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

II. Figure-Detection Cells, A New Class of Visual Interneurones

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Abstract. A new class of large-field tangential neurones (Figure Detection (FD-) cells) has been found and analysed in the lobula plate, the posterior part of the third visual ganglion, of the fly by combined extra- and intracellular recording as well as Lucifer Yellow injection. The FD-cells are likely to play a prominent role in figure-ground discrimination. Together with the Horizontal Cells, the output elements of the neuronal network underlying the optomotor course control reaction, they seem to be appropriate to account for the characteristic yaw torque response to relative motion. The FD-cells might thus compensate for the "deficits" of the Horizontal Cells with respect to figure-ground discrimination (see Egelhaaf, 1985a).

The FD-cells are directionally selective for either front-to-back (FD 1, FD 4) or back-to-front motion (FD 2, FD 3). Their excitatory receptive fields cover part of (FD 1, FD 2, FD 3) or the entire horizontal extent (FD 4) of the visual field of one eye. Their most important common property in the context of figure-ground discrimination is that they are more sensitive to relatively small objects than to spatially extended patterns. Their response to a small figure is much reduced by simultaneous large-field motion in front of the ipsi- as well as the contralateral eye. This large-field inhibition is either directionally selective or bidirectional, depending on the FD-cell under consideration. The main dendritic arborization of all FD-cells resides in the lobula plate. Their axonal projections lie in either the ipsi- or contralateral posterior optic foci and, thus, in the same area as the terminals of the Horizontal Cells. The FD-cells are, therefore, appropriate candidates for output elements of the optic lobes involved in figure-ground discrimination.

Introduction

Flies can easily discriminate an object ("figure") from a textured surround, if they move relatively to each other. During the last years figure-ground discrimination by relative motion has been intensively studied at the behavioural level (Reichardt and Poggio, 1979; Poggio et al., 1981; Reichardt et al., 1983). The characteristic time course of the yaw torque generated by the fly was used in these behavioural experiments as an indicator that the figure had been detected. With respect to the neuronal basis of this visual information processing task it has initially been proposed (Reichardt et al., 1983) that the neuronal network controlling the optomotor yaw torque reaction (e.g. Hausen, 1981; Hausen and Wehrhahn, 1983) might also underly figure-ground discrimination. The Horizontal Cells as the output cells of this network might correspond in this case to the output elements of the neuronal circuit responsible for figure-ground discrimination. The Horizontal Cells receive excitatory and inhibitory input from two retinotopic arrays of small-field movement detectors which respond to front-to-back (progressive) and back-to-front (regressive) motion, respectively (Hausen, 1982a, b). As large-field integrating elements they have specific functional properties which can be related directly to the final behavioural yaw torque response (Hausen, 1981; Reichardt et al., 1983). In the first of this series of papers (Egelhaaf, 1985a) the potential role of the Horizontal Cells in figure-ground discrimination has been reinvestigated. Their functional properties were compared with the predictions inferred from the specific properties of figure-ground discrimination behaviour for the output elements of the underlying neuronal network. It has been concluded that the Horizontal Cells are not sufficient to control yaw torque generation in figure-ground discrimination and that an additional neuronal network is required.

From the "deficits" of the optomotor neurones with respect to figure-ground discrimination the constraints have been inferred that are imposed on the output cells of the postulated additional neuronal

network (Egelhaaf, 1985a). Firstly, the additional output cells should be motion sensitive large-field neurones which respond better to relatively small textured objects than to spatially extended patterns. Secondly, specific heterolateral interactions are required in their input circuitry. As the most obvious consequence of these interactions, the output cells of the network should be inhibited by ipsi- as well as contralateral wide-field motion in either horizontal direction. Thirdly, the additional output cells should usually be excited by progressive motion and inhibited by regressive motion. However, the sign of synaptic transmission of their presynaptic input elements sensitive to regressive motion should be variable and occasionally lead to depolarization of the cell. Alternatively, if this kind of variability were not an intrinsic property of these cells, two parallel sets of output elements are required in addition to the Horizontal Cells, one responsive to progressive, the other to regressive small-field motion. Fourthly, their axonal projections should be appropriate for output elements of the optic lobes involved in the control of yaw torque generation.

A new class of visual interneurones has been found in the lobula plate, the posterior part of the third visual ganglion, which satisfy these conditions, or at least part of them. In this paper the functional and anatomical properties of these cells will be analysed in some detail. Mainly those properties will be addressed which are related to the aforementioned constraints. Possible neuronal mechanisms responsible for these functional properties will be discussed in a theoretical analysis in the subsequent paper (Egelhaaf, 1985b).

Materials and Methods

The experimental apparatus and part of the experimental procedures have been described in the preceding paper (Egelhaaf, 1985a). Only those methods will be described here which were not employed in the preceding study.

All recordings were done from the lobula plate, the posterior part of the third visual ganglion (e.g. Hausen, 1981; see Fig.1 in Egelhaaf, 1985a). The extracellular recordings were done with glass capillaries (borosilicate glass; 1.5mm outer diamter; 1.17mm inner diamter, Hilgenberg) pulled on a vertical puller (Getra, München). The tip diamter amounted to approximately 1μm. The pipettes were usually filled with a 2M KCl-solution and had resistances of 3–8MΩ.

For intracellular recording and dye injection glass micropipettes (borosilicate glass, 1mm outer diamter, 0.57mm inner diameter, Hilgenberg) with taper lengths of less than 10mm and tip diameters smaller than 0.1μm were pulled with a modified MC753 Moving Coil Electrode Puller (Campden Instruments, London). When filled with 2M potassium acetate solution, the electrodes had resistances of 50–100MΩ. For recordings with subsequent dye injection the micropipettes were filled with a solution of 4% Lucifer Yellow CH (Stewart, 1978) in 1MLiCl. Lucifer Yellow CH (EGA, Weinheim) was injected into the cells by DC-iontophoresis with 2–5nA. Usually injection times ranged between 3 and 5min. After injection the animal was left alive for 30–60min to allow the dye to spread into all branches of the injected cell. This measure was taken although inspection of the brain in the opened head capsule under UV-illumination revealed complete overall staining of the cell just after the dye injection was finished.

The preparation was fixed for 1h in a PIPES-formaldehyde fixative (10ml 37% formaldehyde; 90ml 0.1M PIPES (1,4-Piperazinediethanesulfonic acid, SIGMA); 6g saccharose; 1ml 1% $CaCl_2 \cdot H_2O$; pH:7.3), dehydrated for 1h in a mixture containing 25% 2,2-dimethoxypropane, 67,5% methanole, and 7.5% aceton and for 1h in 100% 2,2-dimethoxypropane and embedded in paraffine (Tissue prep, Fisher Scientific; 2 changes). Serial sections (12μm thick) were taken in the frontal plane of the brain on a rotatory microtome (Autocut 1140, Jung), deparaffinized in xylene and mounted in a fluorescence-free medium (Entellan, Merck).

The sections were examined under a fluorescence microscope with epi-illumination (Orthoplan, Leitz). It was equipped with high resolution low power fluorite lenses (Zeiss, Plan Neofluar 16/0.5W-Oel; 25/0.8W-Oel), an automatic Camera (Vario-Orthomat, Leitz) and a HBO 100W mercury lamp. The filters used were as follows: Leitz BP390–490 excitation filters, a Leitz RKP510 dichotic mirror and a Leitz LP515 barrier filter. Stained cells were routinely photographed with Kodak Ektachrome EL135/36 400ASA or 3M Color Slide 1000ASA. The cells were reconstructed from serial sections by sequential projection of the colour slides onto a drawing table.

All positions of the stimulus are given in a head centered coordinate system. ψ denotes the horizontal angular position with respect to the longitudinal axis of the head. $\psi > 0°$ and $\psi < 0°$ correspond to positions in the right and left half of the visual field, respectively. Progressive and regressive motion stand for front-to-back and back-to-front motion, respectively.

Results

A new class of directionally selective motion-sensitive visual interneurones has been found in the lobula plate. Their most prominent functional property is that they are more responsive to the motion of small objects than to large textured patterns. Therefore, they have been termed "Figure Detection" (FD) cells. The intracellularly recorded response pattern of such a FD-cell is displayed in Fig.1. The stimulus conditions were as follows: A textured vertically oriented stripe ("figure") placed in the centre of the cell's excitatory receptive field and a binocular equally textured ground panorama ($-120° \leqq \psi \leqq 120°$) were initially oscillated in phase about the dorso-ventral axis of the fly's head. After two cycles of synchronous oscillation, the ground stopped moving and the figure continued oscillating for another two cycles. As is characteristic for all FD-neurones, their response consists of graded membrane potential changes as well as regular spike activity, when the cell is penetrated in the lobula plate near the convergence region of the main dendrites and the axon.

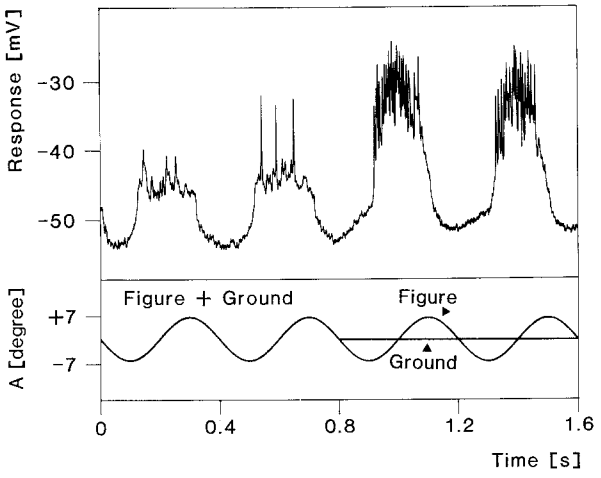

Fig. 1. Intracellular recording of a FD1-cell. This cell was stained with Lucifer Yellow and is shown in Fig. 6a. After two cycles of synchronous oscillation of a 12°-wide textured figure and a binocular ground ($-120° \leqq \psi \leqq 120°$) the ground stopped moving, while the figure continued oscillating for another two cycles. The oscillation frequency amounted to 2.5 Hz, the amplitude to $\pm 7°$. The figure was positioned in the cell's excitatory receptive field at an angular horizontal position of $\psi = 10°$. The cell was penetrated in the lobula plate at the branching point of the main dendrites and the axon. As the other FD-cells, the FD1-neurone is much more depolarized when the figure oscillates in front of the stationary ground than when they move synchronously. Concomitantly, during synchronous oscillation spikes are superimposed only sporadically on the graded depolarizations. In contrast a high-frequency spike train is generated when only the figure moves in the cell's preferred direction

Small-amplitude action potentials are usually superimposed on the graded depolarizations. The FD-cell shown in Fig.1 is depolarized by progressive motion in front of the right eye and hyperpolarized by motion in the opposite direction. In contrast to the optomotor neurones (see Reichardt et al., 1983; Egelhaaf, 1985a), the FD-cells show only a weak excitatory response during synchronous oscillatory motion of figure and ground (time 0–0.8s in Fig.1). Their response is much stronger when the ground stops moving while the figure keeps oscillating in the cell's excitatory receptive field (time 0.8–1.6s in Fig.1).

Four different FD-response types have been found so far. They differ with respect to their preferred direction of motion and their spatial input organization. Due to their small axon diameter (less than 5 μm) it was difficult to record from them intracellularly. Therefore, mainly extracellular recording techniques were employed to study their functional properties quantitatively. Intracellular recording was only used to stain the different cell types and to characterize them qualitatively in order to correlate their structure and function. Although the reasons remain somewhat mysterious, some of the FD-cells could be recorded from much more frequently than others despite intensive search for all of them. Therefore, the different cell types could not be characterized equally well.

1 The FD1-Cell

The FD1-neurone is selectively excited by progressive motion in the frontal part of the eye ipsilateral to its dendritic tree and responds much better to small-field than to wide-field motion. This is illustrated by the spike frequency histogram shown in Fig.2 which represents the response to two cycles of synchronous oscillation of a 12°-wide textured figure and an equally textured binocular ground (wide-field motion) and, subsequently, two cycles of figure motion alone (small-field motion).

1.1 Spatial Input Organization. The excitatory receptive field of the FD1-unit covers along its horizontal axis only the frontal part of the field of view. This is illustrated in Fig.3. In all excitatory receptive field measurements shown in this study a 6°-wide figure was successively oscillated about variable positions. The resulting response to several stimulus presentations was averaged and is plotted against the particular

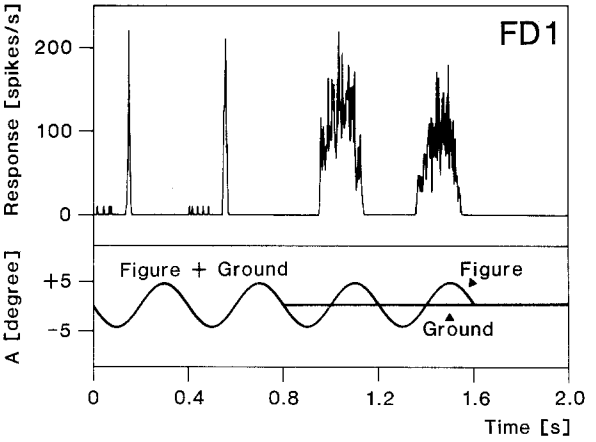

Fig. 2. Response of a FD1-cell to wide-field and small-field motion. After two cycles of synchronous motion of a 12°-wide textured figure and a binocular textured ground, the ground stopped moving while the figure continued oscillating for another two cycles (see bottom traces). Oscillation frequency: 2.5 Hz; oscillation amplitude: $\pm 5°$. This stimulation sequence was followed by an interstimulus interval of 1.2 s. The figure was oscillated within the excitatory receptive field of the cell about an angular position of $\psi = 10°$. With respect to the right eye, movements from $-5°$ to $+5°$ are progressive movements, whereas movements from $+5°$ to $-5°$ are regressive movements. The response curve represents the spike frequency histogram obtained from 32 repetition of the stimulus programme. The cell was recorded from in the mediolateral part of the right lobula plate with an extracellular electrode. Apart from brief transient responses the cell is almost silent during synchronous motion of figure and ground, whereas it shows a strong response when the figure moves progressively in front of the stationary ground

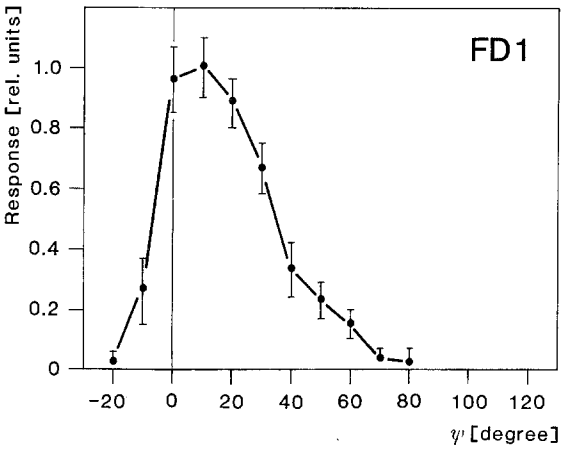

Fig. 3. Horizontal extent of the excitatory receptive field of a FD1-cell. The cell was stimulated by a 6°-wide figure oscillating successively about variable angular horizontal positions with a frequency of 2.5 Hz and an amplitude of ±5°. The resulting response was recorded extracellularly in the medio-lateral part of the right lobula plate. Each data point was averaged from 40 measurements and represents the mean number of spikes per stimulation cycle. The bars denote the corresponding standard deviations. The responses were normalized with respect to the maximal response obtained in this experiment. This spatial sensitivity distribution illustrates that the excitatory receptive field of an FD1-cell is confined to the frontal part of the visual field of the ipsilateral eye

figure position. In this way the horizontal extent of a cell's excitatory receptive field could be explored. The FD1-unit has a prominent spatial sensitivity maximum. Its mean position which has been determined from quantitative receptive field measurements in 7 preparations lies at approximately $\psi = 10°$, as in the example shown in Fig.3. At half-maximum sensitivity the receptive field has an average width of 43° ± 9°. Its frontal boundary lies in the contralateral half of the visual field at about $\psi = -10°$. This coincides well with the margin of the visual field of the right eye (Beersma et al., 1977). The lateral receptive field boundary lies in the range between $\psi = 50°$ and 70°. It should be emphasized that the different values of the receptive field plots do not represent the sensitivity of only a single point in the visual field, but rather a mean sensitivity of the entire area which is stimulated by the oscillating figure. This might slightly enlarge the recorded receptive field width. The vertical angular extent of the excitatory receptive field could not be measured quantitatively with the stimulation apparatus used in this study. Qualitative measurements with hand-held probes revealed that it covers the entire vertical extent of the visual field.

The large-field input organization of the FD1-cell was studied in experiments where a small figure was positioned in the centre of the excitatory receptive field while the ground covered alternatively both eyes, only the right or the left eye, respectively. Figure and ground were oscillated sinusoidally either in phase or in counterphase. Figure 4 shows the pooled data from five different preparations which could be tested each with the complete stimulation programme (see insets in Fig.4). For better comparison, the response amplitudes were normalized with respect to the response induced by figure motion alone. When the binocular ground is oscillated together with the figure the response of the cell is much reduced. This inhibitory effect of wide-field motion is independent of whether figure and ground oscillate synchronously or with a phase shift of 180°. The response is almost as much reduced when the ground stimulates only the eye ipsilateral to the cell's excitatory receptive field. Also under these conditions the reduction of the response does not depend on the direction of ground motion. This only holds, however, if the figure is small in its horizontal extent as compared with the cell's excitatory receptive field (e.g. 6°, as in the experiments shown in Fig.4). If, for instance, a 48°-wide figure oscillates in counterphase with either a binocular or an ipsilateral ground, the

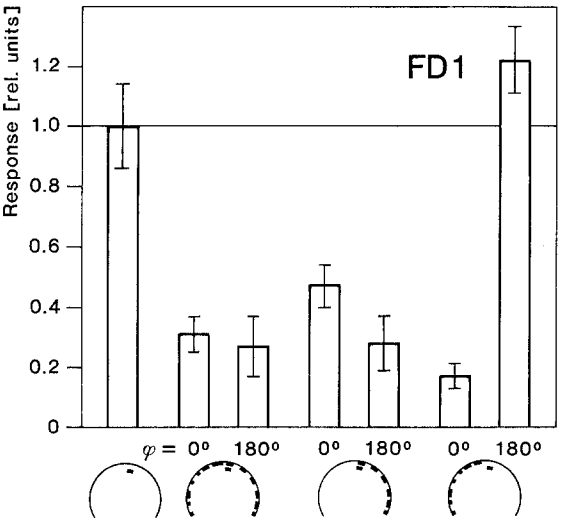

Fig. 4. Large-field input organization of the FD1-cell. A 6°-wide figure was positioned in the cell's excitatory receptive field at $\psi = 10°$. There was either no ground texture or it covered both eyes, the right or the left eye, respectively, as is indicated by the insets. The figure was oscillated either alone or together with the ground. The oscillation amplitude amounted to ±5°, the relative phase between figure and ground to $\varphi = 0°$ or $\varphi = 180°$ and the oscillation frequency to 2.5 Hz. Each column represents the time-averaged response to 230 stimulation cycles obtained from 5 different flies. The response amplitudes were normalized with respect to the response induced by figure motion alone. The vertical bars denote the standard deviation of the mean. The histogram illustrates that the inhibition exerted on the FD1-cell by wide-field motion is not restricted to input from the ipsilateral eye only. Instead, the response is reduced considerably by contralateral regressive motion of the ground ($\varphi = 0°$) and increased slightly by motion in the reverse direction ($\varphi = 180°$)

response amplitude is much less reduced or not reduced at all as compared with the response to figure motion alone. When the ground is located on the contralateral side, the response of the cell diminishes much upon stimulation with synchronous motion of figure and ground. It is not reduced when they are oscillated with a phase shift of 180°. Instead, the response appears to be slightly enhanced.

Since the excitatory receptive field of the FD1-unit is confined to the frontal part of the field of view, the question arises whether its ipsilateral inhibitory input is also spatially restricted or can be induced equally well along the entire horizontal extent of the visual field. This was tested in experiments where one 6°-wide figure (F_1) was oscillated about $\psi = 10°$, while a second figure (F_2) oscillated about variable positions (see inset in Fig.5). The cell's response to motion of both figures in phase (○ in Fig.5) and in counterphase (● in Fig.5), respectively, is plotted against the mean angular position of F_2. When both F_1 and F_2 are located within the excitatory receptive field of the cell and oscillate synchronously the response is slightly enhanced as compared with the response to motion of F_1 alone. In contrast, the response diminishes considerably, when the two figures are oscillated with a phase shift of 180°. Beyond both margins of the excitatory receptive field the effect of F_2-motion is reversed with respect to the phase relations of both figures. In these parts of the ipsilateral as well as the contralateral visual field the response of the FD1-cell is significantly reduced during synchronous motion and slightly enhanced, if it is affected at all, upon motion with a phase shift of 180°.

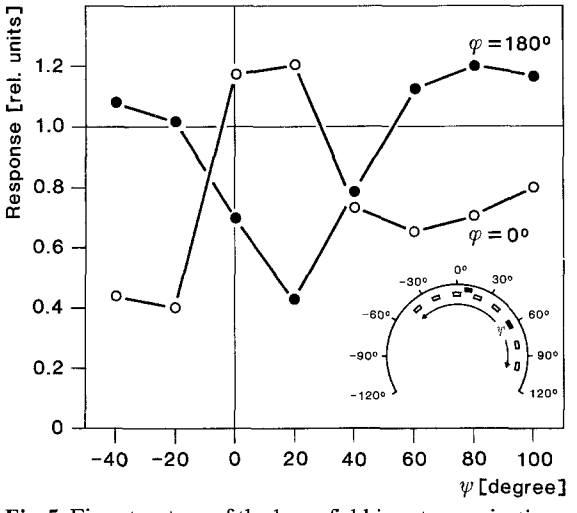

Fig. 5. Fine structure of the large-field input organization of the FD1-cell. A 6°-wide figure (F_1) was oscillated about a fixed position within the cell's excitatory receptive field ($\psi = 10°$), while a second 6°-wide figure (F_2) was oscillated about variable positions (see inset). The oscillation amplitude of both figures amounted to $\pm 5°$, their frequency to 2.5 Hz. They were either oscillated synchronously (○) or with a phase shift of $\varphi = 180°$ (●). The resulting response was normalized with respect to the response to motion of F_1 alone and is plotted against the mean angular position of F_2. Each value represents the time-averaged response to either 32 (○) or 64 (●) stimulation cycles. This experiment reveals that outside of the FD1-cell's excitatory receptive field its response is inhibited by ipsilateral progressive motion as well as regressive motion in front of the contralateral eye. Motion in the reverse directions does not inhibit the cell, but rather increases the response amplitude slightly

On this experimental basis the spatial input organization of the FD1-cell can be summarized as follows. Firstly, the cell is excited by small-field progressive motion and inhibited by regressive motion in a 60°–70°-wide vertically oriented stripe in the frontal part of the visual field. Secondly, it is inhibited by progressive wide-field motion in front of the ipsilateral eye; this inhibitory response component can be induced beyond the lateral margin of the cell's excitatory receptive field. Thirdly, the FD1-cell is inhibited by regressive motion in front of the contralateral eye.

The slightly enhanced response amplitudes during counterphase motion of a figure within the cell's excitatory receptive field and a second stimulus outside the excitatory receptive field (see Figs.4 and 5) can be understood easily, if the large-field inhibition of the cell is mediated by visual interneurones receiving excitatory input from the entire visual field of an eye (see Egelhaaf, 1985b). Due to this hypothesis, the contralateral large-field element in the input circuitry of the FD1-cell is assumed to be excited by regressive motion and inhibited by progressive motion. Given that this presumed large-field element shows a certain level of spontaneous activity, its activity can be decreased and increased with respect to this resting level depending on the direction of motion. Progressive ground motion in front of the contralateral eye, therefore, reduces inhibition on the FD1-cell and, concomitantly, results in a slight increase in its response to a figure moving simultaneously in the excitatory receptive field. This disinhibition is in line with the experimental data (see Fig.4). It should be pointed out that spontaneous activity is a common feature among lobula plate large-field interneurones. The increased response observed during counterphase motion of one figure within and another ipsilateral figure outside the cell's excitatory receptive field (see Fig.5) can be explained in an equivalent way, if one assumes that the FD1-cell's response is reduced by an ipsilateral large-field neurone which is excited by progressive and inhibited by regressive motion.

1.2. Anatomy. Two different anatomical classes of lobula plate tangential neurones have been stained by intracellular Lucifer Yellow injection which had both to be classified as FD1-cells on the basis of three

functional criteria. Firstly, they were directionally selective for progressive motion. Secondly, they were more responsive to small targets than to an extended background structure. Thirdly, their excitatory receptive fields were located within the frontal vertical stripe of the ipsilateral field of view. Due to the short time a stable intracellular recording usually lasted, the spatial input organization of a cell could not be characterized more thoroughly in staining experiments. It should be noted, however, that all cells which conformed to the above criteria in the extracellular analysis could be classified as a single functional class. Hence, at present no unambiguous association of structure and function is possible in the case of the FD1-response type. Nevertheless, it cannot be excluded that with more specific visual stimuli this might eventually turn out to be possible.

The cell type which was stained most frequently in this study (7 injections) is a heterolateral output element of the lobula plate. Due to its axonal pathway it belongs to a class of cells which has been termed by Hausen (in preparation) as "noduli group". It will, therefore, be designated as "$FD1_{nod}$-cell" in the present study. Figure 6a shows a serial reconstruction of a representative of this cell class projected on a semi-schematic frontal view of part of the brain. Its main dendritic tree resides in a thin layer being parallel to the frontal and caudal surface of the lobula plate. It covers almost the entire dorso-ventral extent of the lateral part of this neuropile. Because of the strict retinotopic organization of all visual ganglia this part of the lobula plate represents the frontal vertical stripe of the ipsilateral visual field. This conclusion is in good agreement with the electrophysiologically determined excitatory receptive field of the FD1-neurone (see Fig.3). The axon of the $FD1_{nod}$-cell projects from the lobula plate to the posterior optic foci on the contralateral side of the brain. On its course through the protocerebrum the axon passes the central complex ventrally of the ellipsoid body and directly posterior to the noduli (this pathway is indicated schematically in Fig.1 in Egelhaaf, 1985a). It should be mentioned that the axonal terminal shown in Fig. 6a has only been stained rather faintly and, hence, might not be resolved completely in the reconstruction. The $FD1_{nod}$-cell has a second smaller dendritic tree in the lateral protocerebrum. That this arborization represents an additional input region is suggested by the analysis of cobalt-impregnated cells (Hausen, in preparation). These reveal distinct structural differences between dendrites and axon terminals which cannot be resolved unambiguously on the basis of Lucifer Yellow-stained material. In two cells the additional dendritic tree could not be detected, although they had to be classified as $FD1_{nod}$-cells by their functional properties,

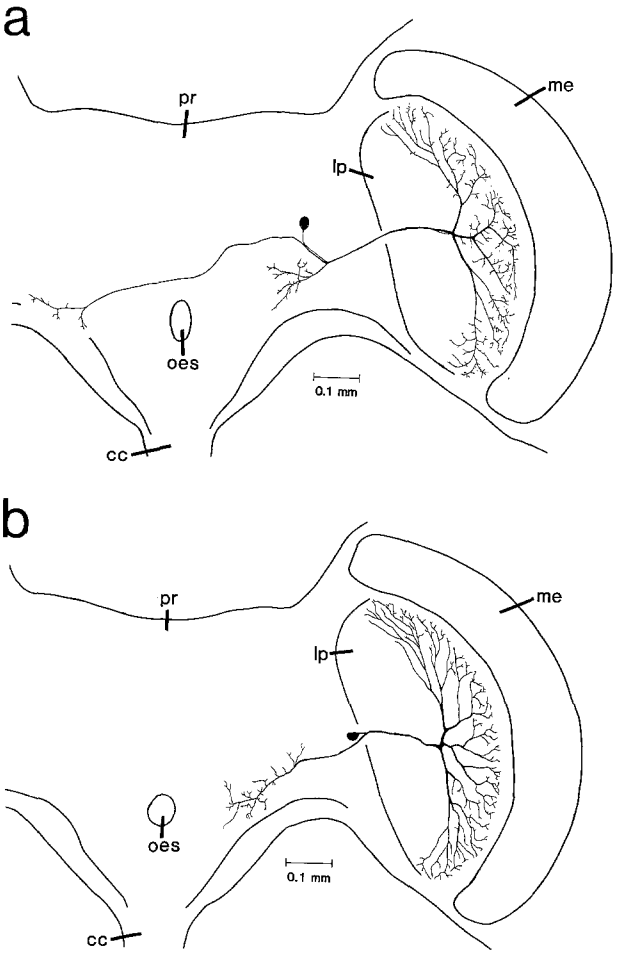

Fig. 6a and b. Structure of the two anatomical representatives of the FD1-response type. Serial reconstructions of intracellular Lucifer Yellow injections. **a** The $FD1_{nod}$-cell; **b** the $FD1_{pof}$-cell. The tracings were obtained from 12 µm frontal sections and show the cells drawn into a semi-schematic frontal view of part of the brain. For further explanations see text. Abbreviations: cc: cervical connective; lp: lobula plate; me: medulla; oes: oesophagus; pr: protocerebrum

main dendritic arborization and axonal projection. This is, however, likely to be due to incomplete staining of the cell, which might well occur when it is penetrated in its axon rather than in its main dendritic tree. It should be noted that both the axon as well as the additional dendritic tree branch off from the main dendrites near their site of convergence and leave the lobula plate as separate, though closely adjacent and in most cases not resolvable fibres. They are accompanied by a third fibre leading to the cell body which is located in the lateral protocerebrum.

The second class of cells with FD1-response properties also represents an output element of the lobula plate. It terminates in the ipsilateral posterior optic foci where it ramifies near the surface of the brain. This is revealed by the reconstruction of Fig. 6b. This anatom-

ical variant of the FD1-response type has been termed $FD1_{pof}$-cell because of its axonal termination site. Its dendritic tree covers a similar area in the lateral lobula plate as the $FD1_{nod}$-cell. Due to the retinotopic organization of all visual ganglia this is expected for a cell with an excitatory receptive field in the frontal part of the field of view. The cell body of the $FD1_{pof}$-neurone lies near the posterior surface of the lateral protocerebrum.

2 *The FD2-Cell*

The functional properties of the FD2-cell have been analysed least thoroughly of all FD-cells. This is because it could be recorded from only intracellularly so far, thus considerably limiting the time available for doing quantitative measurements. It could never be found with electrodes destined for extracellular recording. This is surprising since its dendritic tree covers almost the same area of the lobula plate as the FD1-cell which was recorded from most frequently of all FD-cells.

As the other FD-cells, the FD2-cell is directionally selective and most sensitive to the motion of relatively small targets. In contrast to the FD1-cell, however, it is excited by regressive motion and inhibited by motion in the opposite direction. These functional properties of the FD2-cell are illustrated by the spike-frequency histogram shown in Fig.7. The response amplitude of the cell is considerably larger when the figure oscillates alone and the ground is kept stationary (time 0.8–1.6s in Fig.7) than when they move together (time 0–0.8s in Fig.7).

2.1 Spatial Input Organization. The excitatory receptive field of the FD2-cell is located in the frontal part of the visual field. It could only be tested qualitatively so far. Its maximum of sensitivity lies at angular positions between $\psi = 0°$ and $\psi = 10°$. The frontal receptive field boundary is located between $\psi = -10°$ and $\psi = -5°$ and, therefore, coincides with the margin of the field of view of the ipsilateral eye. Laterally the excitatory receptive field of the FD2-cell reaches as far as approximately $\psi = 60°$. In the vertical direction it covers the entire visual field of the eye. The large-field input organization of the FD2-cell could not be resolved in the intracellular recording experiments of the present study.

2.2 Anatomy. The FD2-cell was stained by intracellular Lucifer-Yellow injection in five preparations. As is illustrated by the reconstructed example shown in Fig.8, it represents an output element of the lobula plate projecting to the ipsilateral posterior optic foci.

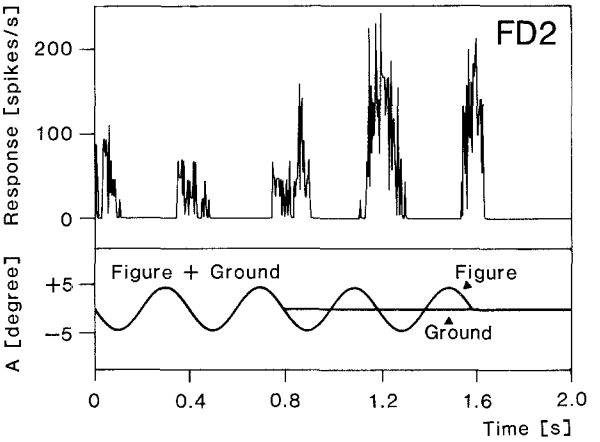

Fig. 7. Response of a FD2-cell to two cycles of synchronous oscillation of a 12°-wide figure and a binocular ground and subsequently two cycles of figure motion alone. The figure was oscillated within the cell's excitatory receptive field about an angular position of $\psi = 10°$. The other stimulus conditions were as described in the legend of Fig. 2. The response curve represents the spike frequency histogram obtained from 16 repetitions of the stimulus programme. The cell was recorded from intracellularly in the medio-lateral part of the right lobula plate. As is characteristic for FD-cells, the FD2-cell responds much stronger to small-field motion as compared to wide-field motion. In contrast to the FD1-cell, it is directionally selective for regressive motion

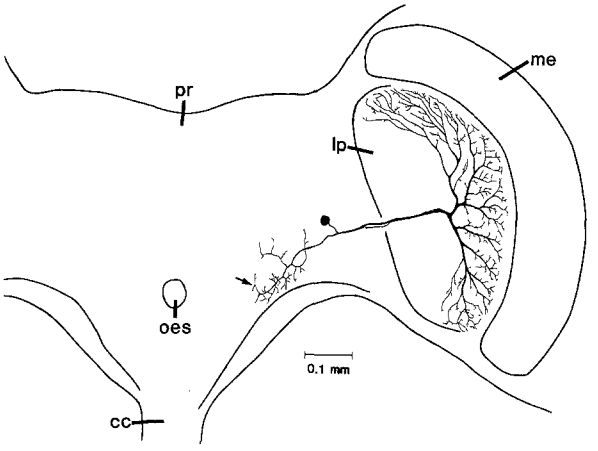

Fig. 8. Anatomical structure of the FD2-cell. Serial reconstruction of intracellular Lucifer Yellow injection. The cell is drawn into a semi-schematic frontal view of part of the brain. The axonal branch projecting frontally most probably into the anterior optic foci is indicated by an arrow. For further explanation see text. Abbreviations: see legend of Fig. 6

Due to its excitatory receptive field in the frontal part of the field of view, its dendritic tree covers the lateral part of the lobula plate along its entire dorso-ventral extent. The main axonal terminal ramifies near the posterior surface of the brain. One terminal branch, however, turns off anteriorly and runs frontally for some 70–90μm (arrow in Fig. 8). It most probably

projects into the area of the anterior optic foci where, in the first place, columnar output elements of the lobula terminate. The cell body of the FD2-cell is located near the posterior surface of the lateral protocerebrum.

3 *The FD3-Cell*

The FD3-cell is excited by regressive motion and inhibited by motion in the reverse direction. This is illustrated by the spike-frequency histogram shown in Fig.9. As is characteristic for FD-cells, the FD3-cell responds best when only a figure with a relatively small angular horizontal extent oscillates in its excitatory receptive field (see Fig. 9 between time 0.8 and 1.6 s). Its response is much reduced when figure and ground oscillate together (see Fig. 9 between time 0 and 0.8 s).

3.1 Spatial Input Organization. The excitatory receptive field of the FD3-cell does not cover the entire horizontal extent of the field of view (Fig.10). It has a maximum at angular positions between 40° and 50° as has been determined from quantitative receptive field measurements in 5 preparations. At half maximum sensitivity the excitatory receptive field has an average width of approximately $62° \pm 7°$. It reaches laterally as far as approximately $\psi = 100°$; its frontal margin lies at an angular position of about $\psi = 20°$. The FD3-cell is so far the only FD-unit which does not receive excitatory input in the most frontal part of the eye. Qualitative measurements with hand-held probes revealed that the excitatory receptive field of the FD3-cell covers the entire vertical extent of the visual field.

The large-field input organization of the FD3-cell was studied quantitatively in the same way as has been described for the FD1-unit. The complete stimulation programme, where a figure in the cell's excitatory receptive field was oscillated in phase or in counterphase together with either a binocular, ipsilateral or contralateral ground, could be tested in five different flies. The results of these experiments are pooled in the histograms shown in Fig.11. In the experiments where a monocular ground was used, the frontal part of the visual field was covered by a 24°-wide mask in order to avoid stimulation of the contralateral eye. The FD3-cell shows a much weaker reaction when it is stimulated by large-field motion as compared with its response to figure motion alone. This inhibition can be observed irrespective of whether the ground stimulates both eyes, only the left or the right eye. Moreover, it is elicited by horizontal ground motion in either direction. In contrast to the FD1-unit, the inhibitory input to the FD3-cell originating from the contralateral eye is, thus, bidirectional. It is more difficult to deduce the spatial input organization of the ipsilateral eye, since here both excitatory as well as inhibitory response components interact in a complicated way. Closer inspection of the histograms shown in Fig.11, however, reveals an interesting response property of the

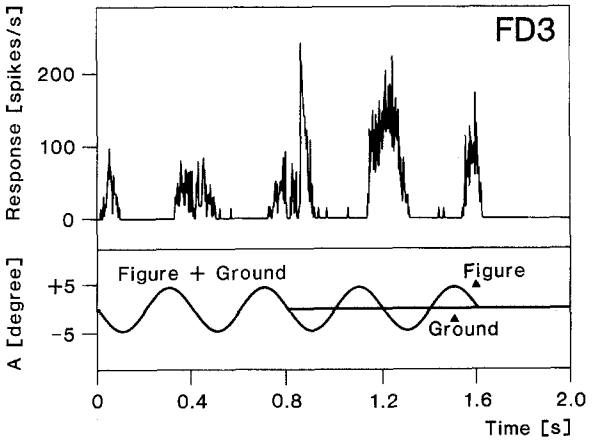

Fig. 9. Response of a FD3-cell to two cycles of synchronous oscillation of a figure and a binocular ground followed by two cycles of figure motion alone. The 24°-wide figure was oscillated in the cell's excitatory receptive field about an angular position of $\psi = 50°$. The details of the stimulus conditions are as given in the legend of Fig. 2. The response curve represents the spike frequency histogram obtained from 32 repetitions of the stimulus programme. The cell was recorded from extracellularly in the centre of the right lobula plate. It is directionally selective for regressive motion and responds much better to small-field than to wide-field motion

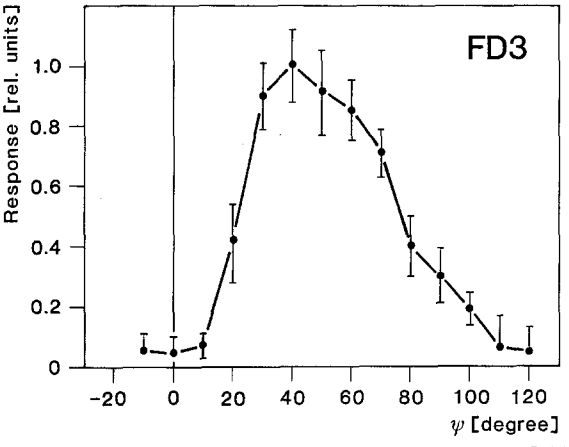

Fig. 10. Horizontal extent of the excitatory receptive field of a FD3-cell. The stimulus conditions and data evaluation were the same as described in the legend of Fig. 3. The cell was recorded from extracellularly approximately in the centre of the right lobula plate. Each data point represents the mean response to 50 stimulation cycles. This spatial sensitivity distribution illustrates that the excitatory receptive field of a FD3-cell covers in its horizontal extent the fronto-lateral part of the field of view. The cell is not excited by motion within the most frontal 10°- to 20°-wide vertical stripe of the visual field

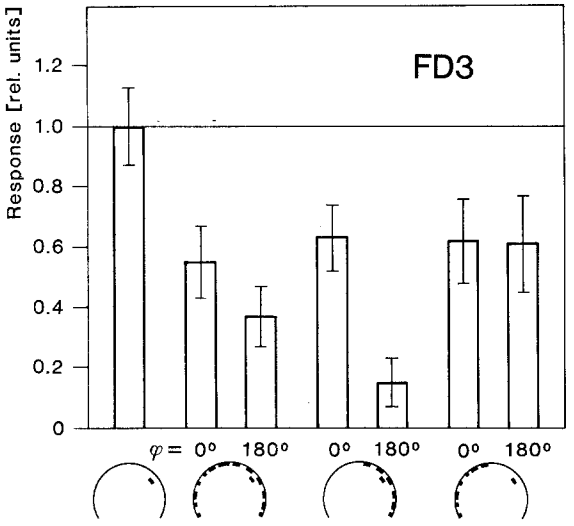

Fig. 11. Large-field input organization of the FD3-cell. The stimulus conditions were the same as in Fig. 4, but the figure was positioned at $\psi = 50°$ in the cell's excitatory receptive field. Its width amounted to 24°, the oscillation amplitude to $\pm 10°$. In the experiments where a monocular ground was used, the frontal part of the visual field was covered by a 24°-wide mask in order to avoid stimulation of the contralateral eye. Each column represents the time-averaged, normalized response to 240 stimulation cycles obtained from 5 different flies. The histogram illustrates that the FD3-cell is inhibited by wide-field motion, irrespective of whether both eyes, only the left or the right eye are stimulated by the ground. Moreover, this inhibition is elicited by horizontal ground motion in either direction

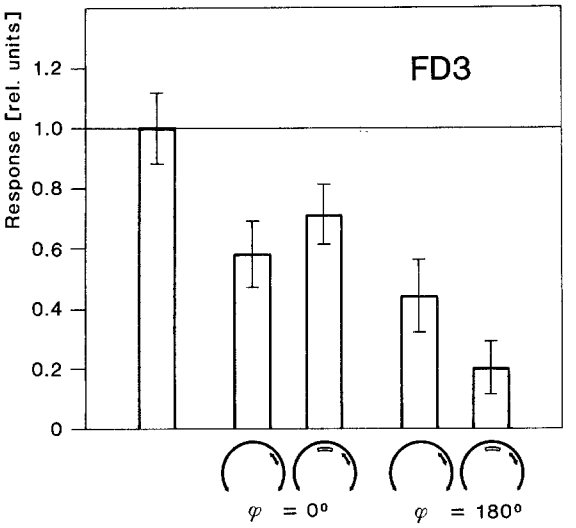

Fig. 12. Fine structure of the large-field input organization of the FD3-cell. The ground covered both eyes and a 24°-wide figure was placed at $\psi = 50°$ in the cell's excitatory receptive field. Whereas the ground was stationary in the left column, it oscillated synchronously ($\varphi = 0°$) or in counterphase ($\varphi = 180°$) with the figure in the experiments shown in the middle and right pair of columns, respectively. The right column of each pair was obtained with a 36°-wide mask positioned symmetrically in the frontal part of the visual field, the left column was obtained without a mask (see insets). The oscillation amplitude of figure and ground amounted to $\pm 10°$. The data of each column were pooled from two flies and represent the time-averaged response to 80 oscillation cycles. They were normalized with respect to the response to figure motion alone. This experiment provides evidence that the FD3-cell is inhibited by regressive wide-field motion along the entire extent of the ipsilateral visual field. In contrast, it is inhibited by ipsilateral progressive motion only within the confines of its excitatory receptive field

FD3-cell which gave a first hint at the fine structure of its ipsilateral input organization. During relative motion of figure and ground with a phase shift of 180° the response of the cell is much more reduced when the ground covers the ipsilateral eye only as compared with its response when the ground extends over both eyes. This finding was surprising at first sight, since under these phase relations both ipsi- as well as contralateral ground motion alone reduce the cell's reaction. If the response to binocular ground motion reflected these monocular inhibitory response components, it should be smaller than either component alone.

These unexpected findings can be understood, if it is assumed that the ipsilateral input to the FD3-cell is organized in principally the same fashion as was found for the FD1-unit. This means for the FD3-cell: Firstly, it should be inhibited by motion opposite to its preferred direction only within the confines of its excitatory receptive field. Secondly, its response should be reduced by large-field motion in the cell's preferred direction along the entire horizontal extent of the ipsilateral visual field. This hypothesis is in accordance with the outcome of the experiment shown in Fig.12. The most frontal part of the visual field was alternately covered by a 36°-wide mask or left open to stimulation, while a binocular ground and a figure at $\psi = 50°$ were oscillated either synchronously or in counterphase. In this way the contribution of the most frontal part of the visual field to the cell's overall response could be analysed.

During synchronous motion of figure and ground the response of the FD3-cell is slightly larger when the frontal part of the visual field is excluded from stimulation. Hence regressive motion beyond the frontal margin of the FD3-cell's excitatory receptive field contributes an inhibitory component to the cell's response. This is expected, if the inhibition induced in the FD3-cell by ipsilateral large-field motion from back-to-front is mediated by a large-field element with a receptive field covering the entire horizontal extent of the ipsilateral field of view.

During relative motion with a phase shift of 180° the response is smaller when the frontal part of the visual field is covered by a mask than when it is exposed to stimulation (Fig.12). This suggests that the

ipsilateral inhibitory input to the FD3-cell induced by progressive motion is restricted to the confines of the cell's excitatory receptive field and is not elicited in the most frontal part of the visual field. The observed decrease in the response of the FD3-cell to counterphase oscillation after masking the frontal part of the visual field can then be interpreted as a disinhibition phenomenon. It has been concluded above that the FD3-cell is inhibited in some way by an ipsilateral large-field element which is selectively sensitive to regressive motion. The response of this presumed large-field neurone to regressive figure motion should decrease by simultaneous progressive motion in the rest of the ipsilateral visual field and, in particular, in the most frontal part of it. This response reduction, therefore, should be more pronounced when during counterphase oscillation of figure and ground the frontal part of the visual field is exposed to stimulation than when it is covered by a mask. As a consequence, the inhibition of the FD3-cell should be reduced when there is no mask leading to an increase in its response amplitude. This expectation is in accordance with the experimental findings shown in Fig.12.

These conclusions on the spatial input organization of the FD3-cell can be summarized as follows. Firstly, the FD3-cell is excited by regressive small-field motion and inhibited by motion in the reverse direction in an approximately 70°–80° wide vertical stripe in the fronto-lateral part of the visual field. Secondly, the cell is inhibited by regressive wide-field motion along the entire horizontal extent of the ipsilateral visual field. Thirdly, the cell's response is reduced by horizontal motion in either direction in front of the contralateral eye.

3.2. Anatomy. The FD3-cell is a heterolateral output element of the lobula plate projecting to the contralateral posterior optic foci. As is illustrated in Fig.13, its main dendritic tree covers the medial part of the lobula plate along its entire dorso-ventral axis. It covers neither the most lateral border of this neuropile nor its proximal part. The outline of the FD3-cell's dendritic tree corresponds, thus, well to the location of its excitatory receptive field (see Fig. 10). As the $FD1_{nod}$-cell, the FD3-neurone belongs to the class of cells which has been described by Hausen (in prep.) as "noduli group". Its axon leaves the lobula plate and projects frontally into the deep protocerebrum. It crosses the midline of the brain posterior to the noduli. It eventually projects backwards and terminates in the contralateral posterior optic foci near the surface of the protocerebrum. This axonal termination area is known from extracellular cobalt impregnation of this cell type (Hausen, in preparation). In the two preparations where I managed to inject the FD3-cell intracellularly with Lucifer Yellow the axon could not be resolved as far (see Fig.13). As the $FD1_{nod}$-neurone, the FD3-cell has an additional ipsilateral dendritic input region near the posterior surface of the lateral protocerebrum. Its cell body is also located in this area.

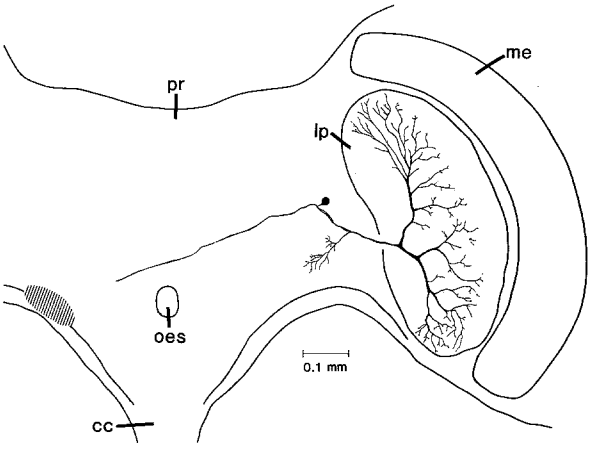

Fig. 13. Anatomical structure of the FD3-cell. Serial reconstruction of intracellular Lucifer Yellow injection. The cell is drawn into a semi-schematic frontal view of part of the brain. Since the axon of the cell could not be stained completely, its termination area in the contralateral posterior optic foci is indicated schematically as it is known from extracellular cobalt impregnation (Hausen, in preparation). For further explanations see text. Abbreviations: see legend of Fig. 6

4 *The FD4-Cell*

The FD4-cell is excited by progressive motion and inhibited by motion in the reverse direction. Its response is strongest when only a relatively small figure moves in its excitatory receptive field (time 0.8–1.6 s in Fig.14), whereas the response amplitude is much reduced during motion of more extended textured patterns (time 0–0.8 s in Fig. 14).

4.1. Spatial Input Organization. The excitatory receptive field of the FD4-cell covers the entire horizontal extent of the ipsilateral visual field. This can be deduced from Fig.15 which represents one out of three examples where quantitative excitatory receptive field measurements could be performed. The cell shown in Fig.15 has its maximum of sensitivity at $\psi = 50°$. Since the sensitivity maxima of FD4-cells are usually not as pronounced as of the FD1- and FD3-cell their locations are scattered within a wider range. In the examples tested quantitatively they were located between angular positions of $\psi = 50°$ and $\psi = 80°$. At half-maximum sensitivity the excitatory receptive field has a width of between 80° and 110°. Its frontal margin coincides with the margin of the ipsilateral eye's field of

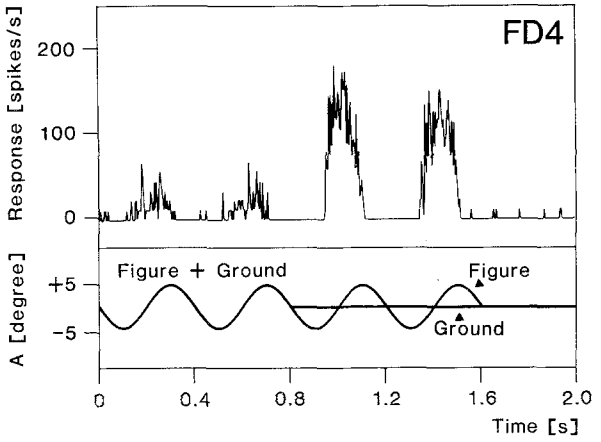

Fig. 14. Responses of a FD4-cell to two cycles of synchronous oscillation of a figure and a binocular ground and subsequently to another two cycles of figure motion alone. The figure had a width of 12° and was oscillated within the cell's excitatory receptive field about an angular position of $\psi = 40°$. The other experimental details are as described in the legend of Fig. 2. The response curve represents the spike frequency histogram obtained from 32 repetitions of the stimulus programme. The cell was recorded from extracellularly in the medial part of the right lobula plate slightly closer to its proximal margin. It is directionally selective for progressive motion and responds much better to the motion of small targets as compared with extended background structures

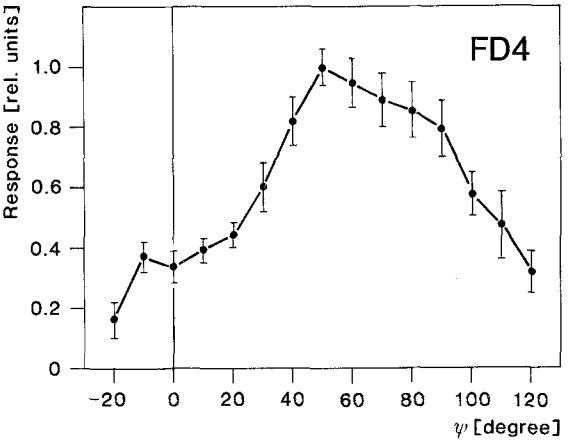

Fig. 15. Horizontal extent of the excitatory receptive field of the FD4-cell. The experimental conditions and data evaluation were the same as described in the legend of Fig. 3. The cell was recorded from extracellularly near the proximal margin of the right lobula plate. Each data point represents the average response to 32 stimulation cycles. This spatial sensitivity distribution illustrates that the excitatory receptive field of a FD4-cell covers the ipsilateral visual field along its entire horizontal extent; this cell type is most sensitive in the lateral part of the eye

view. The postero-lateral margin of the excitatory receptive field could not be determined with the present stimulation device, since it is located beyond a lateral position of $\psi = 120°$. Qualitative measurements with hand-held probes indicate that the excitatory receptive field covers the visual field along most of its vertical axis.

The large-field input organization of the FD4-cell was analysed in principally the same way as has been described for the other FD-cells. Fig. 16 shows the pooled data obtained from 3 different flies where the complete stimulation programme could be tested (see insets). The response to simultaneous motion of figure and ground is smaller than to figure motion alone. This inhibitory influence of large-field motion is independent of whether both, only the left or the right eye are stimulated. Furthermore, it is induced by both clockwise as well as counterclockwise rotation of the ground. The reduction of the response is more pronounced upon stimulation with a binocular ground than with either an ipsi- or contralateral ground alone. This holds for both synchronous as well as counterphase motion. The response to binocular ground motion reflects, at least qualitatively, these monocular inhibitory response components. The FD4-cell differs in this respect from the FD3-unit.

How can these findings be interpreted with respect to the spatial input organization of the FD4-cell?

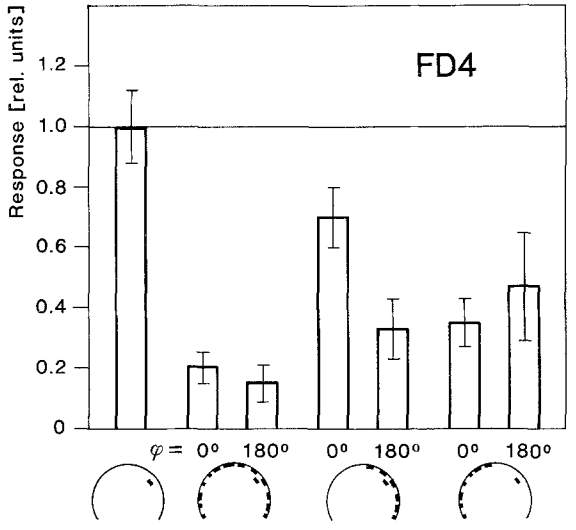

Fig. 16. Large-field input organization of the FD4-cell. The stimulus conditions were the same as in Fig. 4, but the figure was oscillated about $\psi = 60°$ in the cell's excitatory receptive field with an amplitude of $\pm 10°$. The figure width amounted to 24°. In the experiments where a monocular ground was used, the frontal part of the visual field was covered by a 24°-wide mask to prevent stimulation of the contralateral eye. Each column represents the time-averaged response to 120 stimulation cycles obtained from 3 different flies. The response amplitudes were normalized with respect to the response induced by figure motion alone. The histogram illustrates that the response of the FD4-cell is reduced by wide-field motion, irrespective of whether both eyes, only the left or the right eye are stimulated by the ground. Moreover, this inhibition does not depend on the direction of ground motion

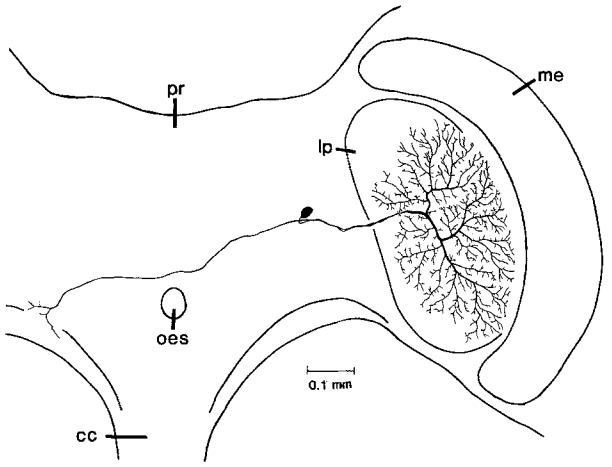

Fig. 17. Anatomical structure of the FD4-cell. Serial reconstruction of intracellular Lucifer Yellow injection. The cell is drawn into a semi-schematic frontal view of part of the brain. For further explanations see text. Abbreviations: see legend of Fig. 6

Phenomenologically, the contralateral inhibitory input to the FD4-cell is bidirectional for horizontal motion. It is more difficult to deduce the spatial input organization of the ipsilateral side, since here both excitatory as well as inhibitory response components interact in a complex way. At least three different response components can be distinguished. Firstly, the FD4-cell is excited by small-field motion from front to back in almost the entire ipsilateral visual field. Secondly, its response is reduced by ipsilateral large-field motion from front-to-back, i.e. in the same direction as the cell's preferred direction. Thirdly, it is inhibited by ipsilateral motion oppositely directed to the cell's preferred direction of motion, i.e. from back-to-front.

4.2 Anatomy. As the $FD1_{nod}$- and FD3-cells, the FD4-neurone is a heterolateral output element of the lobula plate. It belongs to the "noduli group" (Hausen, in preparation) because of its axonal pathway. It could be stained intracellularly with Lucifer Yellow only twice. As the reconstruction of Fig. 17 shows, its dendritic tree covers almost the entire horizontal extent of the lobula plate in its central part. This corresponds well to the horizontal extent of the FD4-cell's excitatory receptive field (see Fig. 15). However, the dendritic tree of the FD4-cell does not cover the entire lobula plate along its dorso-ventral axis. In particular, the dorso-proximal and the most ventro-proximal part of this neuropile are devoid of FD4-dendrites. As a member of the noduli group, the axon of the FD4-cell projects to the contralateral posterior optic foci and terminates there near the surface of the brain. The axonal pathway is the same as has been described for the $FD1_{nod}$- and the FD3-cell. In contrast to these cells, however, no additional dendritic arborization could be detected in the lateral protocerebrum. The cell body of the FD4-cell is located in this area.

Discussion

1 Do the FD-Cells Meet the Conditions for their Potential Role in Figure-Ground Discrimination?

In the preceding paper (Egelhaaf, 1985a) it has been concluded that the Horizontal Cells, the output cells of the neuronal network underlying the optomotor large-field course control reaction (e.g. Hausen, 1981; Hausen and Wehrhahn, 1983; Wehrhahn, 1985), are not sufficient to account for figure-ground discrimination. From the "deficits" of the Horizontal Cells with respect to this information processing task the main conditions have been deduced for the output cells of the presumed additional neuronal network which is required to explain figure-ground discrimination behaviour (see Introduction). These conditions bear upon the spatial integration properties and input organization of the additional output cells, the variability of their response, as well as their axonal projection pattern. Do the FD-cells, which have been described for the first time in this study, comply with these conditions and, thus, qualify for a role in figure-ground discrimination?

1.1 Spatial Integration Properties. It is immediately obvious that the FD-cells meet the first condition, because they are movement sensitive wide-field neurones which respond much better to the motion of relatively small targets than to more extended moving patterns. This is not much surprising, since in all electrophysiological experiments this condition had to be satisfied, before a cell was further tested with respect to the other constraints.

1.2 Spatial Input Organization. The different FD-cells differ with respect to the spatial organization of their inhibitory large-field input. All FD-cells analysed so far receive inhibitory input from the *contralateral* eye. The FD3- and FD4-cell are inhibited by contralateral motion in either horizontal direction and, thus, comply in this regard with the conditions derived from the behavioural analysis. These conditions are not met by the FD1-cell, since its response is only reduced by contralateral motion from back-to-front.

The spatial organization of the inhibitory input to the FD-cells originating from the *ipsilateral* eye is more complex and, therefore, cannot be related as easily to the constraints imposed by figure-ground discrimination behaviour. Whereas in the FD1- and FD3-cell

the inhibitory response component which is mediated by ipsilateral large-field motion is directionally selective and, strictly speaking, does not satisfy the conditions deduced from figure-ground discrimination behaviour, this question cannot yet be answered for the FD4-cell. It should be noted, however, that irrespective of whether the ipsilateral inhibitory input to a particular FD-cell is bidirectional the response of all FD-cells to counterphase motion of a figure and an ipsilateral ground is at least as much reduced as to synchronous motion. This holds at least, if the figure is smaller than the horizontal angular extent of the cell's excitatory receptive field. Although this response reduction during counterphase motion might have different reasons in the different FD-cells, i.e. inhibition via a presumed large-field neurone (see Egelhaaf, 1985b) and/or direct inhibition by the elementary movement detectors, all FD-cells virtually meet the conditions for the ipsilateral input organization of the neuronal elements involved in figure-ground discrimination.

Since the different FD-cells differ in the width and location of their excitatory receptive fields as well as their large-field input organization, the visual field is not organized homogeneously with respect to the detection of small targets. Instead it is compartmentalized into functionally distinct subregions. In particular, its most frontal part differs greatly from the more lateral ones. This aspect of the organization of the neuronal network underlying figure-ground discrimination has not yet been taken into account in the model circuitry proposed by Reichardt et al. (1983). This circuitry has been assumed to be homogeneous along the horizontal axis of the visual field. In all behavioural figure-ground discrimination experiments published so far the figure was never placed in the most frontal part of the visual field. These experiments were, thus, not appropriate to elucidate the compartmentalization of the visual field. The constraints imposed on the neuronal network underlying figure-ground discrimination which have been inferred from them can, therefore, be applied only to the more lateral parts of the visual field. Beyond $\psi = 20°$ the sensitivity of both the FD1- and FD2-cell declines steeply, whereas the sensitivity of the FD3- and FD4-cell increases. Hence, in these more lateral parts of the visual field those cells predominate the others in their sensitivity to small moving targets which comply best with the conditions inferred from the behavioural analysis. In further behavioural experiments also the most frontal part of the visual field needs to be investigated with respect to its specific figure-ground discrimination properties. It should be noted that there are indications from the behavioural analysis of time-averaged reactions that peculiar properties have to be attributed to the most frontal part of the visual field (Reichardt and Poggio, 1979). Therefore, it is not surprising that also the network of FD-cells is not homogeneous with respect to its spatial organization.

1.3 Variability of the Response. Whereas the behavioural response to stimulation with relative motion of figure and ground has been found to be rather variable (Egelhaaf, 1985a) an equivalent degree of variability could not be found in the optomotor neurones. Similarly, the response of the FD-cells does neither differ qualitatively in different preparations nor does it change very much during long-time extracellular recordings (Egelhaaf, in preparation). It is, however, more important in the present context that no FD-cell has ever been found, so far, which depolarized at least occasionally in response to motion opposite to its preferred direction (see Egelhaaf, 1985a). This implies that the variability found in figure-ground discrimination behaviour cannot be explained by the variability in the response properties of a single class of lobula plate output cells. As has already been concluded for the Horizontal Cells (see Egelhaaf, 1985a), a hypothesis originally proposed by Reichardt et al. (1983) to account for the variability of the behavioural reaction, therefore, does not agree with the experimental data.

As an alternative it is proposed that the behavioural variability is the result of differentially weighting the output of parallel neuronal networks with different functional properties. This means in the context of figure-ground discrimination that the Horizontal Cells and part or all of the FD-cells determine to a varying extent the final behavioural output depending on the stimulus conditions but also on the fly's internal state. It will be shown in the subsequent paper (Egelhaaf, 1985b) that this hypothesis can account for the variability of the behavioural data.

1.4 Anatomy. All FD-cells analysed so far have their main telodendritic arborization area in either the ipsi- or contralateral posterior optic foci. The axons of the Horizontal Cells terminate in this region, too, and make synaptic contact with descending neurones (Strausfeld et al., 1984; Hausen, in preparation). These are thought to be connected directly to the motor control centres in the thoracic ganglia. Since there is good evidence for the involvement of the Horizontal system in yaw torque control (e.g. Hausen, 1981; Hausen and Wehrhahn, 1983; Wehrhahn, 1985), it is suggested by the common axonal destination of both cell classes that the FD-cells also play a role in controlling yaw torque generation. Therefore, the FD-cells are likely to act together with the Horizontal Cells as output

elements of the neuronal network underlying figure-ground discrimination.

Two further aspects should be addressed here. Firstly, at least the FD2-cell is likely to be involved in information processing tasks other than figure-ground discrimination. This is suggested by its additional axonal terminal in the anterior optic foci. The landing response can be speculated to represent a possible candidate, since it can be elicited by regressive motion exclusively in the most frontal part of the eye (Wehrhahn et al., 1981). Secondly, it cannot be excluded that there are further FD-cells which have not yet been found. This is indicated by a recently discovered lobula plate tangential neurone which is sensitive to regressive motion (Hausen, in preparation), but has not been characterized functionallly in more detail so far. Since it has almost alike anatomical properties as the $FD1_{nod}$-cell (Hausen, in preparation), it is tempting to speculate that it might be also tuned to small-field motion.

2 Other Cells Selectively Responsive to Small Moving Objects

Visual interneurones which are selectively responsive to the motion of small targets and respond to relative movement in a characteristic way have been found in various parts of the vertebrate visual system (see for instance: cat superior colliculus, Sterling and Wickelgren, 1969; Mason, 1979; Mandl, 1985; cat lateral suprasylvian area: Rizzolatti and Camarda, 1977; v. Grünau and Frost, 1983; cat and monkey striate cortex: Bridgeman, 1972; Hammond and MacKay, 1981; monkey area MT: Miezin et al., 1982; pigeon tectum: Frost et al., 1981; Frost and Nakayama, 1983) as well as in different insect species (Collett, 1971, 1972; Collett and King, 1975; Olberg, 1981; O'Shea and Rowell, 1975; Rowell et al., 1977). Although the mechanisms responsible for the selectivity of these cells to small-field motion have not always been addressed explicitly, they can, roughly speaking, be subdivided in two categories.

The small-field motion sensitive cells found in vertebrates as well as in the pivet hawk moth (Collett, 1971, 1972) and hoverfly (Collett and King, 1975) seem to have one feature in common. Their receptive fields consist of an excitatory field centre and an inhibitory surround. Whereas a response is elicited by motion of a sufficiently small stimulus within the confines of the excitatory receptive field, it is more or less suppressed by stimuli extending into the inhibitory surround. In different cell types these inhibitory surrounds differ in their size and arrangement with respect to the excitatory receptive field centre as well as in their selectivity for the direction of motion. Irrespective of these differences, however, the mechanism for tuning these cells to the motion of small objects is based on the spatial compartmentalization of the receptive field into functionally antagonistic regions. Although this kind of mechanism has been shown to play a role in those FD-cells which cover with their excitatory receptive field only part of the field of view, it is most likely not the decisive determinant of their specific spatial integration properties, as will be shown in the subsequent paper (Egelhaaf, 1985b).

An alternative mechanism for tuning a cell to the motion of small objects that does not rely on centre-surround interactions has been analysed in the input circuitry of the "lobula giant movement detector" (LGMD) neurone in locusts (O'Shea and Rowell, 1975; Rowell et al., 1977). Although its excitatory receptive field covers the entire visual field of one eye, it responds selectively to the motion of small targets. Suppression of its response by large-field motion is due to two separate inhibitory mechanisms. Firstly, lateral inhibition operates between the retinotopically arranged input channels to the LGMD-cell. Secondly, a feed-forward large-field inhibitory input impinges on the LGMD-cell after convergence of its main dendrites near the site of spike initiation. Whereas there are no indications that lateral inhibition plays a role in accomplishing the specific spatial integration properties of the FD-neurones, the model proposed by Egelhaaf (1985a) where the output cell of the network is inhibited directly by another large-field element is reminiscent of the latter inhibitory pathway in the locust system. Whether this equivalence from the circuitry point of view is of similar functional significance in both systems cannot yet be decided. The similarity is probably quite superficial, since this inhibitory pathway in the locust appears primarily to suppress large excitatory transients to wide-field motion before the lateral inhibition network succeeds in suppressing a response to these stimuli anyway.

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