989; van Hateren 1989).

The same theory has been applied to psychophysical data (van Santen & Sperling 1985), although with declining enthusiasm (de Graaf *et al*. 1990, Shioiri & Cavanagh 1990) particularly as non-Fourier stimulus patterns are becoming available. The idea of multiplication of inputs after filtering has been taken over into the modeling of artificial visual systems (Poggio 1983) but with less success because the output must be calibrated for each pattern.

The autocorrelation is based on the mathematical operation of correlation of a moving pattern with itself as seen a moment later in a neighbouring retinal receptor. Correlation of the modulation in two adjacent receptors, with the time delay taken into account, gives the direction. The response plotted against the velocity gives a bell-shaped curve with a peak at a velocity which depends on the spatial frequency of the passing stripes but the response plotted against the temporal frequency of passing stripes is less dependent upon the spatial pattern. The output of this model can be represented simply as the product of a low-pass filter and a high-pass filter behind adjacent visual axes.

A related nonlinear theory, called the energy model (Adelson & Bergen 1985) is based upon rectification of the signal from each input: this model is preferred by Emerson *et al*. (1987, 1990) for directional cells in cat cortex.

Quite a different theory, the gradient model, divides the local temporal gradient of intensity by the local spatial gradient of intensity to obtain the direction and velocity of the stimulus (Fennema & Thompson 1979; Limb & Murphy 1975). This calculation also works in two dimensions (Srinivasan 1990), is suitable for detecting motion of gradients, as well as edges, and has scarcely been looked for in natural visual systems.

Another approach is to assume that detectors which are specific for moving edges are present and to try to separate them and measure their fields despite the abundant evidence of distributed over-lapping parallel processing. This is a common approach for mammalian cortex (Kulikowski & King-Smith 1973) or human vision (Shapley & Tolhurst 1973; Burr *et al*. 1989).

The above mentioned theories depend upon a calculation of a single final output, which yields a quantitative result in few dimensions. Quite a different model (Horridge 1991; Sobey & Horridge 1990) assumes that numerous different neurons, or parts of neurons, on each visual axis of the optic medulla

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respond each in their own way by brief yes or no responses to different transient aspects of the passing visual pattern. These neurons can be modelled as a set of templates each of which is sensitive to one of the possible spatiotemporal combinations of contrast change in adjacent receptors at successive instants. Some of these templates are directional, others non-directional edge detectors; they are nonlinear because they have a threshold. The template theory presents us with a mechanism in which sensitivity to direction is separated from other aspects of the motion and these templates are different for white/black edges and black/white edges. Template responses can be put together in groups as a way of characterizing different kinds of edges, including edges moving at different speeds. Template responses work together like neurons.

Given a choice of several theories, it is not sufficient to show that one of them fits the data. Instead, one looks for critical tests that distinguish between alternatives. Having examined the responses to single edges, bars and the effect of contrast (Horridge & Marcelja 1990*a*, *b*), we now apply another test for multiplication of inputs by reversal of contrast with motion of a two-dimensional random pattern.

### (*a*) *Experimental method*

The stimulus pattern was generated by an Innisfree 'Picasso' image synthesizer fitted with a dual channel texture generator for the production of random pixel checkerboard patterns at 200 Hz refresh rate, which is essential for work with insects. The pattern filled the screen and could be jumped in any direction so that the screen acted as a fixed window within which the pattern moved. Normally the square units of the pattern, 50% dark and 50% bright, subtended 2° at the eye; smaller pixels are less effective as a stimulus. The pattern was jumped by various distances in the period between frames, with or without contrast reversal. The screen was a 11 × 13 cm with greenish-white phosphor, emitting 8 candela $m^{-2}$ in the bright pixels.

Spikes were recorded with intracellular glass or extracellular tungsten microelectrodes in a conventional arrangement. Spikes were collected at a sampling rate of 1 KHz and displayed as post-stimulus histograms with intervals of 40 ms. The data processing was done by an IBM/AT computer fitted with an RW206 processing board which also controlled the visual stimulus generator. Different sequences of stimulation were tested in different experiments, but no significant effects of pattern or pattern sequence were found. The final and preferred method was to record for 2 s then jump one way, record for 6 s then jump back, record for 2 s then start the trace again after a stationary wait for 4 s so that equal intervals of 8 s separate the stimulus jumps. For each stimulus situation 20 or 30 responses were averaged for the histograms (figure 1).

The H1 neuron of the fly was located in the lobula by manipulating the electrode through a hole in the back of the head and was identified by its preferred

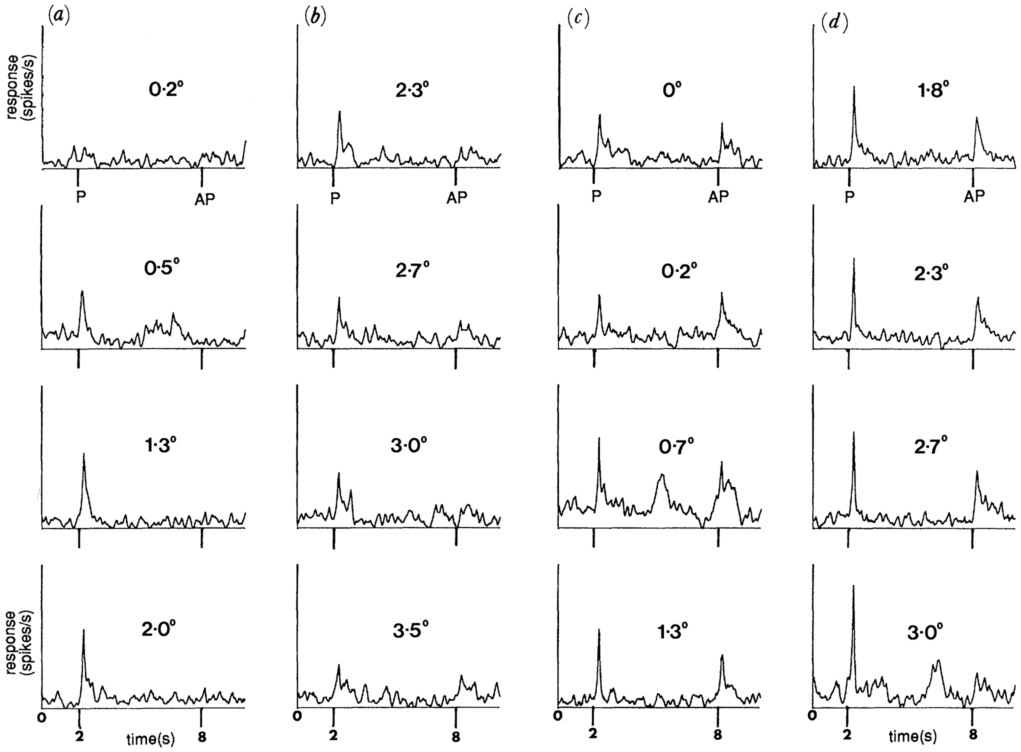

Figure 1. Responses of the H1 neuron of *Calliphora*. Post-stimulus histograms at the different jump amplitudes indicated. (*a*), (*b*) Without contrast reversal there is a response in the preferred direction (P), but usually not in the antipreferred direction (AP) until spurious correlations are reached at large amplitudes of the jump. (*c*), (*d*) With contrast reversal there is a response for jumps in either direction, and also for contrast reversal with no motion. Responses tend to be similar for the two directions except some preparations develop a directional response at large jump amplitudes.

stimulus and direction from the side to the front on the contralateral eye. We used *Lucilia cuprina* and (preferably) *Calliphora stygia*.

The giant directional motion detectors of the butterfly medulla are located in the peripheral layers of the medulla. There are different neurons responding to motion upward (commonest in our recordings) downward, forward along the eye, backward along the eye, all responding to ipsilateral stimulation. Some of these neurons respond also to contralateral stimulation, but this pathway was not tested in the butterfly. We used *Papilio aegeus* for the experiments with random two-dimensional patterns and had previously used *Heteronympha merope* for similar experiments with single bars.

## RESULTS

First, it should be emphasized that the jump of a random pattern on a display screen is not a particularly effective stimulus for directional motion-detector units. Steady motion is much more effective. In addition there is frequently a strong response to the 'off' which is presented to some of the receptors. This response to non-directional temporal contrast is readily seen when the contrast is reversed without any movement of the pattern.

A jump of the two-dimensional random pattern in the preferred direction gives a response which rapidly rises with increasing jump amplitude to a peak near 2° which is similar to the angle between visual axes. The butterfly *Papilio* shown in figure 2, gave a peak at 2.2°, *Calliphora* at 1.8° (figure 3). This is a clear positive result which is to be expected from careful results of stimulation of pairs of photoreceptors (Schuling *et al.* 1989). With increasingly larger jumps the response falls off slowly to an irregular plateau, which we interpret as due to the spurious correlations and large 'on' and 'off' stimuli when the random pattern jumps. To avoid such unwanted correlations with small jumps, we arranged that each pixel on the pattern subtends at least 2° at the eye.

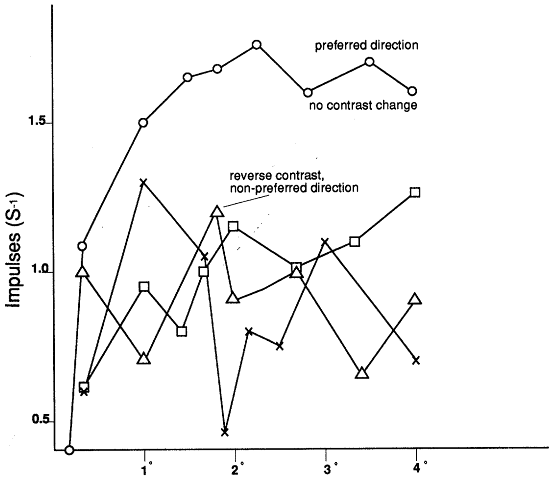

Figure 2. Responses of a giant directional motion-detector of the medulla of the butterfly *Papilio* to jumps of the random-pixel pattern with and without contrast reversals at the jump. (○, no reverse contrast, preferred; □, no reverse contrast, non-preferred; △, reverse contrast, preferred; ×, reverse contrast, non-preferred.

A jump in the antipreferred direction gives a response which rapidly rises only as far as the irregular plateau mentioned above. In the butterflies we saw no inhibition in the antipreferred direction with this stimulus, and interpret this result as due to swamping by the strong 'on' and 'off' responses caused by the jump and to spurious correlations for some jump distances. Some of the H1 responses of the flies, however, were consistently at a lower level for jumps in the antipreferred direction (figure 3*a*).

A reversal of contrast at the time of the jump gives, for either direction, the same irregular plateau for jumps of different sizes in both fly and butterfly. There is no suggestion of a directional preference and the responses are similar to those for a reversal of contrast without motion. This strongly suggests that with contrast reversal there is nothing but 'on' responses originating from half of the pixels on the screen, and 'off' responses from the other 50%, and the motion is not a factor.

We found the same result with the directional motion detectors of the butterfly medulla and the H1 neuron of the fly. In brief, there is no directional response when contrast is reversed at the movement.

### (*b*) *Reversal of contrast sensitivity of templates*

When regular stripes are jumped to the left by a quarter of a wavelength and the contrast simultaneously reversed, they appear to have moved to the right simply because of the phase change. With a single bar, however, a jump by more than half the width of the bar, accompanied by a reversal of contrast, can also generate a stimulus in the reverse direction (figure 4*a*). If the bar jumps to the left by exactly its own width and reverses contrast, the left edge of the bar at $t_1$ coincides in position and polarity with its right edge at $t_2$, so that a small apparent movement either way can easily arise with contrast reversal. What is seen by a visual system, however, depends also on which templates are being used, as will now be considered.

Instead of reversing the contrast of the second part of the stimulus, let us reverse the contrast sensitivity of the second part of the templates. There are three types of templates (figure 4) which are directionally sensitive (Horridge 1991). If we take the templates of the type (−−/−↑) or (↑−/−−) and reverse the contrast sensitivity at time $t_2$, there is no change in directionality (figure 4*b*). If we take templates of the type (↓↑/↑↑) or (↑↑/↑↓) and reverse contrast at time $t_2$, the directionality is reversed (figure 4*c*). Templates of the type (−↑/↑↑) and (↓↓/↓−), however, become non-directional when contrast is reversed at time $t_2$ (figure 4*d*). Therefore if several different templates may be present, the experimental reversal of contrast is not very informative, whatever the experimental result. Alternatively, if there are few templates, inferences about which types are present might be made by such experiments.

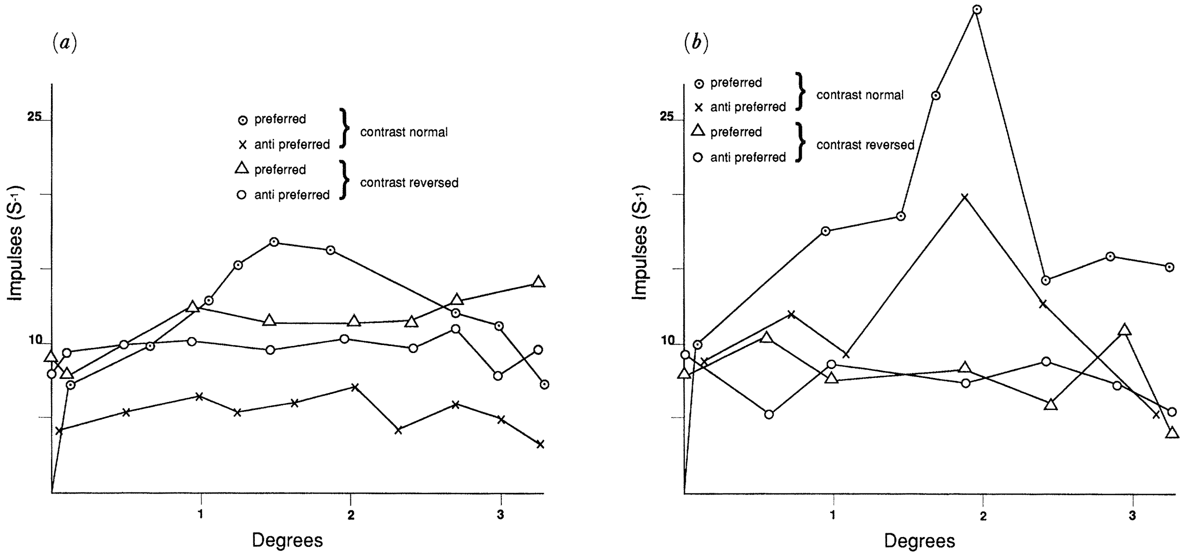

Figure 3. Responses of an H1 neuron of the fly *Calliphora* to jumps of the random-pixel pattern with and without contrast reversal at the jump. (*a*) An individual with lower spike frequency following the jump in the antipreferred direction, and not a high peak in the preferred direction without contrast reversal. (*b*) An individual with a high peak in the preferred direction for a jump of 1.8°. In (*a*) and (*b*) note the responses to contrast reversal with no motion.

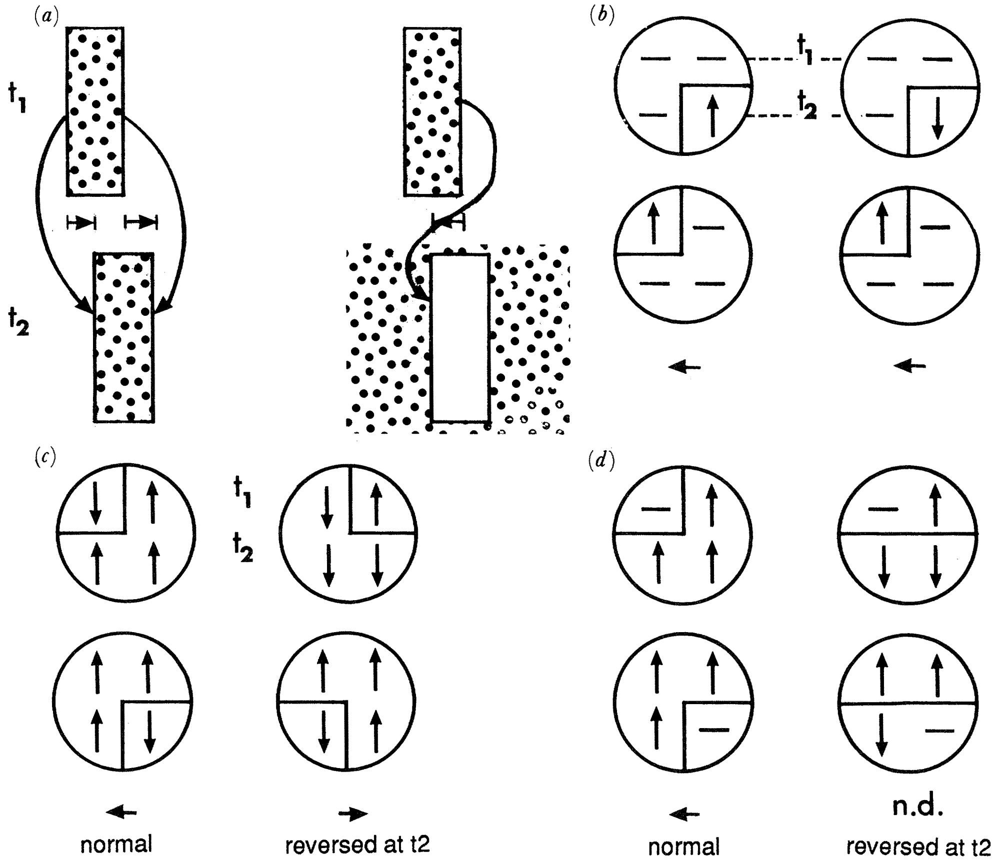

Figure 4. (*a*) Motion of a bar with and without contrast reversal. When the contrast is reversed as the bar jumps by half its width, the best correlation of an edge retaining the polarity indicates a motion the other way. (*b*) Templates of the types (−−/−↑) and (↑−/−−) are unaffected in direction when contrast is reversed at $t_2$. (*c*) Templates of the types (↓↑/↑↑) and (↑↑/↑↓) reverse their directionality. (*d*) Types (−↑/↑↑) and (↑↑/−↑) become non-directional (n.d.).

## DISCUSSION

We have a situation that is characteristic of the course of experimental science. A simple mathematical paradigm looks like a logical representation of the mechanism of motion detection that no amount of observation could refute (Kuhn 1970, p. 78). In this case it is obvious that the autocorrelation of an image with itself which is displaced various distances in space, indicates direction and is a measure of small displacements. For some images, it can measure velocity over a small range but must be calibrated for each pattern. Such a mechanism responds to the passage of each edge, and its summed response therefore depends strongly on the temporal frequency of the stimulus.

Isolated results which could not be explained appeared sporadically. Tests of optomotor neurons of the locust showed that black/white and white/black edges are processed separately (Kien 1974, 1975). Recordings from motion-sensitive neurons of the fly medulla suggested that inhibition is propagated in the anti-preferred direction (Mimura 1975). Stimulation of single fly photoreceptors in succession showed that the directional response depends upon the gradient or edge being of constant polarity when shifted across the receptor array; i.e., contrast reversal abolishes directionality for adjacent receptor pairs (Franceschini *et al.* 1989). Already 25 years ago, Thorson (1966) had suggested many model circuits that would equally well explain the optomotor responses of the locust, but he also used systems analysis with equal numbers of edges of opposite polarity which did not reveal the above anomalies.

In Canberra, the responses of fly and butterfly directionally sensitive neurons to small jumps of single edges also showed that white/black and black/white edges are processed separately, ruling out a symmetrical multiplicative system (Horridge & Marcelja 1990*a*), and that reversal of contrast at the stimulus jump abolishes the directional response to a bar that jumps. We also found that the response to changes in contrast at constant intensity does not depend on $(\text{contrast})^2$, and that responses are readily saturated to contrast (Horridge & Marcelja 1990*b*); therefore sine-wave stimuli are inappropriate.

Once it has achieved the status of paradigm, a scientific theory is declared invalid only if a better candidate is available to take its place. Recently, a theory was developed, considering all possible combinations of temporal contrast at adjacent visual axes and at successive instants as templates which respond or not to the spatiotemporal combination of inputs (Horridge 1991; Sobey & Horridge 1990). One or another of the templates in the model responds to each possible stimulus situation on each visual axis, acting collectively as a parallel distributed processing mechanism. This is a more general and versatile theory than the computational algorithms, and it more closely resembles the way that neurons function. In this model the directional detectors cannot abstract velocity, which is just another feature of a moving edge measured by collaborative responses of several non-directional templates. The results presented here, and in previous papers quoted, do not prove the templates but at least they should draw attention to the need for critical tests.

There appear to be three reasons why the idea of multiplication has been accepted for so long. First, there was little alternative in view. Secondly, in the original positive experimental data, a reversal of contrast may have resembled a phase change because a regular striped pattern was used. Also, the response as a function of contrast could have followed the lower end of an S-shaped curve which happened to fit a square law. Thirdly, the stimulus patterns contained an equal number of dark/light and light/dark edges (even a point source has this effect), so that the summed response resembled a second-order effect such as multiplication or rectification. It is difficult to design test stimuli which avoid this problem.

Looking over 35 years back to the genesis of the autocorrelation theory of motion perception in insects, it is clear that the theory has persisted because autocorrelation of the stimulus with itself is a reasonable way to abstract motion from a moving pattern, irrespective of the actual mechanism in neurons, and that a great deal of quantitative measurements of the final output are compatible with the theory. The difficulty is that curve-fitting does not prove a theory, especially when the natural system has many parallel pathways which have evolved to see motion and therefore its operation and quantitative output has necessarily been selected to generate a correct measure of the motion. It is not surprising that the final response to a stimulus that could occur naturally agrees in some respects with the predictions of correlating the stimulus with itself; any effective mechanism would do so.

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