Biol. Cybern. 52, 267–280 (1985)

Biological Cybernetics

On the Neuronal Basis of Figure-Ground Discrimination by Relative Motion in the Visual System of the Fly

III. Possible Input Circuitries and Behavioural Significance of the FD-Cells

Martin Egelhaaf

Max-Planck-Institut für biologische Kybernetik, Spemannstrasse 38, D-7400 Tübingen, Federal Republic of Germany

Abstract. It has been concluded in the preceding papers (Egelhaaf, 1985a, b) that two functional classes of output elements of the visual ganglia might be involved in figure-ground discrimination by relative motion in the fly: The Horizontal Cells which respond best to the motion of large textured patterns and the FD-cells which are most sensitive to small moving objects. In this paper it is studied by computer simulations (1) in what way the input circuitry of the FD-cells might be organized and (2) the role the FD-cells play in figure-ground discrimination.

The characteristic functional properties of the FD-cells can be explained by various alternative model networks. In all models the main input to the FD-cells is formed by two retinotopic arrays of small-field elementary movement detectors, responding to either front-to-back or back-to-front motion. According to their preferred direction of motion the FD-cells are excited by one of these movement detector classes and inhibited by the other. The synaptic transmission between the movement detectors and the FD-cells is assumed to be non-linear. It is a common property of all these model circuits that the inhibition of the FD-cells induced by large-field motion is mediated by pool cells which cover altogether the entire horizontal extent of the visual field of both eyes. These pool cells affect the response of the FD-cells either by pre- or postsynaptic shunting inhibition. Depending on the FD-cell under consideration, the pool cells are directionally selective for motion or sensitive to motion in either horizontal direction.

The role the FD-cells and the Horizontal Cells are likely to play in figure-ground discrimination can be demonstrated by computer simulations of a composite neuronal model consisting of the model circuits for these cell types. According to their divergent spatial integration properties they perform different tasks in figure-ground discrimination: Whereas the Horizontal Cells mainly mediate information on wide-field motion, the FD-cells are selectively tuned to efficient detection of relatively small targets. Both cell classes together appear to be sufficient to account for figure-ground discrimination as it has been shown by analysis at the behavioural level.

Introduction

A moving object ("figure") can be separated from a textured surround ("ground") on the basis of motion information alone, if both move incoherently. The fly has been used during the last years as a model system to study the neuronal basis of this visual information processing task (Reichardt et al., 1983; Egelhaaf, 1985a, b). In the preceeding papers it has been concluded that figure-ground discrimination is accomplished by the concerted action of two parallel neuronal networks (Egelhaaf, 1985a, b). Their output elements have been suggested to correspond to specific, identified output cells of the lobula plate, the posterior part of the third ganglion in the visual system of the fly. These cells can be subdivided into two functional classes with divergent spatial integration properties. Firstly, the system of Horizontal Cells, for long believed to control the optomotor yaw torque response (for review see Hausen, 1981), respond most strongly to large-field motion and, secondly, the newly discovered Figure-Detection (FD) neurones which are most efficient in detecting the motion of relatively small targets (Egelhaaf, 1985b).

So far, the functional properties of the FD-cells have been characterized phenomenologically (Egelhaaf, 1985b). In this paper it will be studied in what way the neuronal input circuitry of the different FD-cells might be organized in order to account for their specific functional properties. This analysis will be

mainly based on theoretical considerations, because electrophysiological data are not yet available. It will be shown that the properties of the FD-cells can be explained by various alternative model networks. In particular, they can be explained, as has already been done for the Horizontal Cells (Reichardt et al., 1983; Egelhaaf, 1985a), in terms of those model circuits which have previously been proposed to account for figure-ground discrimination at the behavioural level (Reichardt et al., 1983; Egelhaaf, 1985a). The computer simulations based on these models will be compared for specific stimulus conditions with the electrophysiologically determined FD-cell response. Finally, it will be shown in a computer analysis that the FD-cells together with the Horizontal Cells are in fact sufficient to explain all characteristic properties of figure-ground discrimination as they have been revealed in our behavioural experiments (Reichardt et al., 1983; Egelhaaf, 1985a).

Materials and Methods

The preparation, the stimulation apparatus and the extracellular recording techniques are the same as have been described in detail in the preceding papers (Egelhaaf, 1985a, b). The computer simulations were carried out with a Hewlett Packard 86 computer; the programmes were written in BASIC. The positions of the stimulus are given in head centered coordinates; ψ denotes the angular horizontal position with respect to the longitudinal axis of the head; $\psi < 0°$ and $\psi > 0°$ correspond to positions in the left and right half of the visual field, respectively. The terms "progressive" and "regressive" motion denote motion from front-to-back and back-to-front, respectively.

Results

1 Possible Input Circuitries of the FD-Cells: A Theoretical Analysis

The FD-cells are directionally selective, motion sensitive tangential neurones of the lobula plate. Their most characteristic property is that they are more sensitive to the motion of small objects than of more extended patterns (Egelhaaf, 1985b). The FD-cells are distinguished by this property from all lobula plate tangential neurones described so far. They receive at least four different types of motion-sensitive input (Egelhaaf, 1985b): 1) Excitatory input in part of, or the entire ipsilateral visual field. It is induced by small-field motion either from front-to-back (FD1, FD4) or back-to-front (FD2, FD3); the spatial outline of this input defines the particular cell's excitatory receptive field. 2) Inhibitory input in the same part of the field of view, i.e. within the confines of the cell's excitatory receptive field, which is elicited by motion with opposite polarity to the cell's preferred direction of motion. 3) Inhibitory input induced by ipsilateral large-field motion in the cell's preferred direction. 4) Inhibitory input induced by motion in front of the contralateral eye in either progressive (front-to-back), regressive (back-to-front) or both horizontal directions, depending on the FD-cell under consideration.

These different inputs to the FD-cells can be interpreted in terms of the model proposed by Reichardt et al. (1983) to underly figure-ground discrimination behaviour. Possible alternatives will be taken up briefly towards the end of this chapter. As a first approximation, it will be assumed in the models that the FD-cells have the same sensitivity within the confines of their excitatory receptive fields. The FD2-cell had to be omitted from this theoretical analysis, since its input organization could not be resolved with sufficient accuracy (Egelhaaf, 1985b).

A model of the input organization of the FD1-cell can be inferred straightforwardly from the electrophysiological data (Egelhaaf, 1985b) as is shown in Fig. 1a. The model FD1-cell receives excitatory as well as inhibitory inputs from two parallel retinotopic arrays of elementary movement detectors which are sensitive to progressive and regressive motion, respectively. The synapses between the movement detectors and the FD-cell are assumed to operate in the non-linear range of the corresponding transmission characteristic. According to the model of Reichardt et al. (1983), the inhibition mediated by large-field motion is due to pool cells which integrate the movement detector input over the entire visual field of the eye. The pool cells are assumed to saturate. The output of each elementary movement detector is shunted via presynaptic inhibition by these pool cells, before it is summated by the FD1-cell. Since this inhibitory influence can be elicited by large-field motion in front of either eye, the presumed pool cells on both sides of the brain are assumed to be coupled. Since large-field inhibition originating from either eye was found to be selective with respect to the direction of motion (see Figs. 4 and 5 in Egelhaaf, 1985b), the contralateral pool cell is excited by regressive, the ipsilateral one by progressive movement detector input. Both pool cells are assumed to be inhibited by motion in the respective reverse directions. The latter conclusion can be derived from the disinhibition phenomena found in the FD1-cell (Egelhaaf, 1985b).

The models of the input circuitries of both the FD3- and FD4-cell (Fig. 1b and c) can be deduced in a similar way from the corresponding electrophysiological results (Egelhaaf, 1985b). Only four points should be mentioned here. Firstly, apart from the exact location and width of the excitatory receptive fields the excitatory and the different inhibitory ipsilateral inputs

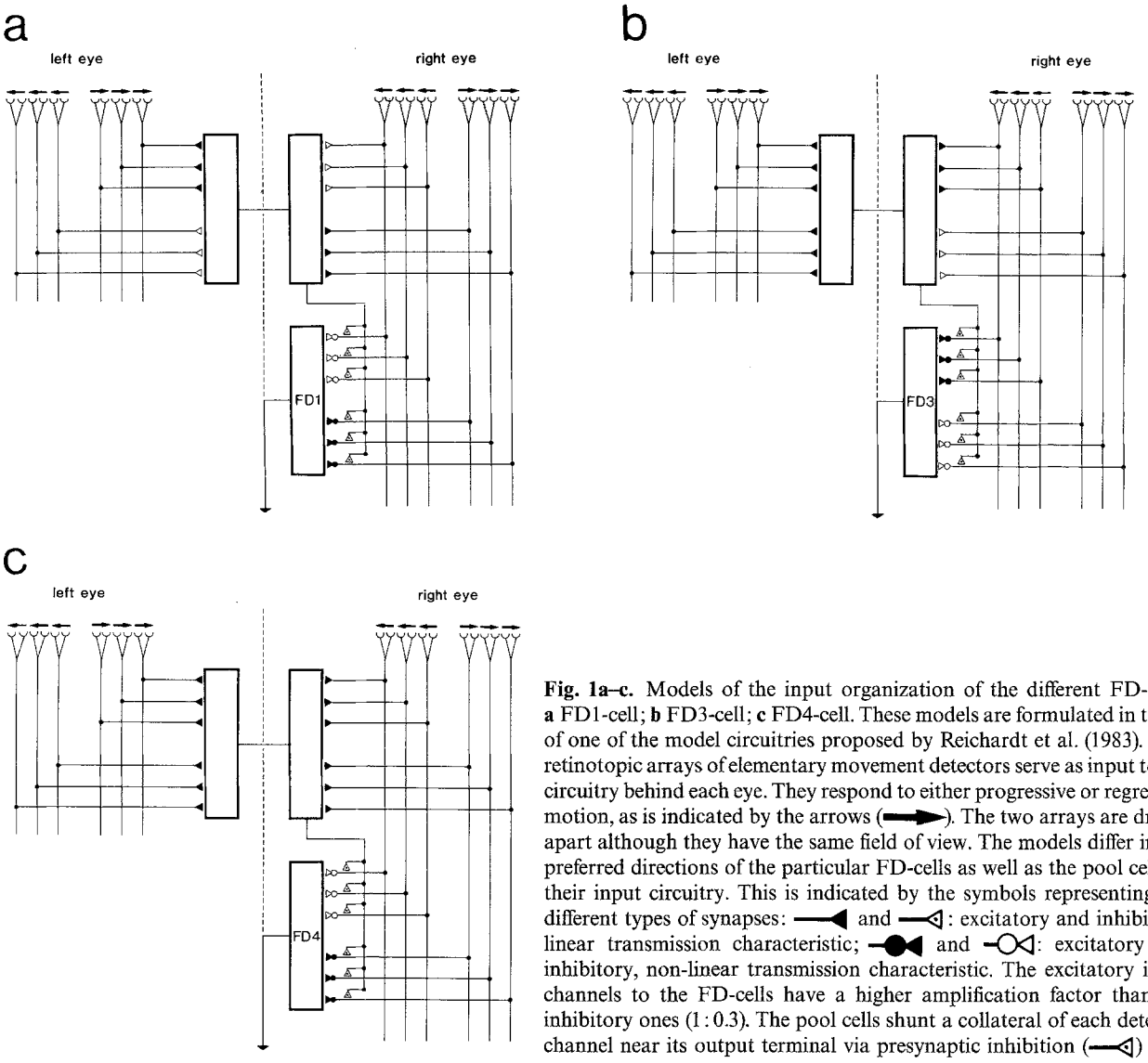

Fig. 1a–c. Models of the input organization of the different FD-cells. **a** FD1-cell; **b** FD3-cell; **c** FD4-cell. These models are formulated in terms of one of the model circuitries proposed by Reichardt et al. (1983). Two retinotopic arrays of elementary movement detectors serve as input to the circuitry behind each eye. They respond to either progressive or regressive motion, as is indicated by the arrows (➡). The two arrays are drawn apart although they have the same field of view. The models differ in the preferred directions of the particular FD-cells as well as the pool cells in their input circuitry. This is indicated by the symbols representing the different types of synapses: —◀ and —◁: excitatory and inhibitory, linear transmission characteristic; —●◀ and —○◁: excitatory and inhibitory, non-linear transmission characteristic. The excitatory input channels to the FD-cells have a higher amplification factor than the inhibitory ones (1 : 0.3). The pool cells shunt a collateral of each detector channel near its output terminal via presynaptic inhibition (—◁)

to the FD1- and FD3-cell are mirror images with respect to their preferred directions (compare Fig. 1a and b). Secondly, the pool cells on both sides of the brain in the input circuitry of all FD-neurones are functionally coupled. Thirdly, in contrast to the FD1-cell the presumed contralateral pool cells of both the FD3- and FD4-cell are excited by motion in either horizontal direction. To be precise, there could be equally well two contralateral pool cells in their input circuitry, one selectively sensitive to progressive, the other to regressive motion. This, however, cannot be resolved by the present analysis and is functionally insignificant in this context. Fourthly, it is not yet clear whether the ipsilateral pool cell in the input circuitry of the FD4-cell is excited by motion in either horizontal direction (Fig. 1c) or by progressive motion only. It cannot easily be decided between these alternatives, since regressive motion inhibits the FD4-cell via its direct inhibitory input along the entire horizontal extent of the ipsilateral visual field and thus might mask an inhibitory response component mediated indirectly by the pool cell.

One problem with respect to all models shown in Fig. 1 remains to be solved in further experiments: There is no experimental evidence so far that the inhibitory input channels to the FD-cells are affected by shunting inhibition via the pool cells as is assumed in Fig. 1. The reason for this is that only the positive response components could be determined with the extracellular recording techniques which were employed for the quantitative characterization of the FD-cells.

Apart from the overall organization of the model circuitries representing the different FD-cells the param-

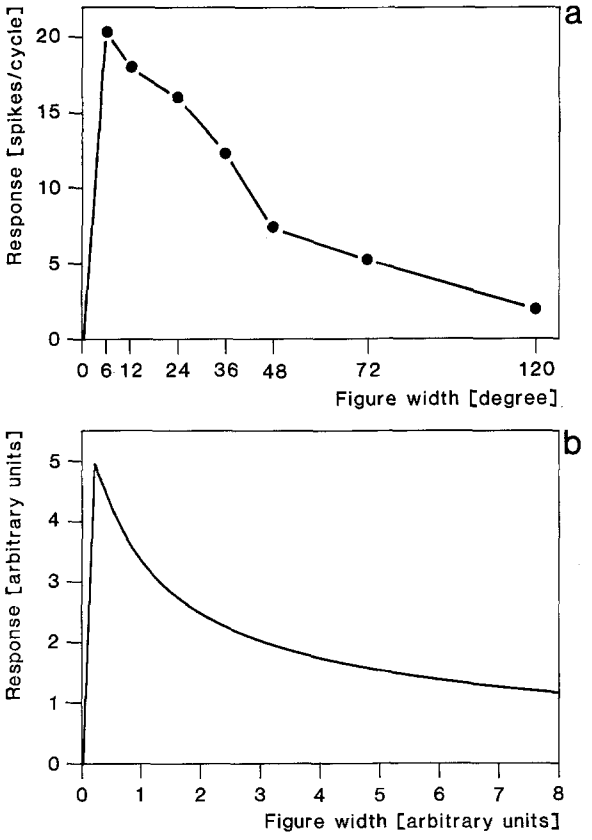

Fig. 2a and b. Experimentally determined **a** and computer simulated **b** response amplitude of a FD-cell as a function of figure width. **a** Stimulus induced responses of a FD1-cell to progressive motion are plotted against the angular horizontal extent of a textured pattern. The pattern was oscillated sinusoidally with a frequency of 2.5 Hz. The oscillation amplitude amounted to $\pm 5°$. The frontal edge of the pattern always oscillated about $\psi = 0°$, whereas the angular horizontal position of its lateral edge depended on its width. The individual data points represent the time-averaged response to 24 stimulation cycles. **b** Simulation of the output cell response to progressive motion of the figure-ground discrimination network [Eq. (1b) in Egelhaaf (1985a)] as a function of the number of excited movement detector channels. Parameter settings of this simulation: $n=3$; $q=0.5$; $\beta=0.1$. For the given parameter settings the computer simulation fits the corresponding experimental data sufficiently well

eters q and n in the corresponding model equations [Eq. (3) in Reichardt et al. (1983), Eq. (1) in Egelhaaf (1985a) see, however, legends of Figs. 3, 4, and 7] need to be specified. These parameters characterize the saturation behaviour of the pool cell and the operating range on the presumed non-linear synaptic transmission characteristic to the output cell of the network, respectively. If q is kept constant, the dependence of the cellular response on the angular horizontal extent of the stimulus is affected sensibly by variations in the parameter n. It follows from Eq. (3) in Reichardt et al. (1983) and Eq. (1b) in Egelhaaf (1985a) that the response of the model output cells decreases with increasing figure width as is characteristic for the FD-cells, if $q \cdot n > 1$. If this condition is met, the experimentally determined relationship between figure width and response amplitude of the cell can be fitted reasonably well by the output of the corresponding model. This is illustrated in Fig. 2 for the FD1-cell. In the simulation (Fig. 2b) n and q amounted to 3 and 0.5, respectively. Despite there is some variability in the steepness of the experimentally measured curves and, concomitantly, in the optimal figure width, these parameter settings were chosen in all computer simulations of FD-cell responses.

The responses of all models shown in Fig. 1 were computed under various stimulus conditions and compared with the corresponding electrophysiological recordings. Only the circuitry with symmetrically organized pool cells representing the FD4-cell (Fig. 1c) and the network with directionally selective pool cells representing the FD1-neurone (Fig. 1a) will be discussed here. Those stimulus conditions were selected for representation in Figs. 3 and 4 which led to the most characteristic response profiles in these cell types.

In Fig. 3 the electrophysiologically determined responses of the FD4-cell to different stimulation situations are compared with the corresponding computer simulations. Apart from Fig. 3a, a vertically oriented textured stripe representing the figure and an equally textured background panorama were oscillated with a phase shift of 90°. Whereas the figure was always placed in front of the right eye in the cell's excitatory receptive field, the angular extent of the ground differed in the different examples. In Fig. 3b it covered both eyes, whereas in Fig. 3c and d it covered only the contra- or ipsilateral eye. For better comparison, the response to figure motion alone is shown in Fig. 3a. The spike frequency histograms of the electrophysiological recordings are fitted quite well by the corresponding computer simulations with respect to their characteristic features under the different stimulus conditions. The simulations match the experimental data similarly well for the other phase relations between figure and ground. It can, thus, be concluded that the model circuitry shown in Fig. 1c with the appropriate parameter settings is, in fact, sufficient to explain the properties of the FD4-cell.

The consequences of directionally selective pool cells are illustrated for the FD1-cell in Fig. 4. They are particularly obvious when the ground stimulates only the contralateral eye, while the figure oscillates in the cell's excitatory receptive field (Fig. 4b–d). In Fig. 4a the ground is stationary and the figure oscillates alone. The asymmetry in the FD1-cell's input organization can be seen in its divergent response profiles to synchronous and counterphase oscillation of figure

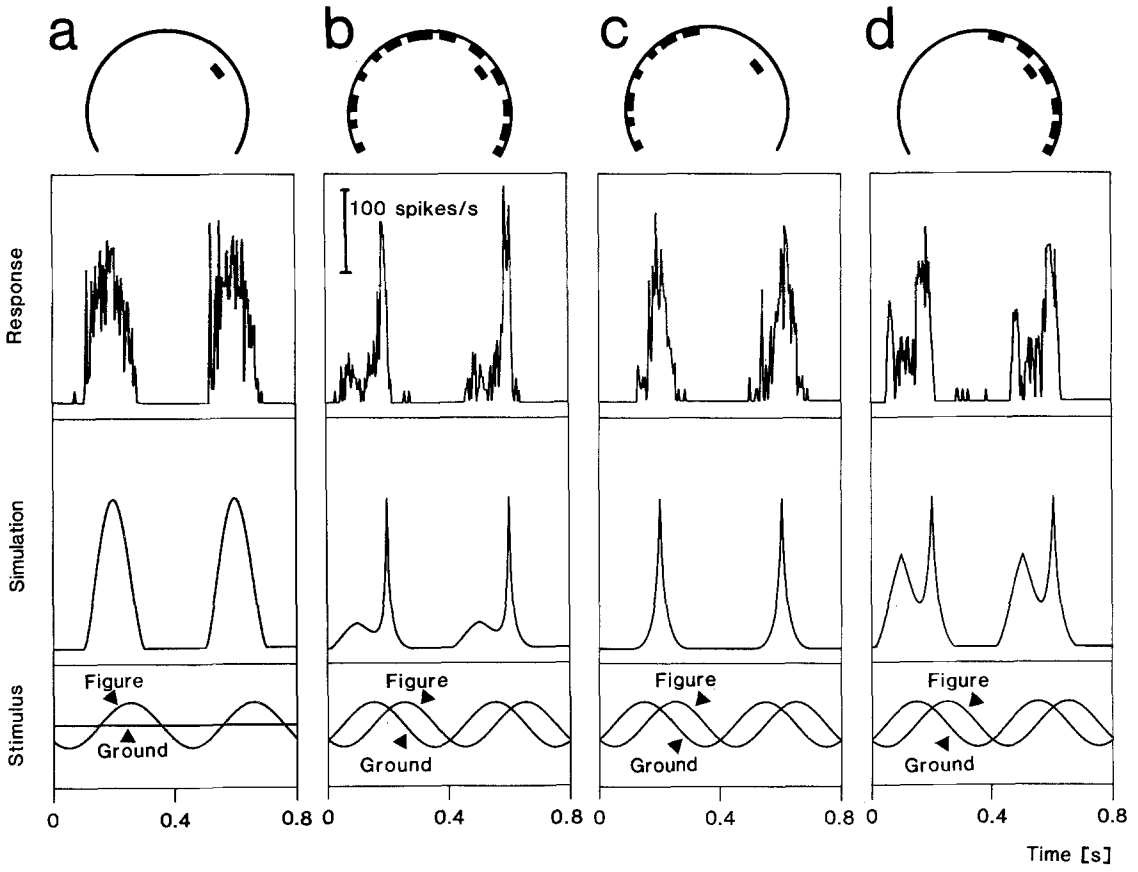

Fig. 3a–d. Comparison of the electrophysiologically determined response of a FD4-cell (upper diagrams) and the response of the corresponding model circuitry (middle diagrams). The stimulus conditions used in the different experiments are indicated in the bottom diagrams and the insets. In **a** the figure was oscillated alone without any ground texture present. The figure and a binocular **b**, a contralateral **c** or an ipsilateral **d** ground were oscillated with a phase shift of $\varphi = 90°$. Upward deflection of the stimulus traces denotes clockwise motion. In the electrophysiological experiments a 24°-wide textured vertical stripe (figure) was positioned at $\psi = 60°$. The oscillation frequency amounted to 2.5 Hz, the oscillation amplitude to $\pm 10°$. In the experiments with a monocular ground the frontal area of the visual field was covered symmetrically with a 36°-wide mask to avoid stimulation of the other eye. The spike frequency histograms of the electrophysiological recordings were averaged from 16 repetitions of the respective stimulus sequences. In the model simulations the response of the output cell of the circuitry shown in Fig. 1c was computed. Since the pool cells on both sides of the brain are bidirectional, the simulations are based on the original model equations of the figure-ground discrimination model [Eq. (3) in Reichardt et al. (1983) and Eq. (1b) in Egelhaaf (1985a)]. The binocular ground stimulated 52, the contralateral ground 30, and the ipsilateral ground 22 detector channels; the figure always stimulated 8 detector channels. The parameter settings used in this simulation: $n = 3$; $q = 0.5$; $\beta = 0.05$. Since the experimentally determined cellular responses show delays with respect to the stimulus, the computed response curves are shifted accordingly. For better comparison with the spike frequency histograms, only the positive response components are shown in the simulations. The simulations fit the electrophysiological recordings quite well with respect to their characteristic time course under the different stimulus conditions

and ground (compare Fig. 4b and d). This difference is closely matched by the corresponding computer simulations based on the model circuitry of Fig. 1a. The experimental results are fitted equally well for a phase shift of 90° between the figure and the contralateral ground (Fig. 4c), but also when the ground covers the ipsilateral or both eyes (not shown). Hence, it can be concluded that the model representation of Fig. 1a is, in fact, sufficient to account for the response characteristics of the FD1-neurone.

One observation in the response of both the FD1- and FD4-cell deserves further attention. There is hardly a difference between the time course of the experimentally determined response of both cell types to relative motion of the figure and a contralateral ground with a phase shift of 90° (compare Figs. 3c and 4c). This is surprising because of the differently organized large-field input to both types of FD-cells. The corresponding computer simulations certainly differ from each other in the fine structure of their time course. However, these differences are obviously too insignificant to be resolvable against the noise background and variability in the electrophysiologically recorded cell response.

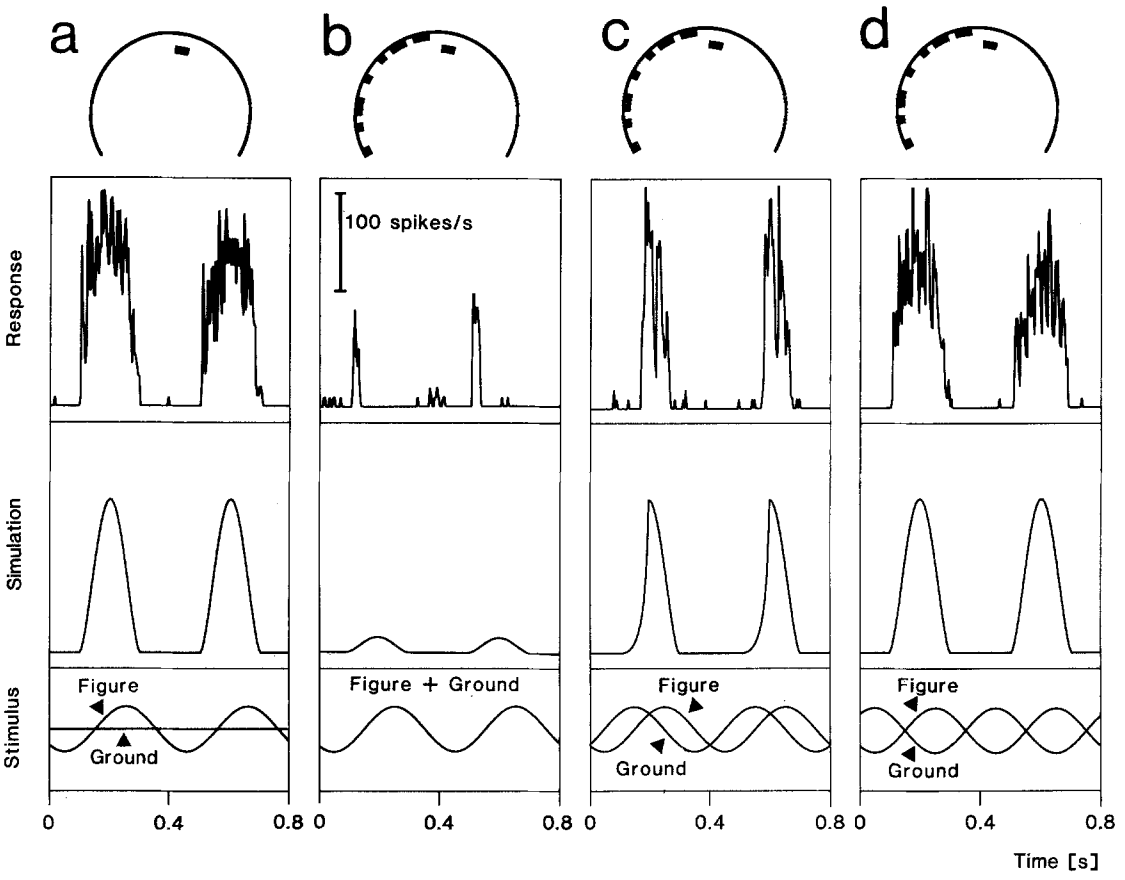

Fig. 4a–d. Comparison of the electrophysiologically determined response of a FD1-cell (upper diagram) and the response of the corresponding model circuitry (middle diagrams). The stimulus conditions used in the different experiments are indicated in the bottom diagrams and the insets. Upward deflection of the stimulus traces denotes clockwise motion. In all electrophysiological experiments a 6°-wide figure was positioned in the cell's excitatory receptive field at $\psi = 10°$, while the ground covered only the contralateral eye. In **a** the ground was stationary and the figure oscillated alone. Figure and ground oscillated synchronously ($\varphi = 0°$) in **b** or with a phase shift of $\varphi = 90°$ or $\varphi = 180°$ in **c** and **d**, respectively. The oscillation frequency amounted to 2.5 Hz, the oscillation amplitude to $\pm 5°$. The spike frequency histograms of the electrophysiological recordings were averaged from 32 repetitions of the respective stimulus sequences. In the model simulations the response of the output cell of the circuitry of Fig. 1a was computed. Since the two pool cells are directionally selective, the computer simulations are based on a modified version of Eq. (3) in Reichardt et al. (1983) and Eq. (1b) in Egelhaaf (1985a): The excitatory and inhibitory inputs to the pool cells are given a positive and negative sign, respectively. The ground stimulated 30 detector channels, the figure only 8. The parameter settings used in this simulation: $n = 3$; $q = 0.5$; $\beta = 0.05$. Since the experimentally determined cellular responses are delayed with respect to the stimulus, the computed response curves are shifted for better comparison by the respective delays. Only the positive response components are shown in the computer simulations. The experimental data fit the corresponding computer simulations sufficiently well with respect to their characteristics features under the different stimulus conditions

Despite the relatively good correspondence between the response properties of the FD-cells and the computer simulations of their respective model counterparts the circuitries shown in Fig. 1 represent only rather crude approximations to reality. The three major simplifications which have been made in establishing the model circuitries pertain to the implicit assumption that the receptive fields of the FD-cells are organized homogeneously along both axes of the eye. Firstly, all input channels in the models contribute equally to the overall response of the model output cells; they have not been weighted according to their position in the visual field, although the FD-cells have characteristic single-peaked sensitivity distributions for the horizontal extent of their receptive fields (Egelhaaf, 1985b). This simplification does, however, not seriously affect the performance of the model circuitry, as long as the stimulus patterns oscillate about fixed positions with relatively small amplitudes, as was the case in all experiments shown in Figs. 3 and 4. Nevertheless, this simplification can be easily overcome by weighting the movement detector channels appropriately. Alternatively, spatial weighting of local motion information might be accomplished, as has been proposed for the Horizontal Cells (Hausen, 1981), by supplying the representation area of specific

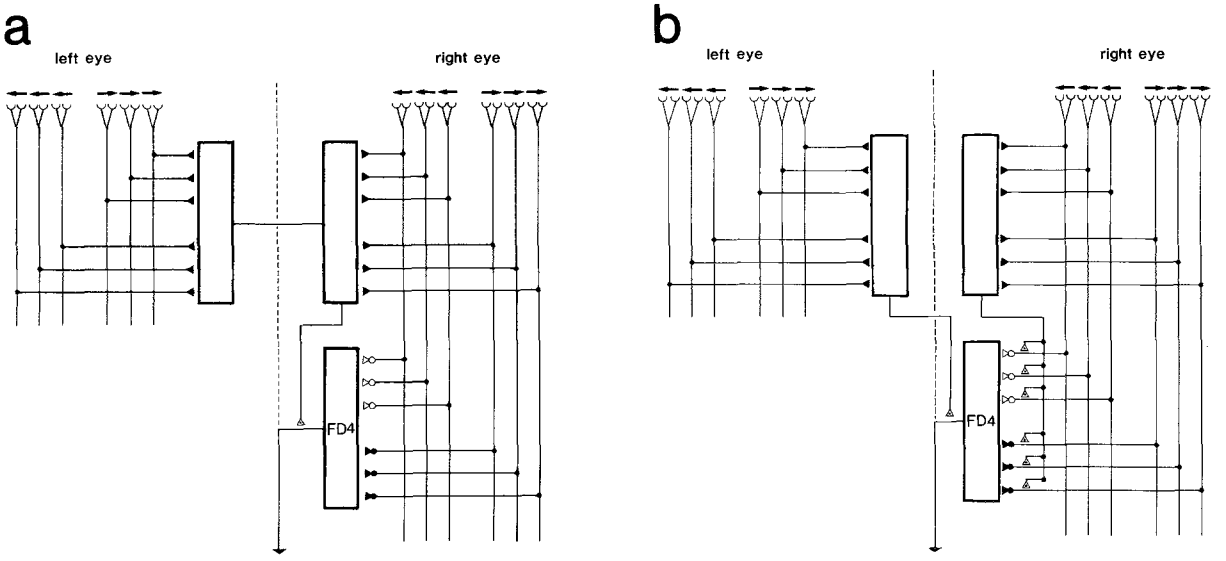

Fig. 5a and b. Alternative models of the input circuitry of the FD4-cell (see Fig. 1c). In **a** the heterolateral pool cells are coupled and directly inhibit the output cell of the network via synapses of the shunting type. In **b** the pool cells of both halfs of the brain operate independently from each other. Whereas the ipsilateral pool cell interacts with the individual elementary movement detectors, the contralateral one inhibits the output cell directly. The symbols used are the same as is explained in the legend of Fig. 1

parts of the visual field with a higher density of input synapses than other parts. Secondly, for certain FD-cell types (FD1, FD2, FD3) the excitatory receptive field is limited in its angular horizontal extent and, thus, smaller than the receptive field of the presumed ipsilateral pool cell. Computer simulations on the basis of more refined model circuitries which allowed for pool and output cells with different spatial extension clearly revealed that this does not qualitatively affect the principal constraints imposed on the circuitry. Certainly, the condition of non-linearity of synaptic transmission to the output cell of the network can be restrained to a certain degree, if this cell receives direct excitatory input from only part of the visual field. However, the observed steep decrease in the response amplitude of the FD1-cell with increasing width of the stimulating pattern (see Fig. 2) cannot easily be explained if synaptic transmission to the FD1-cell were linear. It seems, therefore, to be necessary that the input synapses of the FD-cells operate in the non-linear range of the transmission characteristic, even if the excitatory receptive field of the cell covers only part of the field of view. Thirdly, it could not be tested with the stimulation device used in this study (see Egelhaaf, 1985a), whether the FD-cells have the same spatial integration properties along their vertical and horizontal axes, as has been implicitly assumed in the models. Further experiments are needed to resolve whether this assumption is justified.

So far the input circuitries of the different FD-neurones have been formulated in terms of only one of the models proposed by Reichardt et al. (1983). The FD-cell's functional properties, however, can also be interpreted by the alternative model circuit proposed by Reichardt et al. (1983) where a recurrent pathway interacts with the individual movement detectors prior to summation of their signals by the pool cells. Moreover, they can be accounted for by the model, where the output cell of the network is inhibited directly by the pool cells rather than presynaptically (Egelhaaf, 1985a), but also by networks which take up elements of the different aforementioned model schemes. It is obvious that further more complex alternatives are conceivable. Only two possible alternative circuitries for the FD4-cell will be discussed here which are of similar complexity as the corresponding network shown in Fig. 1c. Figure 5a shows a network in which both pool cells are coupled and directly inhibit the output cell. It should be noted that this model is mathematically equivalent to a network where both pool cells are uncoupled and synapse independently onto the output cell (not shown). In the model circuit shown in Fig. 5b both pool cells operate independently from each other. Whereas the ipsilateral pool cell interacts with the individual elementary movement detectors, the contralateral one inhibits the output cell directly. As can be shown by computer simulations the output of both model networks is very similar to the one shown in Fig. 1c and, therefore, might represent the input circuitry of the FD4-cell equally well.

It can be concluded that the characteristic functional properties of a given FD-cell can be accounted for by various neuronal circuitries with different

topological organization. This leaves several possibilities for the actual realization of the input circuitry of the different FD-cells in the fly's brain. It should be noted, however, that all these model circuits have in common that the FD-cells are inhibited in some way by cells which represent information on wide-field motion. The information to decide between the alternative models might be gained indirectly from further, more specific functional tests of the FD-cells or, better, from a direct neurophysiological analysis of their input circuitry.

2 From the Neuronal to the Behavioural Level: FD- and Horizontal Cells are Sufficient to Explain Figure-Ground Discrimination Behaviour

It was not possible to establish the Horizontal Cells as the only output elements of the neuronal network controlling yaw torque generation in response to relative motion of figure and ground (Egelhaaf, 1985a). The FD-cells seem to be appropriate to compensate for the "deficits" of the Horizontal cells with respect to figure-ground discrimination and could, thus, represent the required additional output cells of the network (Egelhaaf, 1985b). Therefore, in the final step of this analysis one has to return from the neuronal to the behavioural level by demonstrating on the basis of computer simulations that the Horizontal Cells together with the FD-neurones are in fact sufficient to explain all characteristic properties of figure-ground discrimination behaviour. These computer simulations are based on a composite neuronal model which is shown in Fig. 6. Despite its complicated appearance, it is simply composed of the model circuits which have been derived for the Horizontal Cells (Fig. 10 in Egelhaaf, 1985a; see also Reichardt et al., 1983) and the FD-neurones (Fig. 1), respectively. In the sequel I shall simplify this analysis slightly, since I do not consider the most frontal vertical stripe of the visual field. As has been discussed in Egelhaaf (1985b), in this small area of the field of view figure-ground discrimination differs from the remaining major part of the eye and is not yet fully understood. Beyond angular horizontal positions of approximately $\psi = +20°$ those FD-units predominate the others in their efficiency to detect small moving objects which virtually satisfy the conditions for an output element of the neuronal network underlying figure-ground discrimination. Therefore, apart from the Horizontal Cells only the FD3- and FD4-neurone will be taken into account. The output signals of these parallel subcircuits can be weighted independently and are assumed, as a first approximation, to contribute linearly to the behavioural response. To distinguish the model cells from the real ones in the fly's brain the model cells will be referred to in quotation marks.

Although there are now a great number of different behavioural experiments, the outcome of only a few of them will be compared with the corresponding computer simulations of the model shown in Fig. 6. In particular, it will be concentrated on the variability of the characteristic features of the response to relative motion of figure and ground (Egelhaaf, 1985a). This variability in the time course of the torque response pertains mainly to two response components which could be resolved best when figure and ground oscillated with a phase shift of 90°: Firstly, the characteristic response peak which is induced when the figure still moves progressively while the ground reverses its direction of motion (see Figs. 3 and 7 in Egelhaaf, 1985a). Secondly, a response peak which occasionally emerges when the direction of ground motion reverses while the figure still moves regressively (see Fig. 5 in Egelhaaf, 1985a). These features reveal best the specific role each of the three types of output cells shown in Fig. 6 is likely to play in figure-ground discrimination.

In the computer simulations of Fig. 7 the three types of output cells of the network (see Fig. 6) contribute to a varying degree to its total response. Whereas the "FD3-cell" has been chosen for convenience not to contribute to the reaction in the examples shown here (weighting factor 0), the contribution of the "Horizontal system" and the "FD4-cells" varies inversely from Fig. 7a to d. In Fig. 7a the "Horizontal system" clearly predominates the response of the network. Under these conditions the time course of the response to relative motion of figure and ground with a phase shift of 90° is not much changed as compared to synchronous motion. Accordingly, the characteristic response peak can hardly be discerned. On the other hand, in the example of Fig. 7d the "FD4-cells" predominate the "Horizontal system", which leads to sharp response peaks during relative motion with a much larger amplitude than the reaction to synchronous motion of figure and ground. The examples displayed in Fig. 7b and c are intermediate in this respect between these extreme cases. It can be, thus, concluded, that the entire range of variability found in the expression of the response peak induced by progressive figure motion can be explained by differentially weighting the output of the FD4- and Horizontal Cells before they converge on a final common path (compare Fig. 7 with Figs. 3 and 7 in Egelhaaf, 1985a).

The response peak which is occasionally generated upon regressive figure motion can be explained in a similar way. This time, however, the FD3-cell will play the major role. As a precondition it needs to be assumed that this cell type contributes a component to the yaw torque response that is oppositely directed to the direction of stimulus motion. Or to put it into other words, upon regressive motion the FD3-cell elicits a

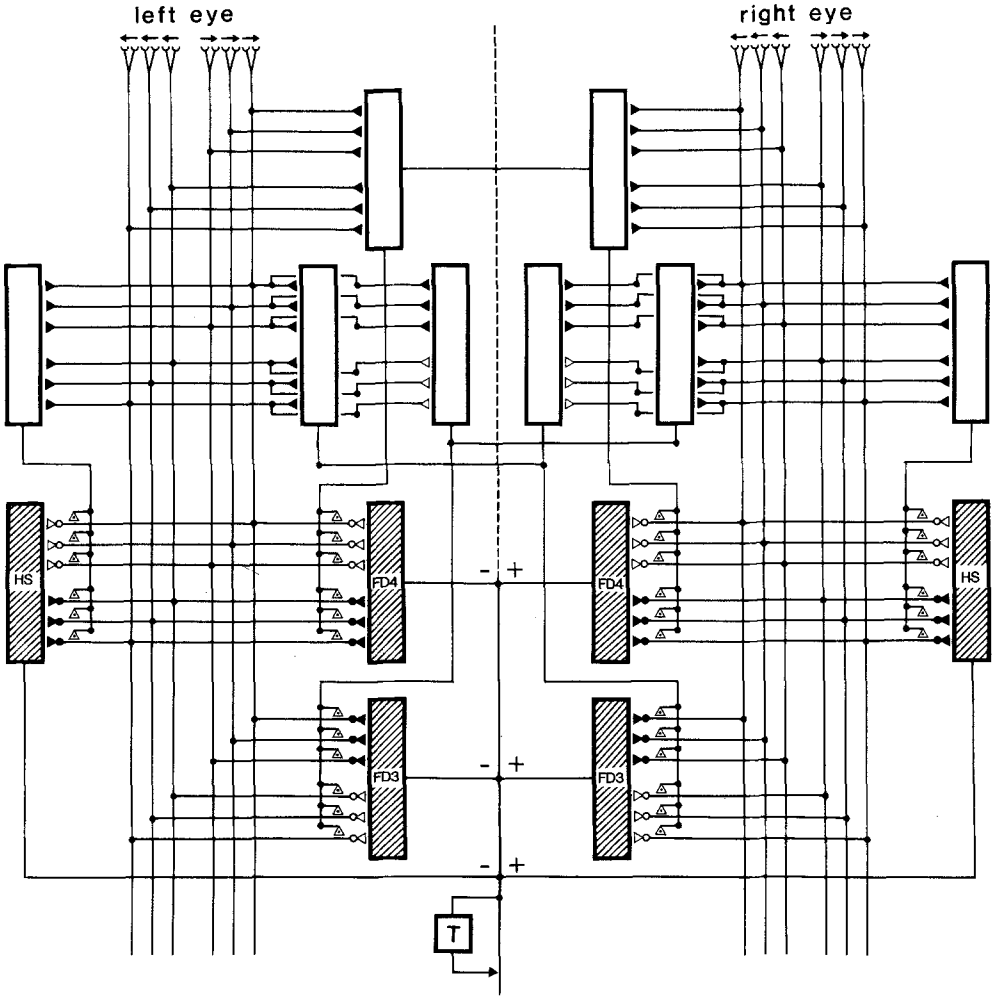

Fig. 6. Outline of a model circuitry which is sufficient to account for figure-ground discrimination behaviour in the major part of the visual field, except its small most frontal area. In contrast to the models shown in Figs. 2 and A1 in Egelhaaf (1985a), the network shown here is composed of the model networks of the Horizontal Cells (HS) (see Fig. 10 in Egelhaaf, 1985a) and the FD-neurones and their particular input circuitries (Fig. 1). It should be noted that it represents only one of several possible alternatives and relies exclusively on presynaptic shunting inhibition to achieve the characteristic spatial integration properties of the different output cells. The cells in the circuitry which are known from direct electrophysiological analysis are hatched. The symbols used are the same as is explained in the legend of Fig. 1. The final motor output is controlled by the output cells of the network via a direct channel and a channel *T* producing the running average of the direct output signal. Before convergence on a common path the signals of the output cells can be weighted independently

response towards the position of the figure rather than in its direction of motion. Provided these assumptions were correct this might well lead to the response peak, observed during relative motion with a phase shift of 90° when the figure moves regressively while the ground reverses its direction of motion. This is substantiated by the computer simulations shown in Fig. 8. While the contribution of the "FD4-cells" to the total behavioural response has been held constant throughout Fig. 8, the "FD3-cell" contributes a varying part increasing from Fig. 8a to d, where it has finally been given the same weighting factor as the "FD4-cell". Accordingly, the response peak to regressive motion continuously increases until it has almost the same size as the response peak induced by progressive motion. Hence, it is suggested that the entire range of variability found with respect to this response component can be accounted for by differentially weighting the output of the FD3-cell (compare Fig. 8 with Fig. 5 in Egelhaaf, 1985a).

On the basis of these computer simulations it can, thus, be concluded that together with the Horizontal system the FD-cells are sufficient as output elements of the optic lobes to account not only for some behavioural key experiments, but for the entire range of variability observed in the torque response of the fly to relative motion of figure and ground. It should be emphasized that this conclusion is independent of the

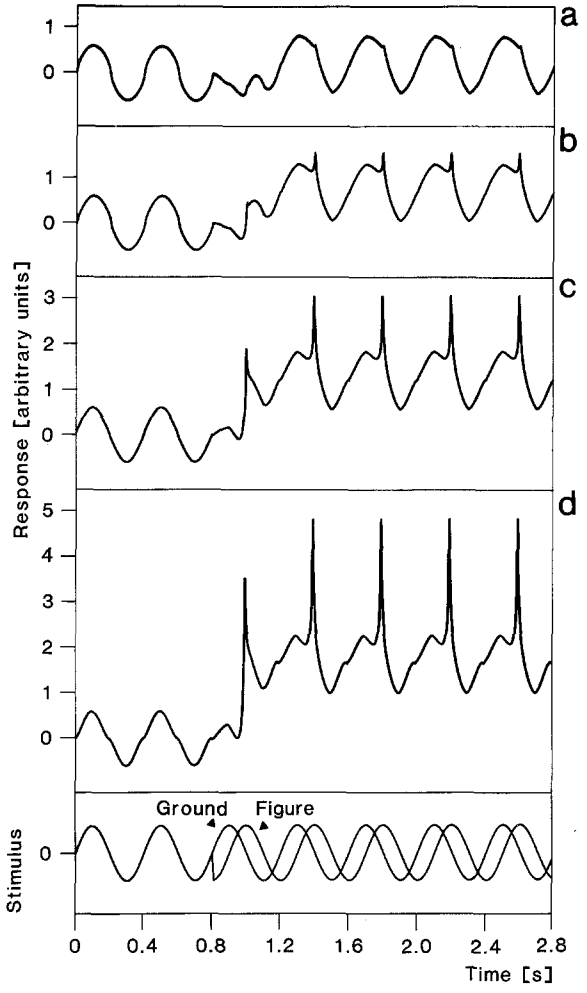

Fig. 7a–d. Computer simulation of the behavioural experiment shown in Fig. 2 in Egelhaaf (1985a). This computer simulation was done on the basis of the model circuitry displayed in Fig. 6 with parameter settings for the different parallel subcircuits as have been determined for the Horizontal system, the FD3- and FD4-cells. In the different simulations the three types of output cells of the network contribute to a varying degree to the total response. Whereas the "FD3-cell" did not contribute to the reaction (weighting factor 0), the ratio of the contribution of the "Horizontal system" and the "FD4-cell" varies ("HS": "FD4" = 10:1 in **a**; 1:1 in **b** 0.2:1 in **c**; 0:1 in **d**). Since the ipsilateral pool cell of the FD3-cell is assumed to be directionally selective for motion, the simulation of the FD3-cell response is based on a modified version of Eq. (3) in Reichardt et al. (1983) and Eq. (1b) in Egelhaaf (1985a): The excitatory and inhibitory inputs to the ipsilateral pool cell are given a positive and negative sign, respectively. The simulations of the FD4- and the Horizontal Cells are based on equations as explained in the legend of Fig. 3 and in Egelhaaf (1985a), respectively. The parameters used in these simulations: "HS": $n=1.25$; $q=0.5$; $\beta=0.05$; "FD3", "FD4": $n=3$; $q=0.5$; $\beta=0.05$. The number of channels stimulated by the ground amounted to 52, the number of channels stimulated by the figure to 8. The running average time was 0.4 s. After two cycles of synchronous motion of figure and ground the relative phase was switched to $\varphi=90°$. For better comparison, the response amplitudes were normalized with respect to the response induced by synchronous motion of figure and ground. These simulations illustrate that the entire range of variability found in the amplitude of the response peak induced by progressive figure motion can be accounted for by differentially weighting the FD4- and Horizontal Cell output before they converge on a final common path

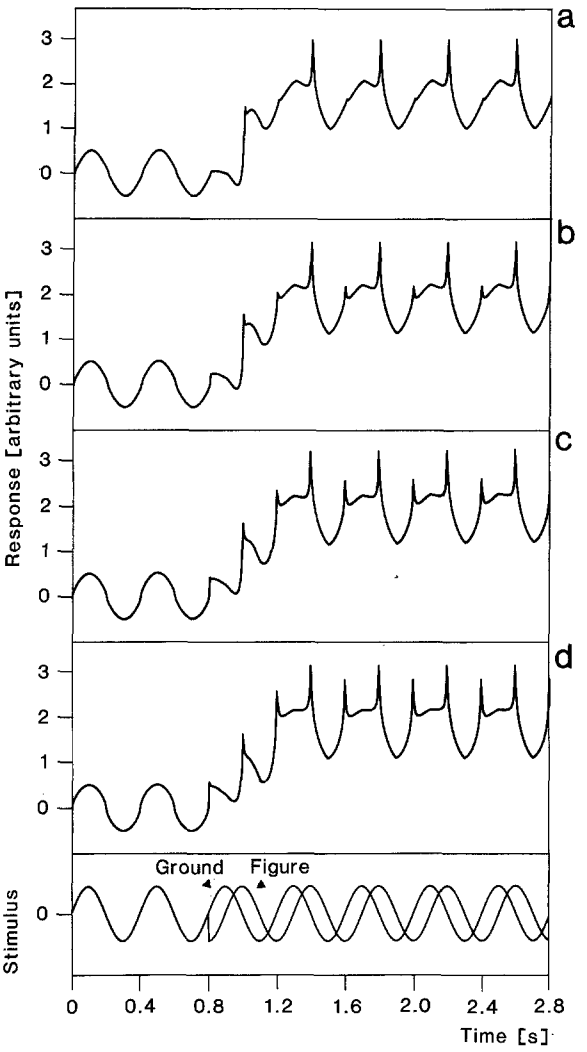

Fig. 8a–d. Computer simulation of the behavioural experiment shown in Fig. 5 in Egelhaaf (1985a). The simulation was done, as explained in the legend of Fig. 7, on the basis of the model circuitry displayed in Fig. 6. As in Fig. 7 the contribution of the three types of output cells of the network to the total response amplitude varied. Their ratio amounted to: "HS": "FD3": "FD4" = 0.275:0.1:1 in **a**; 0.35:0.4:1 in **b**; 0.425:0.7:1 in **c**; 0.5:1:1 in **d**. The other parameters of these simulations were the same as specified in the legend of Fig. 7. The "FD3-cell" contributes a component to the total response that is directed oppositely to the direction of stimulus motion. The running average time amounted to 0.4 s. After two cycles of synchronous motion of figure and ground the relative phase was switched to $\varphi=90°$. As in Fig. 7, the response amplitudes were normalized with respect to the response to synchronous motion of figure and ground. These simulations illustrate that the entire range of variability found in the amplitude of the response peak induced by regressive figure motion can be attributed to a variable contribution of the FD3-cell to the total torque response

particular mechanisms which finally will turn out to be responsible for the characteristic properties of these cells. It depends, however, on the precondition that these parallel output cells can be weighted differentially and independently with respect to their contribution to the overall motor output, before they converge on a common path.

Discussion

This and the preceding papers (Egelhaaf, 1985a, b) are a further step towards unravelling the neuronal mechanisms which allow the fly to discriminate an object in front of a textured background. Behavioural and electrophysiological experiments as well as computer simulations led to a neuronal model network which is sufficient to account for figure-ground discrimination by relative motion. The output elements of this network are suggested to correspond to specific, identified output cells of the lobula plate, the posterior part of the third visual ganglion. According to their divergent spatial integration properties these cells can be subdivided into two functional classes which perform different tasks in figure-ground discrimination: Whereas the Horizontal Cells mainly mediate information on wide-field motion (e.g., Hausen, 1982a, b; Reichardt et al., 1983), the FD-cells are selectively tuned to efficient detection of relatively small targets (Egelhaaf, 1985b).

1 Organization of the Neuronal Circuit

The specific spatial integration properties of the FD-cells can be accounted for by modified versions of the model circuitry proposed by Poggio et al. (1981) and Reichardt et al. (1983) but also by various alternative model networks. Despite of their different operations, all these alternative models lead to essentially the same response properties of their output cells. It seems, therefore, that with our present knowledge on the functional properties of the FD-cells it cannot be resolved which alternative comes closer to the actual neuronal network implemented in the fly's brain.

1.1 The Retinotopic Input to the Circuitry. All circuitries proposed in this study receive direct excitatory and inhibitory input from a retinotopic array of two classes of small-field elementary movement detectors. These movement detectors were assumed to be directionally selective for either progressive or regressive motion. The synapses between the movement detectors and the output cells of the network were concluded to operate with a non-linear transmission characteristic. How do these assumptions fit into the framework of available data on the structural and functional properties of the optic lobes?

There are various lines of evidence that the main input to the lobula plate large-field tangential cells is in fact by a large number of retinotopic small-field elements. Firstly, there is a good correspondence between the outlines of the dendritic arborizations of these tangential cells and the projection map of their visual fields onto the retinotopically organized lobula plate (Hausen, 1981; for the FD-cells see Egelhaaf, 1985b). Secondly, upon ipsilateral stimulation pronounced graded de- and hyperpolarizations, rather than discrete postsynaptic potentials are induced in the dendritic tree of the lobula plate tangential cells (Horizontal Cells: e.g., Hausen, 1982a; FD-cells: Egelhaaf, 1985b). This suggests the idea of a large number of independently firing presynaptic elements rather than only one or few large-field neurones (see Hausen, 1976, 1982a). Thirdly, retinotopically organized movement-specific nervous activity has been identified in the lobula plate with the radioactive deoxyglucose technique by comparing stimulated and unstimulated regions of the ganglia (Buchner et al., 1984).

Anatomical candidates for this retinotopic small-field input are two classes of columnar neurones which connect the proximal medulla (T4-cells) and the posterior lobula (T5-cells) to the lobula plate, respectively (Strausfeld, 1976, 1984). Whether these cell types are sensitive to motion has not yet been shown electrophysiologically. It should be noted, however, that movement sensitive units (Bishop et al., 1968; McCann and Dill, 1969; Mimura, 1971, 1972; DeVoe and Ockleford, 1976; DeVoe, 1980) as well as movement-specific deoxyglucose activity labeling (Buchner et al., 1979; Buchner et al., 1984) have been found in the medulla.

In conclusion, the assumption that the main input to the figure-ground discrimination network is provided by retinotopically organized small-field movement detectors is quite in accordance with the available neurophysiological and anatomical data. It should be emphasized, however, that the specific properties of the movement detectors are not critical for the capability of the proposed circuits to discriminate relative motion. In the computer simulations presented in this study the amplitude of the signals carried by the input channels to the network has simply been assumed to be proportional to the pattern velocity. More recent computer simulations with movement detectors as input elements to the figure-ground discrimination network lead to essentially the same conclusions (Guo and Reichardt, in prep.).

1.2 Organization of the Large-Field Input. The characteristic spatial integration properties of the FD-cells are assumed to result from the specific interaction of large-field neurones in their input circuitry. These pool cells are assumed to interact by shunting inhibition either presynaptically with each elementary movement detector or directly with the FD-cells. Although these presumed pool cells have not yet been identified neurophysiologically, their principal spatial input organization could be indirectly inferred from the functional properties of the FD-cells. In this respect, two main conclusions emerge from the analysis of the FD-cells. Firstly, the receptive fields of the presumed pool cells in the input circuitry of each FD-cell cover altogether the entire horizontal extent of the visual field of both eyes. Secondly, the ipsilateral as well as

contralateral presumed pool cells have specific preferred directions of motion. In the topologically simplest version of the models they are either directionally selective or bidirectional, depending on the FD-response type under consideration (see Fig. 1). Therefore, the spatial organization of the information processing stage preceding the output elements of the figure-ground discrimination network appears to be more complicated than has been imagined on the basis of behavioural experiments alone (see Reichardt et al., 1983).

The models for the different FD-cells shown in Figs. 1, 5, and 6 have been formulated so that as few pool cells as possible are postulated in the input circuitry of each FD-cell. However, if one regards the network of FD-cells as a whole, one can result in a more parsimonious solution with respect to the minimal number of pool cells required. To achieve this end the bidirectional pool cells in the input circuitry of the FD3- and FD4-cell have to be divided into two directionally selective ones with opposite polarity. This has, of course, no influence on the response properties of these FD-cells, but might be reasonable with respect to the potential neuronal substrate in the brain, since only directionally selective large-field units have been described so far in the lobula plate. Under these conditions a minimum of two pool cells in each half of the brain, one responding to progressive, the other two regressive motion, would be sufficient to account for the spatial integration properties of all output cells of the optic lobes involved in figure-ground discrimination. As a precondition for such a scheme it is demanded that these pool cells operate independently from each other and interact in specific combinations with the different FD-cells.

Are there any cellular candidates which might represent the pool cells in the input circuitry of the FD-cells? It seems to be reasonable to search for them in the lobula plate, since there reside a wealth of tangential cells representing wide-field motion information (Hausen, 1981, in preparation). Several of them can be speculated as being appropriate for a role as pool cell in figure-ground discrimination. Only one possibility will be discussed here that emanated from a recent study of Hausen (in preparation). It concerns the CH- and the H5-neurones, both being centripetal elements projecting to the lobula plate from either the ipsi- or contralateral posterior optic foci of the ventral protocerebrum, respectively. Whereas the CH-cells respond selectively to ipsilateral progressive and contralateral regressive motion (Hausen, 1976, 1981; Eckert and Dvorak, 1983), the H5-neurone is excited by ipsilateral regressive and contralateral progressive motion (Hausen, in preparation). From their anatomy both cell types seem to be destined to reconvey information to the lobula plate and to interact in some way with the retinotopic array of input elements or directly with the dendritic tree of other tangential cells. Therefore, it is highly suggestive to speculate that they play a role in the input circuitry of the FD-cells.

2 How Does the Circuit Account for Variability in Figure-Ground Discrimination Behaviour?

When taking a closer look at the outcome of the behavioural figure-ground discrimination experiments, it is obvious that a fly does not respond in the same way at different times to identical visual stimuli. This is not particularly surprising since, in addition to its visual afferences, an animal has to make allowance for both non-visual sensory input as well as its "internal state" in order to behave in an adaptive way in a richly structured natural habitat. The variability in the behavioural response of the fly to relative motion has been proposed to result from differential weighting of the different parallel output cells of the visual ganglia involved in yaw-torque control. This hypothesis could be shown by computer simulations to be in accordance with both the available behavioural results as well as the data on the Horizontal system and the FD-neurones. Since these cell classes show very stereotyped response patterns to a given stimulus (see also Hausen, 1984) and do not reveal anything like the variability found at the behavioural level, none of them can account for the behavioural variability on its own. Two further conclusions are suggested by these results. Firstly, the biophysical mechanism proposed by Reichardt et al. (1983; see also Egelhaaf, 1985a) is not responsible for the variability observed in figure-ground discrimination behaviour, because it relies on variable response profiles in the output elements of the underlying neuronal network. Secondly, the processing of visual information is performed rather independently from the influence of other non-visual sources up to as high a level of integration as the lobula plate tangential neurones. Any pronounced non-visual input contributing to the variability in figure-ground discrimination behaviour interferes with the main pathways computing visual information at some stage subsequent to the lobula plate. The latter conclusion is in accordance with recent anatomical results (Strausfeld and Bacon, 1983; Strausfeld et al., 1984). At the level of descending neurones which are postsynaptic to the lobula plate output elements there are extensive non-visual input connexions mediating ocellar, mechanosensory and olfactory information but also input from the central protocerebrum.

3 Significance of Two Circuits with Different Spatial Integration Properties

Every biological information processing system is understood as a phylogenetic adaptation to the specific

problems it encounters in its natural environment. For this reason, the functional significance of the neuronal networks contributing to the fly's yaw torque response to relative motion can only be assessed appropriately, if one knows their specific computational tasks. On the one hand, the yaw torque generated by the fly in the optomotor reaction to large moving patterns has been regarded for long as a specific means to counteract unintended deviations from the flight course by minimizing rotations relative to the environment (e.g. Fermi and Reichardt, 1963; Götz, 1964, 1968; McCann and MacGinitie, 1965). On the other hand, the characteristic time course of the yaw torque resulting in a turn towards the target was used in our behavioural experiments on figure-ground discrimination as the indicator that the target had been detected (Reichardt and Poggio, 1979; Reichardt et al., 1983; Egelhaaf, 1985a). The computational goal of discriminating a moving target in front of a background structure can, thus, be concluded to be the fixation of the target in the frontal part of the fly's visual field.

A visual information processing system designed to detect and fixate small moving targets is certainly most efficient in doing so, if it is tuned selectively to the appropriate target size. On the other hand, a system primarily involved in optomotor course control should be sensitive for wide-field motion. Since fixation of small objects and stabilization of flight course are different tasks it would be attractive from a computational point of view, if the underlying neuronal circuits were kept separate. Hence, it is not very surprising that one actually finds two anatomically and functionally distinct subcircuits implemented in the fly's brain which seem to be suitable for these different goals. Both are tuned to a different range of target size. The network assumed to underly the optomotor course control with the Horizontal Cells as its output elements is relatively, though not completely, insensitive to variations in stimulus width (Hausen, 1981, 1982b; see also Egelhaaf, 1985a). On the other hand, the network of FD-cells is much more sensitive to small-field than to wide-field motion. It appears, thus, to be well suited for detecting and fixating efficiently a small target. Hence, the relevant information for optomotor course control and fixation of moving targets is represented separately at the level of output elements of the optic lobes and, thus, can be utilized independently and to a variable extent in different information processing tasks, such as figure-ground discrimination. Although both parallel networks are involved in generating the characteristic time course of the yaw torque response to relative motion of a figure and a background structure, the figure is detected and fixated the better the higher the relative contribution of the FD-cells to the final behavioural response.

4 Why Does the Detectability of a Figure not Depend on the Direction of Background Motion? A Possible Explanation

There is one decisive difference between the perception of relative motion in humans and figure-ground discrimination in the fly. In humans a figure can be discriminated in front of a background structure by movement information alone, if both move in opposite directions (e.g. Baker and Braddick, 1982; van Doorn and Koenderink, 1982). Consequently, for oscillatory movement with a phase shift of 180° the figure is easily detectable in psychophysical tests, whereas the figure remains hidden in the ground, if they have the same texture and move synchronously. In contrast, a figure cannot be discriminated by the fly against an equally textured ground, if they are oscillated in counterphase with the same frequency and amplitude, but is detected easily for other phase relations (Reichardt and Poggio, 1979; Reichardt et al., 1983; for specific changes of the phase dependence of figure-ground discrimination at low oscillation frequencies, see Reichardt and Poggio, 1979). It should be noted, however, that the figure remains hidden in the ground during synchronous and counterphase oscillation only as long as they have the same texture, contrast and speed. If they differ in these characteristics, as is usually the case under natural conditions, the figure can be detected even during synchronous and counterphase oscillation (Reichardt and Poggio, 1979; Guo and Reichardt, in preparation). For given differences in speed and/or texture between figure and background the figure is then equally detectable irrespective of whether they move in the same or in opposite directions. This characteristic feature at the behavioural level is well reflected at the underlying neuronal level in the large-field input organization of the FD-cells (Egelhaaf, 1985b).

This different performance of man and fly in the evaluation of relative motion is, however, only surprising as long as one does not take into account that the actual goal of figure-ground discrimination in the fly is the detection and subsequent fixation of a target. In this context, the above peculiarity of fly figure-ground discrimination means that for a given position and velocity of the figure the same turning amplitude is induced irrespective of the direction of ground motion. This is likely to be advantageous, if a target has to be tracked against a background that frequently reverses its direction of motion relative to the eye. As is indicated by a recent study (Wagner, 1985), this is just what can be observed during pursuit manoeuvres of freely flying flies: The pursuing fly does not follow at an angular velocity which is proportional to the change in the flight path of the leading fly, but usually executes a sequence of 10–20 fast turns per second which lead to retinal large-field motion of continually changing sign.

Hence, in this respect the specific properties of figure-ground discrimination and, accordingly, the underlying neuronal networks appear to be well adapted to the particular needs a tracking fly encounters under natural conditions.

Acknowledgements. I am indebted to W. Reichardt for numerous discussions and continuous support of this study. K. Hausen, H. Wagner, C. Wehrhahn, and J. Zanker are all thanked for reading and criticizing previous versions of the text. The figures are due to the skill of K. Bierig, I. Geiss, and L. Heimburger. The manuscript was typed by I. Geiss.

This work is part of a doctoral dissertation submitted to the University of Tübingen (FRG) and was supported by the Max-Planck-Gesellschaft.

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Received: May 3, 1985

Martin Egelhaaf
Max-Planck-Institut
für biologische Kybernetik
Spemannstrasse 38
D-7400 Tübingen
Federal Republic of Germany

Verantwortlich für den Textteil: Prof. Dr. W. Reichardt, Max-Planck-Institut für biologische Kybernetik, Spemannstr. 38, D-7400 Tübingen. Verantwortlich für den Anzeigenteil: E. Lückermann, Springer-Verlag, Kurfürstendamm 237, D-1000 Berlin 15, Fernsprecher: (030)8821031, Telex: 01-85411. Springer-Verlag, Berlin · Heidelberg · New York · Tokyo. Druck der Brühlschen Universitätsdruckerei, Gießen. Printed in Germany.