

A Neuronal Circuitry for Relative Movement Discrimination by the Visual System of the Fly

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We propose the basic structure of a neuronal circuitry possibly underlying the detection of discontinuities in the optical flow by the visual system of the housefly. The main features of the circuitry are: binocular cells summate elementary movement detectors over a large visual field and inhibit each one of them; inhibition is of the shunting type, with an inhibitory equilibrium potential very near the resting potential. A specific model implementing our proposal accounts for all the behavioral data on relative movement discrimination, including the characteristic dynamics of the response.

Motion in the visual world generates a distribution of apparent velocities on the eyes. Discontinuities in this "optical flow field" are a good indication of object boundaries and can be used to segment images into regions that correspond to different objects [2, 5]. In particular, the relative movement of an object against a background can be used to reveal its presence and to delineate its boundaries. The human visual system is very efficient at exploiting this fact [6]. Quite similarly, a fly is able to detect and discriminate an object that moves relative to a ground texture [13, 3].

Behavioural Analysis

A behavioral analysis has already led to a characterization of the algorithm used by the fly to perform this computation, which amounts indeed to the detection of discontinuities in the optical flow [9, 11]. We measured the torque response of a housefly to a textured small figure oscillating sinusoidally with a certain frequency and amplitude in front of a similar ground texture. The latter was also oscillated with the same frequency and a given phase in front of

one or both compound eyes. Flies usually fixate, i.e. fly towards, a small contrasted object on a white background. Similarly, detection of a figure in front of a ground can be seen in the torque response of the fly as a fixation attempt "superimposed" on the usual optomotor response (which follows the oscillatory movement of the ground). Under normal conditions, the housefly optimally detects the figure for phase 90° and 270° ; detection decays from 90° (270°) to 180° (0°) where it is negligible (in the time-averaged reaction). In the absence of a ground pattern the position-dependent response of the fly is mostly due to asymmetric movement detectors (and in part to flicker detectors, their relative importance being set by the time course of the stimulus [14]). The analysis of the figure-ground discrimination task established that the corresponding algorithm relies on an inhibitory multiplication-like operation between the elementary movement detectors stimulated by the ground texture and the figure. This interaction is, at least in our time-averaged experiments (at 2.5 Hz oscillation frequency), symmetric, i.e. movement back-to-front (regressive) is equally effective as movement front-to-back (progressive) in inhibiting the reaction to both progressive and regressive movement.

Constraints on the Neuronal Circuitry

In this paper we wish to suggest the basic structure of a neuronal circuitry for figure-ground discrimination via relative movement by the visual system of the fly *Musca domestica*. This circuitry may be located in the lobula complex whose anatomy and physiology are suggestive of the major aspects of our model. Whereas we were previously restricted to the analysis of the time-averaged behaviour, we have now measured the fine dynamics of the torque response at the onset and in the stationary phase of relative movement. Two main results have been thus obtained:

1) Since the kinetics of the response is a characteristic signature for every specific phase condition, we were able to confirm that the figure-ground effect exists not only under binocular but also under monocular stimulation by the ground texture. Rather surprisingly, the dynamics of the fly's torque is basically the same if figure and ground are oscillated in front of the right eye (ipsilateral stimulation) or if the figure oscillates in front of the right eye and the ground texture in front of the left eye (contralateral stimulation).

2) The torque response of the fly follows the oscillation of a given pattern, as it is well known from studies of the optomotor behaviour. Our data clearly show that the amplitude of the response increases with the movement amplitude whereas it is almost independent from the dimensions of the pattern, suggesting a quite specific gain control mechanism. Similarly, the effect of the small figure in determining the phase of the optomotor response is as large as the ground's despite their different areas.

Full details of these and further experiments will be published elsewhere. They have prompted us to consider a neural circuitry implementing our algorithm and obeying the following constraints: 1) The circuitry should automatically provide a gain control mechanism for the overall optomotor reaction. 2) The (inhibitory and nonlinear) interaction between movement detectors is not realized through a lateral inhibitory network but rather through large field-movement-selective neurons inhibiting elementary movement detectors. 3) The model should reproduce the characteristic dynamics of the response for all phases between figure and ground and for the various types of binocular and monocular stimulations.

Neuronal Circuitry

We wish to put forward a simple circuitry satisfying these restrictions. The full binocular circuitry is outlined in Fig. 1. The circuitry has a retinotopic array of elementary movement detectors as its input. We have made the usual assumption that all cells only carry positive signals: in particular, detectors for progressive movement are separate from the detectors for regressive movement. Large-field cells (S_L and S_R) summate the elementary movement detectors over a large part of the visual field and receive a similar contralateral input. They inhibit through shunting inhibition the single elementary detectors, irrespectively of their preferred direction. All movement detectors are then summated by another large-field cell (X_L and X_R). Before summation, each input undergoes a nonlinear transformation like a squaring operation, representing either the nonlinear

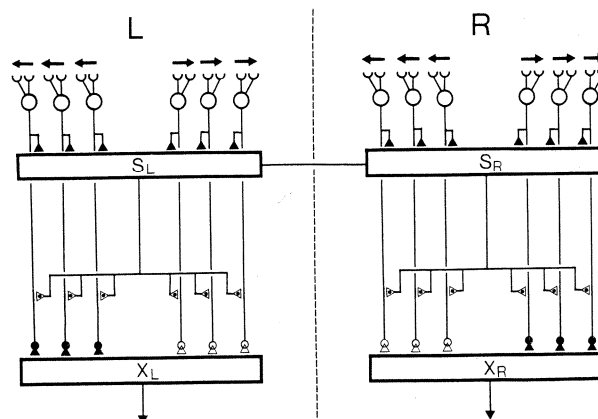


Fig. 1. The skeleton of the neuronal circuitry proposed in the paper, for the right (R) and for the left (L) eye. A retinotopic array of elementary movement detectors serves as input to the circuitry. In the right eye a pool neuron (S_R) summates the movement detectors responding to progressive (regressive) movement, as well as the input from its contralateral homologue (S_L). Its output is assumed to undergo a saturation effect (modeled by taking a fractional power—0.6—of it) and to shunt each elementary movement detector via presynaptic inhibition. The synapses involved (\bowtie) should therefore inhibit (opening ionic channels with an equilibrium battery close to the resting potential) the output terminal of each elementary movement detector. The output cell X summates the progressive (excitatory, \bullet) and the regressive movement detectors (inhibitory, \ominus). Progressive channels have a higher amplification than the regressive ones, possibly because of the different ionic batteries. The synapses on the X cell are assumed to operate with a nonlinear input-output characteristic, leading to postsynaptic signals that are the square of the inputs. Not shown here and not simulated in Fig. 2 is the transformation on the X cell output by a feedback loop including a low-pass filter in its path, leading to the DC shift in the response to the onset of relative movement. Several features of this model could be changed, as explained in the text, without changing its basic properties

presynaptic-postsynaptic characteristic at the synapse (see for instance [7]) or local active properties of the postsynaptic membrane. The last cells (X_L and X_R) would then directly drive the behavioural response. Extensive computer simulations suggest that the basic features of our model are so far sufficient to account well for all the main properties of the figure-ground effect. Figure 2, for instance, shows the computed response for two characteristic phase situations (0° and 90°). The comparison with the behavioural torque response is indeed satisfactory in all experimental situations, including the relevant time-averaged responses discussed by Reichardt and Poggio [11]. Among the main properties of the behavioural response which are accounted by the model of Fig. 2, we list the following ones: a) the amplitude of the optomotor response is rather invariant for the size of the pattern but increases with increasing velocity; b) a figure oscillating with 0° phase but a smaller (larger) amplitude than the ground induces a repulsion (attraction) in

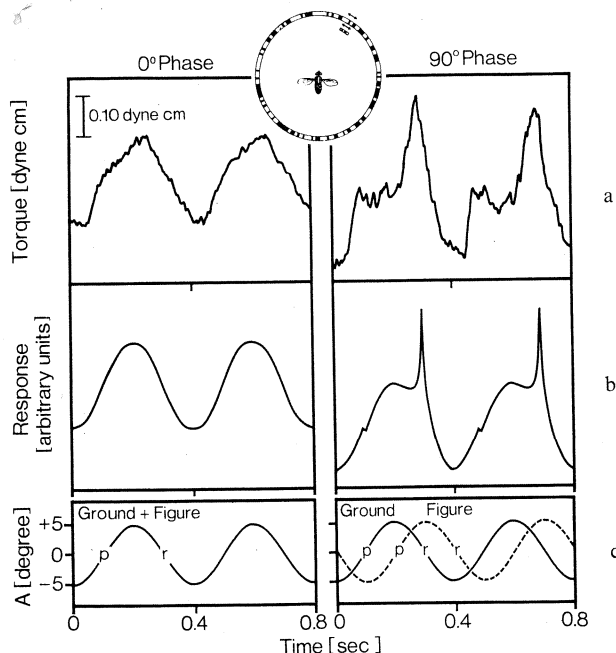


Fig. 2. A small textured stripe (12° width) is sinusoidally oscillated in front of a texture background (see inset) with an amplitude of $\pm 5^\circ$ and a frequency of 2.5 Hz. (a) The torque generated by the fly for 0° (left) and 90° (right) phase shift between figure and ground. (c) The actual time course of the stimulus (p and r denote progressive and regressive motion on the right eye). A is the angular position relative to the stripe mean position $\Psi = 30^\circ$ (right eye). (b) The output of the model of Fig. 1 in arbitrary units. We have assumed that the output of the elementary movement detectors follow closely the sinusoidal stimuli. The output of the simulation has been shifted by a fixed phase to account for the (unknown) phase shift of the movement detectors' signal. The experiments (as the simulation) refer to the stationary phase of the response, at least 1 sec after the onset of relative motion. For 90° phase shift there is a clear positive DC component (not shown here) in both the experimental data and the model simulation

the fly's response; c) there is no (time-averaged) attraction — i.e. no fixation attempt — if the figure is stationary and only the ground texture moves; d) a small screen between figure and ground does not affect the response; e) finally, dynamics and DC values of the torque can be accurately reproduced for monocular and binocular stimulation at all phases.

The model presented in Fig. 1 serves to illustrate the two critical features of the circuitry we propose: 1) the inhibition between movement detectors required by our analysis [11] is mediated by large-field cells with ipsilateral and contralateral inputs from elementary movement detectors; 2) the multiplication-like characteristic of this inhibitory interaction is implemented by inhibition of the shunting type, which is probably presynaptic [8] to the output cell and involves the opening of ionic channels with an equilibrium potential near the resting potential. Another possibility is postsynaptic inhibition of the type

proposed by Torre and Poggio [12]. In the latter case a terminal of the S cell and of a single movement detector should synapse close to each other on a third neuron, the S cell being inhibitory and the movement detector being excitatory. We wish to point out that shunting inhibition is probably the mechanism used by the nervous system to implement a multiplication-like operation [10], as it is required in the figure-ground and in the directional movement algorithms.

We regard these two features as critical. Experimental evidence against any one of them would seriously undermine our proposal. All other aspects of our model are much more open and are not yet uniquely determined by the data available to us. In particular, inhibition is not necessarily of the forward type, as in the specific model of Fig. 1. Computer simulations of recurrent schemes in which the S_L and S_R cells shunt the single movement detectors prior to summation, suggest that such models could reproduce satisfactorily the main properties of the forward scheme. Similarly, the synaptic nonlinear amplification of the single channels (see Fig. 1 and legend) is probably not an essential feature of the circuitry. In the model of Fig. 1 it is responsible for the "spiky" shape of the response at 90° (see Fig. 2), characteristic for behaviour of *Musca*. All other properties, however, can be reproduced without it. All time-averaged responses, in particular, can be fully accounted for in terms of just shunting inhibition without further nonlinearities, consistently with a previous analysis [11]. Interestingly, the fruitfly *Drosophila* [1] and probably the blowfly *Calliphora* (according to our preliminary experiments) do not show such a "spiky" behaviour. Their response could be simulated by the model of Fig. 1 with linear synapses on the X cells. Synapses with either linear or nonlinear characteristics are well known (see [8]); furthermore, the degree of nonlinearity strongly depends on the value of the presynaptic resting potential [7]. In the case of a recurrent scheme with linear synapses the response of the X cell would mirror the activity of the ipsilateral S cell. We cannot exclude that nonlinear synapses on the S cells may also produce a "spiky" response, although instability problems arise which require a careful analysis.

Discussion

Additional experiments are needed to clarify the open aspects of our proposal. Electrophysiological data will play an especially important role. Intracellular recordings from identified horizontal cells in the lobula plate of *Calliphora* (H cells, see [3]) have already revealed that these cells seem to behave as the X cells of our model with recurrent shunting inhibition and linear

synapses (on the X cells). They show clear influence of the figure-ground phase and gain control properties for the size of the pattern, similarly to the behavioural response. Thus, one may speculate that their activity may be rather close to the behavioural response of *Calliphora*, although it does not show the shift in the baseline which is characteristic for the torque response. We turn now to this point.

Behavioural data reveal that the typical dynamic pattern of the torque corresponding to a phase shift of 90° is very often accompanied, at the onset of relative movement, by a shift in the baseline of the response. This is neither explained by the model presented in Fig. 1, nor by its variations discussed above. It can be, however, reproduced by adding to the overall output of the circuit its running time integral (over a relatively long time, i.e. 0.5 s). Our computer simulations show that this assumption is fully adequate to account for our behavioural data. Interestingly, the same transformation is probably performed on the signal involved in the vestibulo-ocular reflex and in the oculomotor system in primates, i.e. a pulse of activity is transformed into the sum of a pulse and its integral before reaching the motoneurons. The purpose of this transformation on the X cell signal may be somewhat similar to the case of oculomotor control: to ensure that rotation of the fly is a smart flick in response to a sudden stimulus, while integrating the motor command into a smooth signal. Bypassing of the integration stage improves the high-frequency response, compensating for the low-pass properties of the motor dynamics. Notice that the transformation of a signal into the sum of the signal and its low-pass version may be implemented very simply by a positive feedback loop with a low-pass filter in the feedback path. An attractive feature of this scheme is that the time constant of the resulting integration is independent from the value of the time constant of the filter in the feedback loop. An arbitrarily high value can be simply set by an appropriate choice of the feedback gain. A local circuit that could implement this scheme should probably involve non-spiking neurons and usual tonic excitatory synapses with a resting flow of transmitter. The electrophysiological data seem to suggest that this feedback loop

is located at a later stage, possibly at the level of the motor output.

In summary, the basic structure of the proposed circuitry consists of wide-field binocular cells which summate an array of elementary movement detectors and inhibit each one via inhibition of the shunting type. The specific model of Fig. 1 also illustrates how to translate our previous (algorithmic) analysis into a specific neural implementation which is physiologically plausible.

So far as we can tell, it is basically compatible with the old and new experimental data, but it must be regarded as little more than a very useful starting point to devise new critical experiments. Some of its specific functional properties, most notably its gain control and integration features are certainly relevant also for normal optomotor stimuli not involving relative movement.

Full details of the model, including the new experimental data on which it is based, will be published elsewhere.

We would like to thank L. Heimbürger for drawing the figures, I. Geiss for typing the manuscript and B. Rosser for reading an early version of it.

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Received February 9, 1981