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The Elementary Movement Detection Mechanism in Insect Vision

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The elementary movement detection mechanism in insect vision

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SUMMARY

In insects, the elementary movement detection (EMD) mechanism is based on a nonlinear asymmetric interaction between signals mediated by adjacent points of the sampling lattice of the eye. The nature of this nonlinear interaction is still somewhat controversial: whereas Schmid & Bülthoff (1988) suggested that it is inhibitory, Franceschini *et al.* (1989) reported that it is facilitatory. Despite the conflicting reports, we show that experimental evidence to date favours an inhibitory interaction. This paper attempts to resolve the conflict by disproving a hypothesis by Franceschini *et al.* (1989) suggesting that only a facilitatory mechanism can account for the response of a fly wide-field movement-detecting neuron (H1) to sequential stimulation of a pair of adjacent photoreceptors. It is shown here that the responses of a directionally selective movement-detecting neural network architecture, based on lateral inhibitory interactions, match very well the recorded responses of the fly H1 neuron.

1. INTRODUCTION

There are many reasons why animals need to detect motion; most of them utilize motion information, for example, to separate a figure from the ground, determine a three-dimensional (3-D) structure, avoid an obstacle, chase a prey, or escape a predator. Thus, nature has equipped even simple animals with directionally selective movement-detecting (DSMD) units. These units respond vigorously to motion in a particular direction, known as the preferred direction, and feebly or not at all to motion in the opposite, or null direction (Barlow *et al.* 1964; Bishop *et al.* 1968; Hausen 1981; Holden 1977; Horridge *et al.* 1965; Marchiafava 1979; Michael 1968). It is now a well-established fact that an inhibitory mechanism is responsible for direction selectivity in the vertebrate retinae. Since Barlow & Levick (1965) demonstrated that inhibition is the mechanism underlying direction selectivity in rabbit retinal ganglion cells, many investigators have confirmed their report in the rabbit and several other species (Ariel & Adolph 1985; Ariel & Daw 1982; Holden 1977; Marchiafava 1979; Michael 1968).

It has been shown that direction selectivity in retinal ganglion cells is based upon sequence discrimination between small-field synaptic subunits, or elementary movement detectors (EMDs) (Barlow & Levick 1965; Michael 1968). The initial stages of movement detection in insects also appear to be based on sequence discrimination by EMDs. Both behavioural and electrophysiological experiments suggest that movement detection takes place between adjacent channels (Kirschfeld 1972; Bishop *et al.* 1968; Horridge & Marcelja 1990; McCann 1973; Zaagman *et al.* 1978; Riehle & Franceschini 1984; Franceschini *et al.* 1989). For example, sequential stimulation, confined to pairs of identified photoreceptors in single ommatidia, induced optomotor turning reactions in the fly (Kirschfeld 1972). Riehle & Franceschini (1984) recorded a sequence-dependent response in the H1 neuron by activating two adjacent cartridges with stimulation of the photoreceptor pair (R1, R6) within a single ommatidium. In particular, they found that the sequence R1→R6 evoked an excitatory response whereas the sequence R6→R1 induced an inhibitory response or no response at all, which was in accordance with the preferred and null directions of the H1 neuron, respectively.

There have been, however, conflicting reports regarding the nature of the mechanism underlying direction selectivity in the insect visual system. Schmid & Bülthoff (1988), based on neuropharmacological coupled with electrophysiological experiments, suggested that inhibition is the mechanism mediating directional selectivity in the fly visual system, whereas Franceschini *et al.* (1989), based on electrophysiological experiments, concluded that facilitation rather than inhibition is responsible for directional selectivity. Yet an earlier report (Mimura 1972) suggests that both mechanisms are involved: facilitation in the preferred direction and inhibition in the null direction. It is our aim here to resolve the conflict.

This paper is organized as follows. In the next section, we will discuss the EMD mechanism in insect vision. Then we will present a directionally selective movement detecting neural network architecture, which could settle the conflict. Simulation results of the neural network responses to moving stimuli are

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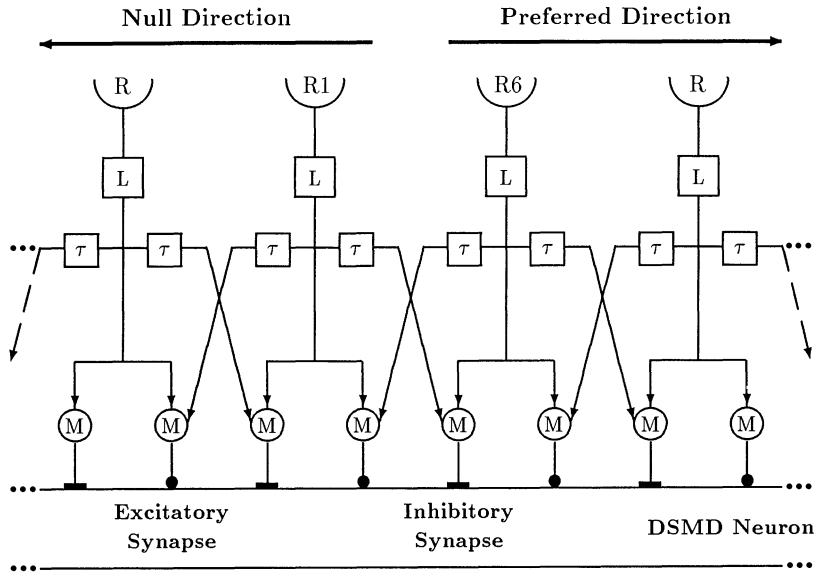

Figure 1. The DSMD neural network architecture. The DSMD neuron receives excitatory and inhibitory signals from an array of functionally identical EMDs (M-units), which differ only with respect to the orientation of their sampling bases, i.e. preferred directions. The basic information flow from the photoreceptors (R-units) to the DSMD neuron, through the lamina (L-units), is represented by a puppet. The legs of the puppet transmit signals to its knees (M-units) where they interact with the delayed signals (box τ), carried laterally by the puppet arms of the neighbouring columns. (After Bouzerdoum 1991.)

presented in § 4. The paper ends with a discussion and some concluding remarks.

2. ELEMENTARY MOVEMENT DETECTION

The primary visual system of insects is composed of a pair of compound eyes and three visual ganglia in each optic lobe, namely the lamina, the medulla, and the lobula or lobula complex, which is divided into an anterior part,the lobula, and a posterior part, the lobula plate. The medulla is the most peripheral structure in which movement detection takes place; although searched for, responses to movement have not been recorded in the lamina (DeVoe 1980; Horridge *et al.* 1965; Mimura 1975). The lobula plate, however, is regarded as the motion computation centre in some insect orders such as Diptera and Coleoptera. It is characterized by a group of wide-field directionally selective movement-detecting (DSMD) neurons (Strausfeld 1989; Hausen & Egelhaaf 1989; Hausen 1984, 1981). This group of neurons comprises several classes of tangential cells, which respond to whole-field horizontal or vertical motion. They may provide inputs to the 'slow' descending movement-detecting neurons identified recently by Horridge & Marcelja (1992) in the brains of fly, butterfly, dragonfly, and locust. One particular lobula plate DSMD neuron that has been consistently investigated for the past three decades is the H1 neuron of the fly (Bishop *et al.* 1968; Franceschini *et al.* 1989; Hausen 1981, 1984; Horridge & Marcelja 1990; Riehle & Franceschini 1984; Zaagman *et al.* 1978). It is a giant heterolateral spiking neuron which responds selectively to horizontal regressive motion. Its main function appears to be the control of insect optomotor reactions (Hausen 1981, 1984; Hausen & Egelhaaf 1989).

Although the large-field DSMD neurons of the lobula plate differ in their preferred direction and receptive field organization, they have the same functional organization and share a common network of presynaptic units derived from the medulla (Strausfeld 1989; Hausen 1981, 1984). It is not yet known whether these presynaptic units are motion sensitive or motion insensitive. It is, however, well known that the wide-field DSMD neurons receive their inputs from large retinotopic arrays of small-field elementary movement detectors (Hausen 1984; Hausen & Egelhaaf 1989). It cannot yet be decided whether these small-field EMDs reside in the medulla, lobula, or lobula plate; nevertheless, it is widely believed that they operate on the principle of a nonlinear asymmetric interaction of signals derived from adjacent cartridges of the ommatidial lattice (Kirschfeld 1972; Franceschini *et al.* 1989; Hausen 1984; McCann 1973; Riehle & Franceschini 1984).

There are mainly two general schemes for implementation of the nonlinear asymmetric interaction: one is facilitatory, the other is inhibitory. The facilitatory mechanism selects the preferred direction by detecting a specific conjunction of excitation. The inhibitory mechanism, however, works by rejecting the null stimulus (non-preferred motion) by a veto operation. Which of these two general schemes is responsible for direction selectivity in the insect visual system is still the source of some controversy. By combining neuropharmacology and electrophysiology, Schmid & Bülthoff (1988) demonstrated that the inhibitory neurotransmitter gamma-amino-butyric acid (GABA) is responsible for direction selectivity in

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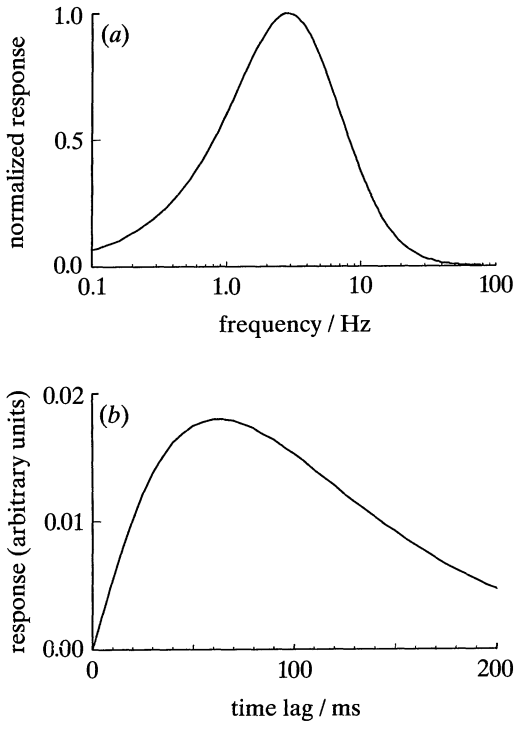

Figure 2. Characteristic responses of the neural network model of figure 1. (*a*) Normalized response as a function of the temporal frequency of a moving sinusoidal grating. (*b*) Response as a function of the time lag between the onsets of two sequential flashes.

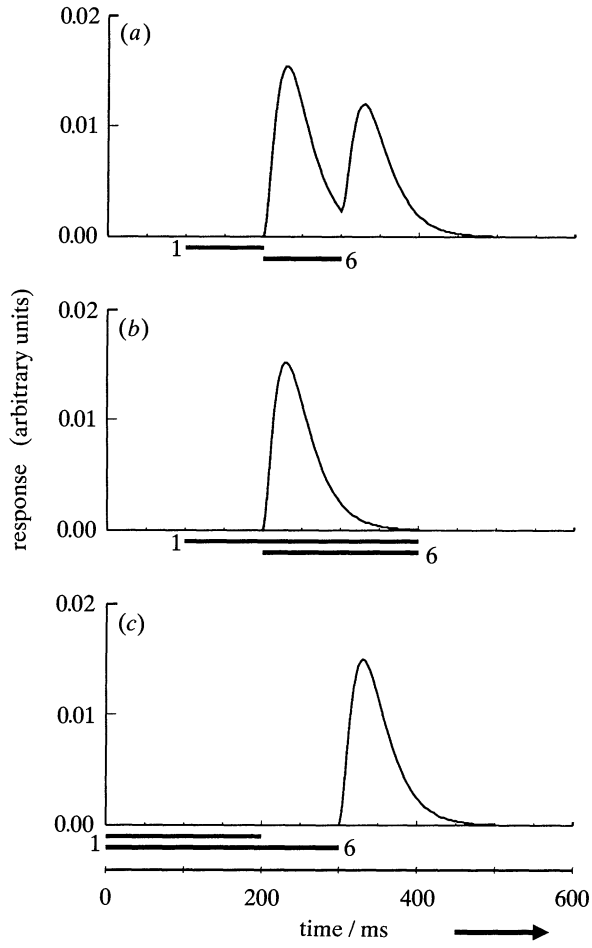

Figure 3. Response of the neural model of figure 1 to stimulation of the receptor pair (R1, R6) with a sequence of flashes mimicking motion in the preferred direction. The horizontal bars under each plot indicate the time and duration of stimulation of R1 and R6.

the fly. Their experiments showed that the direction selectivity of H1 was abolished by injection of picrotoxin, an antagonist of (GABA), into various parts of the brain; the direction selectivity of H1 was restored by injection of GABA. They hence concluded that the mechanism mediating direction selectivity in the fly is inhibitory. Osorio (1986) has reported involvement of the inhibitory process in the mechanism of direction selectivity of a group of movement detectors in the locust medulla.

Egelhaaf *et al.* (1990) have suggested that the abolishment of the H1 directional selectivity by injection of picrotoxin is due to blocking of the inhibitory synapses feeding the H1 neuron and not to blocking of the inhibitory interactions at the EMD level. Their conclusion was, however, based on the assumption that the EMD input channels are linear. This may not be true since it is believed that the EMD inputs are mediated by ON or OFF transient channels (Franceschini *et al.* 1989; Horridge & Marcelja 1990). Furthermore, in their experiments Egelhaaf and his colleagues injected picrotoxin into the fly's haemolymph, which resides next to the third visual ganglion. Thus, it is possible that not all inhibitory synapses at the EMD level were blocked. Schmid & Bülthoff's experiments showed that, by injection of picrotoxin into the medulla, the spike activity of the H1 neuron was completely suppressed for a short period. This can happen only if the inhibitory interactions at the EMD level are blocked and the inhibitory synapses feeding the H1 neuron are not; for then the H1 neuron receives from the EMDs signals which are equal in magnitude and opposite in polarity (see figure 1).

Franceschini and his colleagues showed that microstimulation of a pair of photoreceptors having adjacent visual axes (R1 and R6), singly or simultaneously, does not elicit any response unless the stimulus intensity is very high. But when stimulation of R6 is preceded by that of R1, the H1 neuron fires. Furthermore, the evoked response was always time locked with the second flash (Riehle & Franceschini 1984; Franceschini *et al.* 1989). They concluded, therefore, that the priming flash on R1 must have exerted a facilitatory influence rendering the secondary flash on R6 more effective. By contrast, Mimura (1972) reported that both excitatory and inhibitory processes subserve directional selectivity. He suggested that the inhibitory process is activated in the null direction, whereas the excitatory process is activated in the preferred direction. In the next section we will present one possible neural network architecture which could resolve the conflict.

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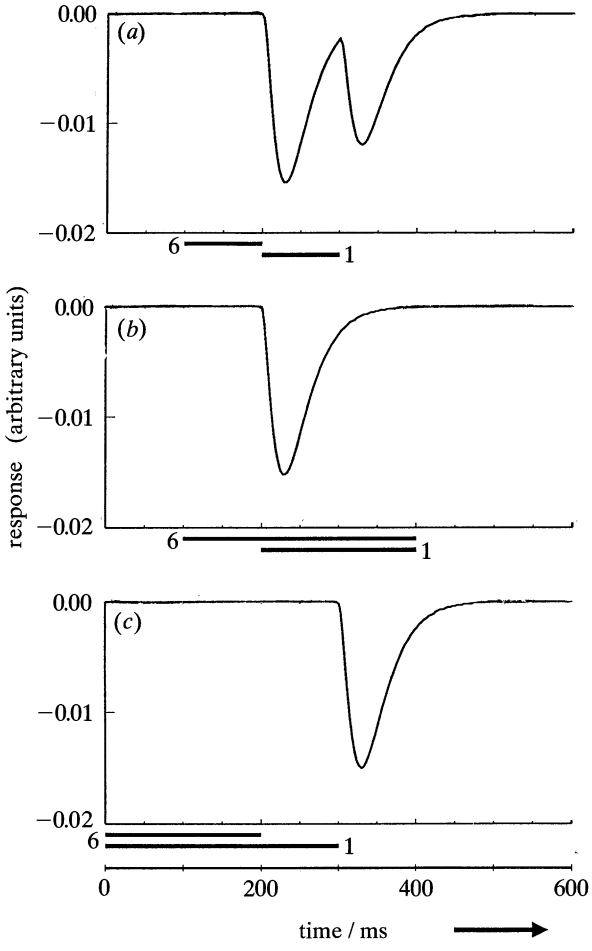

Figure 4. Response of the neural model of figure 1 to stimulation of the receptor pair (R1, R6) with a sequence of flashes mimicking motion in the null direction. The horizontal bars under each plot indicate the time and duration of stimulation of R1 and R6.

3. THE NEURAL NETWORK ARCHITECTURE

The visual system of insects is characterized by a retinotopic organization. The three visual ganglia are organized into parallel synaptic compartments or columns that are retinotopically connected. Both lamina and medulla contain as many columnar neuropils as there are ommatidia in the retina. The medulla, where movement detection first takes place, is also characterized by an extensive network of lateral connections. Each synaptic column in the lamina, known also as an optic cartridge, receives direct inputs from a set of photoreceptors sharing the same field of view, and projects outputs to one medullary column only. The periodicity of the lamina and medulla, however, is coarsened by the columnar neurons of the third visual ganglion, the last orderly projection of the visual field; each column in the lobula or lobula plate receives inputs from several medullary columns. For a detailed neuroanatomical description see, for example, Strausfeld (1989, 1976); Hausen & Egelhaaf (1989); Hausen (1984, 1981).

The conflict over the nature of the EMD mechanism may be resolved by considering the spatial arrangement and nature of synaptic contacts of the input elements conveying motion signals to the wide-field tangential cells. There exists convincing evidence that these tangential neurons receive both excitatory and inhibitory inputs from large retinotopic arrays of small-field EMDs which possess opposite orientations, or preferred directions (Hausen 1981, 1984; Hausen & Egelhaaf 1989; Franceschini *et al.* 1989). Consequently, movement in a particular direction (the preferred direction) activates mainly the excitatory inputs, whereas movement in the reverse direction excites the inhibitory ones. This confirms Mimura's report since we believe that the units he recorded from were mostly large-field DSMD neurons. Although his report is accurate, it does not concern the mechanism underlying direction selectivity at the level of the small-field movement detectors. Franceschini and his colleagues, however, have apparently reached their conclusion by assuming that the photoreceptor pair (R1, R6) activates only one pair of EMDs having opposite orientations and conveying antagonistic signals to the H1 neuron. This, however, does not explain the fact that stimulating either receptor singly induced an excitatory response when the stimulus intensity was very high (figure 2G in Riehle & Franceschini 1984); for if stimulation of one receptor leads to an excitatory response, stimulation of the other receptor must induce an inhibitory response.

Figure 1 illustrates the basic functional structure describing the flow of motion information from the photoreceptors to a DSMD neuron. The DSMD neuron receives excitatory and inhibitory signals from an array of functionally identical EMDs (M-units) which differ only with respect to the orientation of their sampling bases, i.e. their preferred directions. The basic information flow from a lamina cartridge (box L) to the DSMD neuron is represented by a puppet. The legs of the puppet transmit signals to its knees (M-units) where they interact with the delayed signals (box τ), carried laterally by the puppet arms of adjacent columns.

The interaction at the knees is of the veto type; nevertheless, it can still explain the results obtained by Franceschini *et al.* For example, stimulating two photoreceptors, singly or simultaneously, activates synchronously an equal number of EMDs conveying opposite signals which lead to mutual cancellation; hence, no response is evoked in the DSMD neuron. By contrast, when sequentially flashing a pair of adjacent receptors, a delayed signal from the first flash, carried laterally, vetoes one of the excitatory signals generated by the second flash. This upsets the balance between the activated excitatory and inhibitory synapses, thereby inducing either an excitatory or an inhibitory response, depending upon whether the flash sequence mimics motion in the preferred direction (R1→R6) or motion in the null direction (R6→R1). Bacause the signals generated by the first flash are opposite and cancel each other, the response of the DSMD neuron is always time locked with the onset of the second flash; unless, of course, the excitatory and inhibitory synapse are not perfectly balanced, in which case a single flash induces excitation if the excitatory synapse is dominat-

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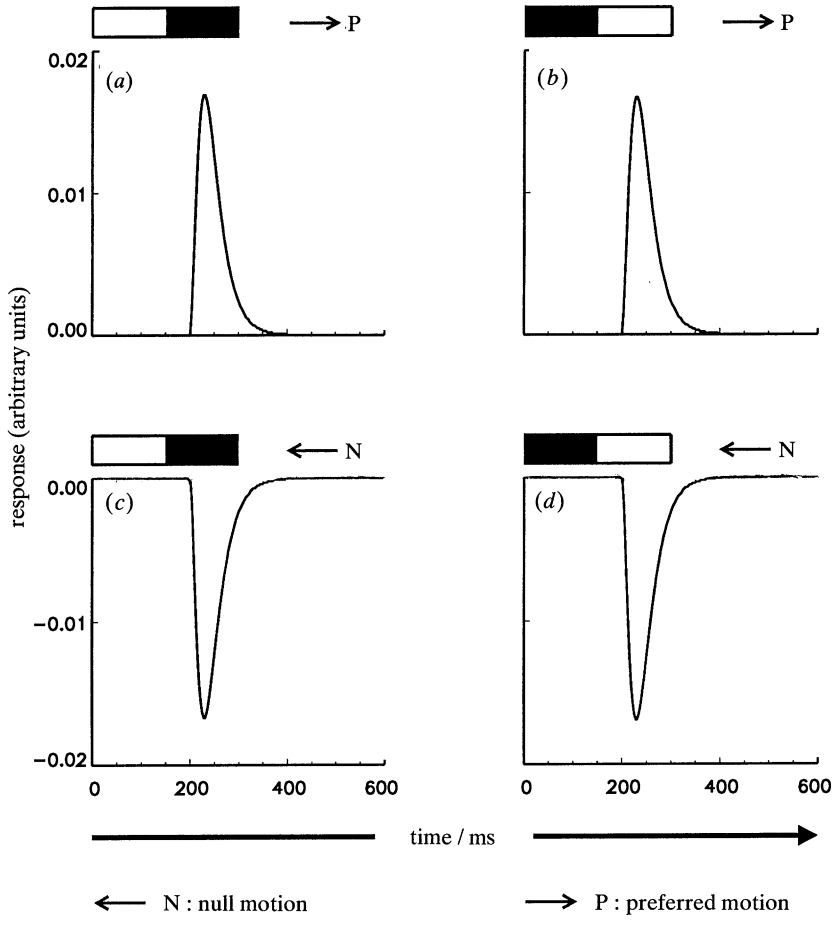

Figure 5. Response of the neural network to a jumping edge. At $t=0$ the edge, whose orientation (black–white or white–black) is indicated above the plot, appears over the receptor pair (R1, R6). After 200 ms, it jumps by one receptor (*a*) and (*b*) to the right, or (*c*) and (*d*) to the left. The responses are directional regardless of edge orientation.

ing. This shows that inhibitory interactions at the EMD level can explain the experimental results of Franceschini *et al.*; hence, it cannot be concluded, simply on the basis of their results, whether the mechanism mediating directional selectivity is facilitatory or inhibitory. To further support this claim, we will next examine the responses of the neural network model of figure 1 to different types of moving objects, and show that they closely match those of the H1 neuron.

4. THE NEURAL NETWORK RESPONSE

We now present simulation results which show that our neural network model, based on an inhibitory interaction, can account for the recorded responses of the H1 neuron to a variety of moving stimuli. In the simulations, the input signal was passed through a log transformation, representing the transformation at the photoreceptor level. A laminar unit (L-Unit, figure 1) was simulated as the subtraction of the receptor output from the output of a low-pass filter. This operation, with the appropriate time constant, has the effect of inverting the photoreceptor response, a function performed by the large monopolar cells (LMCs) of the lamina (see, for example, Laughlin 1989). Then, after the signal is magnified, it is rectified to produce transient responses of ON and OFF nature; it has now become apparent that in the insect visual system the motion signals are carried through separate ON- and OFF-channels (Franceschini *et al.* 1989; Horridge & Marcelja 1990; Riehle & Franceschini 1984). The outputs of the ON- and OFF-channels are low-pass filtered and passed laterally to interact, respectively, with the outputs of the ON- and OFF-channels in the adjacent columns. The interaction at the knees of the puppet (M-Unit, figure 1) is of the shunting inhibitory type. Numerous studies suggest that the dominant factor in GABA-mediated postsynaptic inhibition is of the shunting type, for the GABA site is thought to reside on chloride (Cl) channels, whose equilibrium potential is close to the membrane resting potential in some neurons. If we hypothesize that the membrane resting potential is equal to the equilibrium potential of the Cl channels, then the response $m(t)$ of an M-Unit is described by

$$dm/dt = x(t) - am(t) - cy(t)m(t), \qquad (1)$$

where a is a positive constant, representing the passive decay rate of the membrane voltage $m(t)$, $x(t)$ is the output of the ON or OFF transient channel, $y(t)$ is the

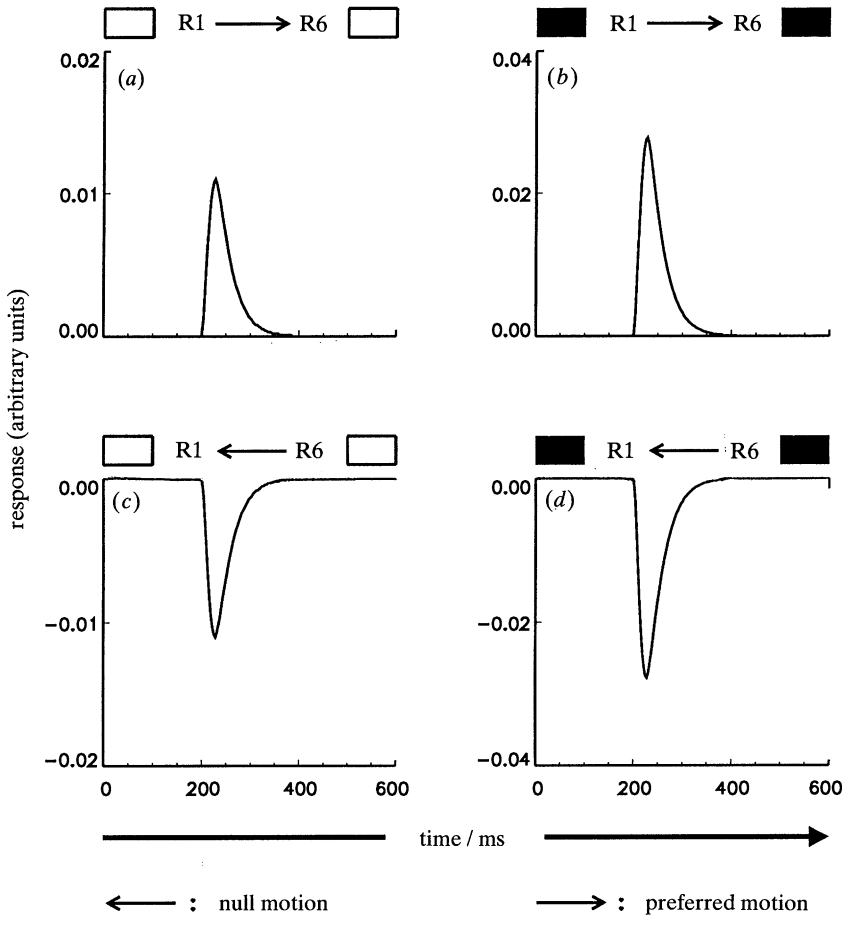

Figure 6. Response of the neural network to a jumping thin bar. At $t = 150$ ms, a bright or dark bar appears over one receptor, and disappears at $t = 175$ ms. Then, at $t = 200$ ms, the same bar reappears over a neighbouring receptor (*a*) and (*b*) to the right, or (*c*) and (*d*) to the left. The responses are directional regardless of bar contrast.

signal from the lateral branch, and c is a positive constant representing the connection strength; for a derivation see, for example, Bouzerdoum (1991).

The spatial integration of local movement signals at the level of the wide-field DSMD neurons is, in principle, almost linear if the activation of single input channels produce only minute voltage changes at the output sites of the dendrites. If we assume it to be linear, then the effects of the excitatory and inhibitory synaptic contacts of the individual EMDs with the DSMD neurons are, respectively, additive and subtractive. Thus, if we denote by $m_{E_j}(t)$ the signal mediated by the jth excitatory synapse and by $m_{I_j}(t)$ the signal mediated by the jth inhibitory synapse, then, to first order, the response of the DSMD neuron is given by

$$R(t) = \sum_j m_{E_j}(t) - m_{I_j}(t), \qquad (2)$$

where the summation operation is carried over all j indices for both ON and OFF channels, and the rates of change of $m_{E_j}(t)$ and $m_{I_j}(t)$ are given by equation (1).

The parameters a and c and the time constants of the low-pass filters were chosen so as to account for the characteristic response of the H1 neuron to a moving sinusoidal grating, and to sequential flashing of two adjacent receptors. Zaagman *et al.* (1978) recorded from the H1 neuron of the blowfly *Calliphora erythrocephala* the response to a moving sinusoidal pattern; they found that the steady-state response increases with temporal frequency to peak at approximately 4 Hz, and falls off sharply above this value. In fact, all lobula plate DSMD neurons that have been tested so far exhibit similar responses; the response range covers about 3 log units, and the response peaks are consistently found at 1–5 Hz (Hausen 1981, 1984; Horridge & Marcelja 1992). Franceschini *et al.* (1989) recorded from the H1 neuron of *Musca domestica* after sequentially flashing the photoreceptor pair (R1, R6). The response increased with the time lag between the onsets of the two flashes to a peak value near 50 ms, after which the response decreased slowly; the neuron ceased to respond when the time lag was around 230 ms. Figure 2 presents the response of our neural network model as a function of temporal frequency of a moving sinusoidal grating (figure 2*a*), and as a function of the time lag between the onsets of two sequential flashes on adjacent receptors (figure 2*b*). The network parameters used to obtain these responses are: $a = 0.08$ ms^{-1}, $c = 0.05$, and 50 ms as time constant for the low-pass filters. These values of the model parameters were determined by visual inspec-

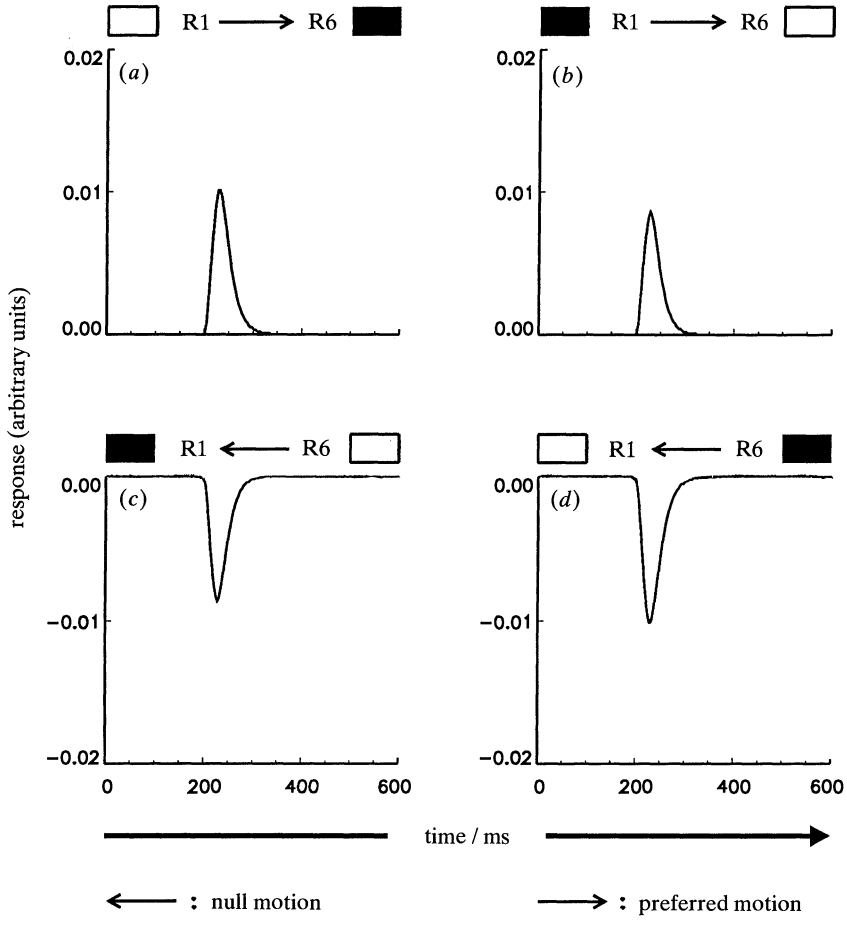

Figure 7. Response of the neural network model to contrast reversal. The stimulus conditions are the same as those of figure 6, except for reversal of contrast at the jump, i.e. a black bar becomes white and vice versa. The responses are directional despite contrast reversal.

tion, and were used in all the simulations throughout this paper. We should note that the response here represents the actual membrane voltage, or the deviation of the membrane voltage from the resting potential, rather than the firing rate of the neuron. To obtain the response as firing rate, the output of the DSMD neuron should be passed through a rectifying nonlinearity.

(*a*) *Response to sequential flashing*

Simulations of the neural network responses to light flashes showed that stimulating a pair of receptors singly or synchronously does not evoke any response in the DSMD neuron (results not shown). However, stimulating the two receptors with a sequence mimicking motion in the preferred direction (R1→R6) induces an excitatory response (figure 3). Note that the response of the network is always time locked to the onset or offset of the second flash. Note also that the response to a sequence of nonoverlapping light flashes, with a short time lag between their onsets, consists of two prominent peaks (figure 3*a*); the first peak is caused by the ON-response (figure 3*b*) and the second one by the OFF-response (figure 3*c*). The responses of the network to sequences mimicking motion in the null direction (R6→R1) are shown in figure 4. These responses are equal but of opposite polarity to those shown in figure 3; they are inhibitory responses.

These responses are similar to those recorded by Franceschini *et al.* (1989) from the H1 neuron. Our results confirm that not only a facilitatory but also an inhibitory mechanism can explain their results. Furthermore, responses similar to those recorded by Schmid & Bülthoff (1988), when injecting the lobula plate with picrotoxin, have also been obtained (not shown). In particular, when partly blocking the inhibitory synapses feeding the DSMD-neuron (figure 1), the response to the null sequence decreases in magnitude and then reverses sign; it becomes equal to the preferred response when all synapses inhibiting the DSMD-neuron are blocked.

(*b*) *Response to jumps*

The responses of the neural network to an object (an edge or a bar) jumping over a distance equal to the distance between neighbouring receptors, are presented in figures 5 and 6. Figure 5 shows that, regardless of its orientation, an edge jumping in the preferred direction induces excitation (figure 5*a*,*b*), whereas an edge jumping in the null direction causes

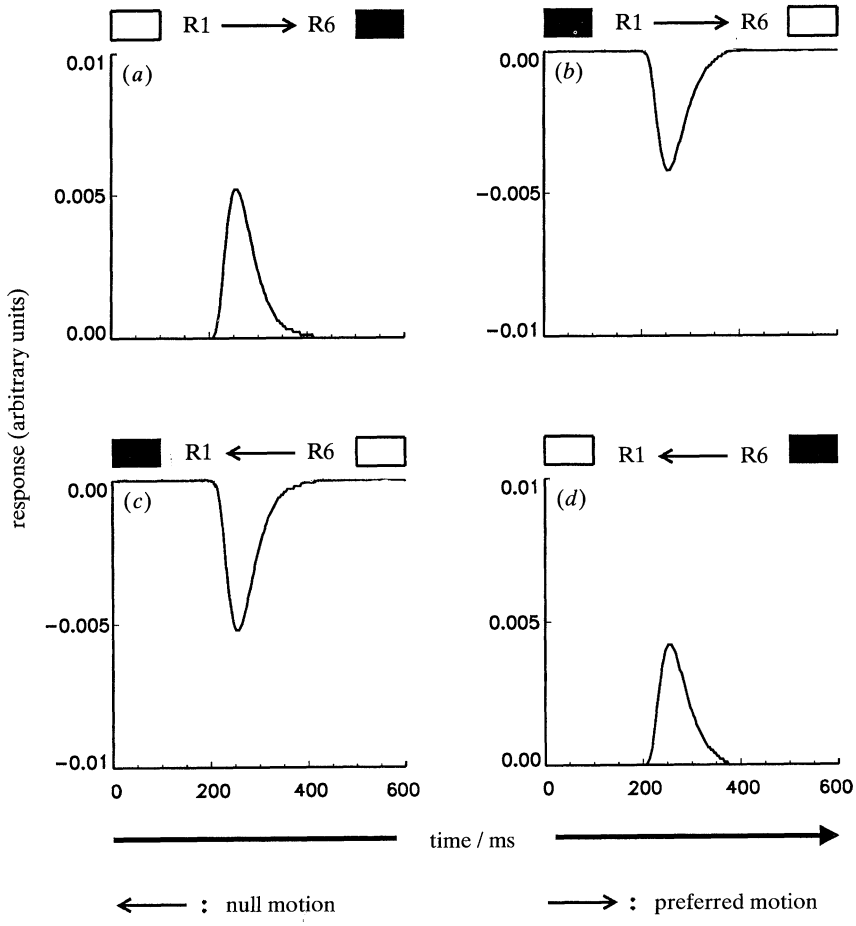

Figure 8. Response of the neural network to contrast reversal. At $t = 50$ ms, a bar appears over one receptor. Then, at $t = 200$ ms, the bar reappears, with its contrast reversed, over a neighbouring receptor. Here, (*b*) a jump in the preferred direction can cause a negative response, and (*c*) a jump in the null direction can cause a positive response.

inhibition of the DSMD-neuron (figure 5*c*,*d*). The dependence of directionality upon contrast was tested by jumping a thin light or dark bar in the preferred and null directions. The results are presented in figure 6, which shows that the preferred direction of the neural network model (figure 1) does not depend on the sign of contrast. In other words, both a bright and a dark bar evoke an excitatory response when jumping in the preferred direction (figure 6*a*,*b*), and an inhibitory response when jumping in the null direction (figure 6*c*,*d*). Notice, however, that the dark bar elicits a stronger response than the bright bar.

This phenomenon has also been observed in the recorded responses of the H1 neuron of *Calliphora stygia* by Horridge & Marcelja, who also found that the directionality of the H1 neuron does not change with edge orientation or bar contrast (figures 2 and 5; Horridge & Marcelja 1990). However, they found that the H1 neuron may lose its directionality by reversing the contrast of the jumping bar. More specifically, when there is a time lag during the jump the H1 neuron preserves its directionality (figure 5; Horridge & Marcelja 1990), but when there is no time lag, i.e. the second bar appears, contrast reversed, simultaneously with the disappearance of the first one, the H1 neuron seem to lose its directionality (figure 6; Horridge & Marcelja 1990).

The responses of our neural network to bars which reverse contrast at the jump are depicted in figures 7 and 8. Despite contrast reversal, the network preserves its directionality when there is a time lag between the disappearance and reappearance of the bar (figure 7). Yet, the network may lose its directionality if there is no time lag during the jump (figure 8). Although the onset of the dark bar followed by the offset of the light bar constitutes a preferred OFF-sequence in figure 8*b*, the response is inhibitory. The reason for reversal of directionality in (figure 8*b*,*d*) is that the sequence caused by the onset and offset of the black and white bars, respectively, evokes only a weak excitatory (figure 8*b*) or inhibitory (figure 8*d*) response in the DSMD neuron, for the time lag of the sequence is too long (150 ms). This weak response is dominated by an opposite ON-response induced by the simultaneous appearance and disappearance of the white and black bars, respectively. As the ON-response caused by the offset of the black bar is not exactly the same as the ON-response caused by the onset of the white bar, there is an imbalance between the excitatory and inhibitory signals fed to the DSMD neuron: two adjacent

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EMDs are inhibited simultaneously, but their two immediate neighbours are not, which gives rise to an excitatory or inhibitory ON-response. The opposite happens when reversing the contrast of the bars (figure 8*a*,*c*).

5. DISCUSSION AND CONCLUSION

The elementary movement detector is the minimum prerequisite structure for directionally selective detection of motion in the visual field. It is based on the principle of a nonlinear asymmetric interaction between adjacent channels. The initial stages of movement detection in insects appear to be based on sequence discrimination by EMDs. There have been, however, conflicting reports regarding the nature – facilitatory or inhibitory – of the mechanism mediating the asymmetrical interaction at the level of insect small-field movement detectors. It was argued here that experimental evidence to date favours an inhibitory interaction (Schmid & Bülthoff 1988; Osorio 1986). The suggestion of Franceschini *et al.* (1989) that an inhibitory interaction cannot explain the responses of the H1 neuron to micro-stimulation of a pair of adjacent photoreceptors was disproved by showing that a neural network model, based on an inhibitory interaction, can account for their experimental results.

Our model was shown to account for the steady state as well as the transient responses of insect DSMD neurons (see also Bouzerdoum 1991; Bouzerdoum & Pinter 1992). Except for some minor discrepancies, the responses of our model agreed very well with those recorded from the fly H1 neuron. The discrepancies are partly due to the choice of model parameters such as the filter time constants; the data we tried to fit are from different fly species, yet we used the same model parameters. For example, the responses recorded by Horridge & Marcelja (1990) from *Calliphora stygia* are more sluggish than those recorded by Franceschini *et al.* (1989) from *Musca domestica*; our model parameters were, however, chosen to fit the latter results. Another source of discrepancy is that our model responses represent the deviations of the membrane voltage from the resting potential rather than the firing rates of the neuron. This, however, can easily be fixed by passing the output of the neural network through a rectifying nonlinearity. We have also assumed that the excitatory and inhibitory channels (EMDs) conveying signals to the DSMD neuron are exactly the same, i.e. they share the same parameter values. However, it may not be possible for nature to duplicate exactly a neural structure several thousand times; there is evidence that the DSMD neurons in the lobula plate of the fly do not receive equal signals from the excitatory and inhibitory EMDs (Egelhaaf *et al.* 1989). This would explain why stimulation of a single receptor evokes a response in the H1 neuron when the stimulus intensity is very high (Riehle & Franceschini 1984).

In conclusion, elementary movement detection is based on sequence discrimination between adjacent subunits. In insects, the mechanism of sequence discrimination is probably caused by lateral interactions of the inhibitory type; this phenomenon is simply known as directional lateral inhibition. Although we cannot conclusively determine, on the basis of our results solely, whether the EMD mechanism in insects is facilitatory or inhibitory, these results coupled with the experimental data of Schmid & Bülthoff (1988) strongly suggest that it is inhibitory. More conclusive experiments are required though to unravel the mystery of the EMD mechanism in insect vision.

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