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

I. Behavioural Constraints Imposed on the Neuronal Network and the Role of the Optomotor System

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Abstract. A fly can discriminate an object ("figure") from its background on the basis of motion information alone. This information processing task has been analysed, so far, mainly in behavioural studies but also in electrophysiological experiments (Reichardt et al., 1983). The present study represents a further attempt to bridge the gap between the behavioural and the neuronal level. It is based on behavioural and electrophysiological experiments as well as on computer simulations. The characteristic properties of figure-ground discrimination behaviour impose specific constraints on the spatial integration properties of the output cells of the underlying neuronal network, the heterolateral interactions in their input circuitry, as well as on the range of variability of their response. These constraints are derived partly from previous behavioural studies (Reichardt et al., 1983), partly, however, from behavioural response characteristics which have not been addressed explicitly so far. They are interpreted in terms of one of the alternative model circuits shown by Reichardt et al. (1983) to be sufficient to account for figure-ground discrimination. It will be demonstrated, however, that this can be done equally well by means of a further alternative model circuit. These constraints are used in the electrophysiological analysis for establishing visual interneurones as output elements of the neuronal network underlying figure-ground discrimination.

In the behavioural experiments on figure-ground discrimination as well as on the optomotor course control the yaw torque generated by the tethered flying fly under visual stimulation was used as a measure for the strength and time course of the reaction. Therefore, it has initially been proposed that the three Horizontal Cells, which are regarded as the output elements of the neuronal network underlying the optomotor reaction (e.g. Hausen, 1981), might also control yaw torque generation in figure-ground discrimination (Reichardt et al., 1983). New behavioural data show, however, that the Horizontal Cells do not meet all the constraints imposed on the presumed output cells of the figure-ground discrimination network: (1) The Horizontal Cells are not sensitive enough to motion of small objects. (2) The heterolateral interactions within their input circuitry are not in accordance with the behavioural data (see also Reichardt et al., 1983). (3) The variability found in the time course of certain components of the yaw torque response to relative motion of figure and ground cannot be explained by their response characteristics. Hence, the Horizontal Cells cannot account for figure-ground discrimination on their own and additional output cells of the optic lobes with different functional properties are required to accomplish this task.

Introduction

An object ("figure") can, at least in principle, be discriminated from a structured background on the basis of differences in structure, colour, luminance, and contrast. However, even if figure and ground do not differ in these features, they can be separated when they move relatively to each other. This has been shown in psychophysical experiments for the human visual system (e.g. Baker and Braddick, 1982; van Doorn and Koenderink, 1982; Regan and Beverley, 1984), but might be particularly important for fast flying organisms, since these are likely to rely strongly on motion information for partitioning their visual surround into objects and background structures. Thus it was not surprising that visually guided behaviour based on the evaluation of motion information and, in particular, figure-ground discrimination play a prominent role in fly orientation (e.g. Virsik and Reichardt, 1974, 1976; Collett, 1980; Bülthoff, 1982; Reichardt et al., 1983; Wagner, 1985). It should be noted that in this series of papers (Egelhaaf, 1985a, b) as well as in previous

studies (Reichardt and Poggio, 1979; Poggio et al., 1981; Reichardt et al., 1983) figure-ground discrimination by relative motion exclusively refers to the *detection* of motion discontinuities in the retinal velocity field, rather than to the exact delineation of the object boundaries. This distinction is not an arbitrary one, since both tasks are different from a computational point of view. They appear to be kept separate even in the human nervous system (e.g. Marr, 1982; Hildreth, 1984; Regan and Beverley, 1984).

1 The Fly as a Model System for Solving Visual Information Processing Tasks

The fly represents a good model system for studying visual information processing, since this can be done at both the behavioural as well as the neuronal level. A clear understanding of the behavioural level is crucial, even if one is primarily concerned with a neurophysiological analysis. This is because complex systems, such as a nervous system, generally cannot be understood by simple superposition of the properties of their components. Consequently, one cannot understand properly what information is processed in a particular part of the nervous system on the basis of neurophysiological studies alone as long as one has no clear concepts of what needs to be explained there. These concepts can only be derived from an understanding of the performance of the entire system (e.g. Harmon, 1970).

In animals information about the performance of visual information processing can only be gained from their motor activity. In this respect the yaw torque generated by the fly about its vertical axis represents a sensitive and conveniently measurable indicator. This measure is of functional significance, since it represents the most important rotational degree of freedom in visual orientation behaviour. It has been applied successfully during the last decades in studying various basic visual information processing tasks (for review see Reichardt and Poggio, 1976; Poggio and Reichardt, 1976) and, in particular, most recently figure-ground discrimination (Reichardt and Poggio, 1979; Poggio et al., 1981; Reichardt et al., 1983).

The main advantage of the fly's brain for analysing visual information processing at the neuronal level is that this can be done, at least partly, on the basis of neurones (or cell types) which can be identified individually in different preparations. The main pathway from the eye to the central brain is through three consecutive visual ganglia, the lamina, medulla and the lobula-complex which is subdivided into the anterior lobula and the posterior lobula plate (Fig. 1; e.g. Strausfeld, 1976). Despite extensive transformation of the input information, the spatial retinotopic order remains preserved along this pathway due to a columnar organization of the visual ganglia. The point-to-point representation of visual space is abandoned in the lobula plate, where the information is integrated by some 20–30 anatomical classes of large tangential neurones over part of, or even the entire visual field (Hausen, 1981; in prep.). Some of them make synaptic contact with descending neurones which are thought to project directly to the motor control centres in the thoracic ganglia. As large-field integrating elements, these neurones have very specific functional properties which can be related directly to the final behavioural output (e.g. Hausen, 1981) and, therefore, represent an ideal starting point for any electrophysiological analysis of a visual information processing task such as figure-ground discrimination.

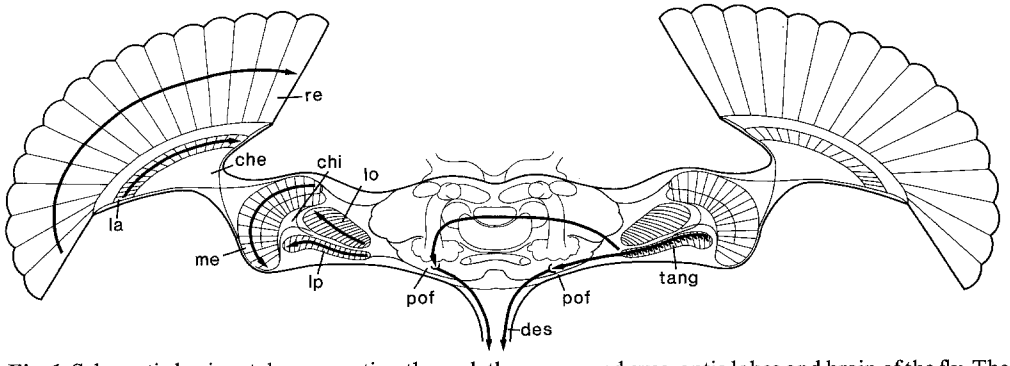

Fig. 1. Schematic horizontal cross-section through the compound eyes, optic lobes and brain of the fly. The ommatidia in the retina and the corresponding columns in the visual ganglia are indicated by thin lines. The arrows in the left optic lobe indicate the retinotopic projection; its horizontal axis is inverted along the pathway by two chiasmata. In the right lobula plate the location of the tangential neurones is indicated schematically. Only those pathways from the lobula plate to the protocerebrum are marked by arrows which are relevant in this and the subsequent papers (Egelhaaf, 1985a, b). One of them projects close to the posterior surface of the brain to the ipsilateral posterior optic foci, the other through the deep central protocerebrum to the contralateral posterior optic foci. Both output projections are assumed to be synaptically linked to descending neurones which terminate in the motor control centres of the thoracic ganglia. Abbreviations: des: descending neurones; che: external chiasma: chi: internal chiasma; la: lamina; lo: lobula; lp: lobula plate; me: medulla; pof: posterior optic foci; re: retina; tang: tangential neurones (modified from Hausen, 1981)

2 Figure-Ground Discrimination of the Fly: A Brief Review

Flies do not only turn towards small contrasted objects moving on a homogeneous background (Reichardt, 1973; Reichardt and Poggio, 1976); they even fixate and track a target in front of a ground panorama with identical texture, if they move relatively to each other (Virsik and Reichardt, 1974; 1976). This means in the special case of figure and ground oscillating with the same frequency and amplitude that a phase shift between figure and ground is required for the figure to be detected (Reichardt and Poggio, 1979). Within a certain frequency range the fly optimally discriminates the figure for a relative phase of 90° and 270°. Detection decays from 90° (270°) to 180° (360°) phase shift where it is negligible in the time averaged reaction.

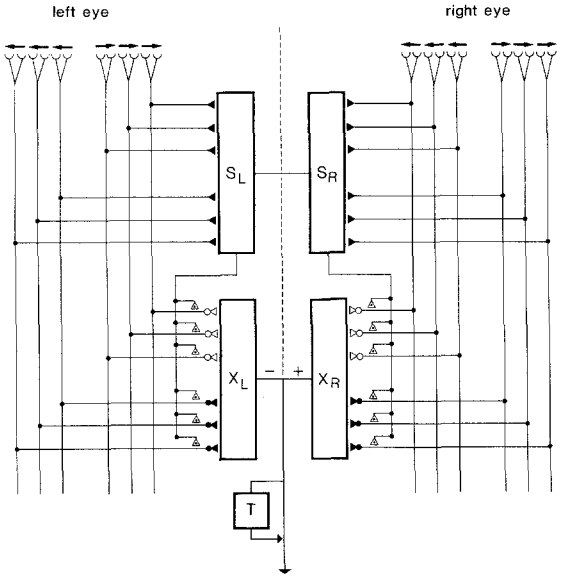

Fig. 2. Neuronal model circuitry proposed on the basis of behavioural experiments to underly figure-ground discrimination. This model is topologically equivalent to the circuit shown by Poggio et al. (1981) and Reichardt et al. (1983). Outline of the network. Two retinotopic arrays of elementary movement detectors serve as input to the circuitry behind each eye. Considering only the right eye, they respond selectively to progressive (—▶) and regressive (◀—) motion, respectively. The two arrays are drawn apart from each other, although they have the same field of view. The pool cell S_R receives excitatory input from all movement detector channels (—◀) irrespective of their preferred direction. It is coupled with its contralateral homolgue S_L. The output of the pool cell is assumed to saturate. It shunts a collateral of each detector channel near its output terminal via presynaptic inhibition (—◁). The output cell X of the network summates the progressive (excitatory —●◀) and regressive (inhibitory —○◁) movement detectors. The progressive channels have a higher amplification than the regressive ones (1 : 0.3). The synapses on the output cell are assumed to operate with a non-linear transmission characteristic. The final motor output is controlled by the X-cells via a direct channel and a channel T producing the running average of the X-cell output

On the basis of further behavioural experiments possible circuitries were proposed to be sufficient to account for figure-ground discrimination behaviour (Poggio et al., 1981; Reichardt et al., 1983). These circuits were formulated and graphically represented in a way lending themselves well to an interpretation in cellular terms.

The main properties of one of these model circuits can be summarized as follows (see Fig. 2). One pool cell on each side of the brain (cell S in Fig. 2) summates the output of two retinotopic arrays of small-field elementary movement detectors, one responding to front-to-back (progressive) the other responding to back-to-front (regressive) motion. In accordance with the behavioural experiments both pool cells have been assumed to be completely coupled. The output cells of the network (X-cells in Fig. 2) are excited by the progressive and inhibited by the regressive movement detectors. Prior to summation by the X-cells the progressive and regressive channels are differentially weighted (1 : 0.3) and shunted via presynaptic inhibition. Since the model equations have been discussed intensively before (Reichardt et al., 1983), only the final equation relating the output of the network $y(t)$ to the amplitude of the movement detector output $w_i(t)$ will be given here:

$$y(t) = \frac{\sum_{i=1}^{N} |w_i(t)|^n \cdot \operatorname{sign}(w_i(t))}{\left(\beta + \left(\sum_{i=1}^{N} |w_i(t)|\right)^q\right)^n}, \tag{1a}$$

where N denotes the number of detector channels, β the coefficient of shunting inhibition, $q<1$ approximates a saturation characteristic of the pool and n represents the non-linearity in the synaptic transmission between input channels and the output cell X. With $w_i(t) = w_j(t)$ for all i, j Eq. (1a) reduces to the much simpler form

$$y(t) = \frac{N|w(t)|^n}{(\beta + (N|w(t)|)^q)^n} \cdot \operatorname{sign}(w(t)). \tag{1b}$$

The response becomes independent of figure width if $n=2$ and $q=0.5$; for $n>2$ the response decreases, for $n<2$ it increases with increasing figure width. The motor output of the network is controlled by the X-cells via a direct pathway and a channel T computing the running average of the X-cell output. If the time constant of the running average is chosen to be large enough, the mean torque response is shifted to positive (or negative) values during relative motion and, after a transition period, the time course of the torque signal directly reflects the time course of the output cell response. It should be noted that although these circuitries were only meant to represent the logical

organization of the network underlying figure-ground discrimination, they impose constraints on its actual implementation in the fly's brain and could, thus, be tested in neurophysiological experiments.

3 Organization of the Paper

Although the main objective of this and the subsequent papers (Egelhaaf, 1985a, b) is to unravel parts of the neuronal circuitry underlying figure-ground discrimination in the fly, electrophysiological experiments constitute only one part of them. This is because it was not possible to interpret newly discovered cells properly with respect to their potential involvement in figure-ground discrimination, as long as the constraints imposed on such cells by the specific properties of this task were not known. In the present paper these constraints are derived from behavioural experiments and formulated in terms of the model shown in Fig. 2. An alternative cellular model is proposed in an Appendix. It leads to essentially the same predictions for the functional properties of the output cells of the neuronal network underlying figure-ground discrimination. Since for methodological reasons all electrophysiological experiments could be carried out on the blowfly *Calliphora* only, while most behavioural experiments were done with the housefly *Musca*, it will be shown in control experiments that both species do not differ with respect to figure-ground discrimination behaviour. In a previous study (Reichardt et al., 1983) it has been proposed that the three Horizontal Cells which are believed to control the optomotor yaw torque response (Hausen, 1981; Hausen and Wehrhahn, 1983) might represent also the output elements of the network underlying figure-ground discrimination. The present analysis, however, reveals that the Horizontal Cells are not sufficient for this task and additional output cells are required. Appropriate candidates for this role will be analyzed in the subsequent papers (Egelhaaf, 1985a, b).

Materials and Methods

1 Definitions

All positions of the stimulus are given in a head centered coordinate system. The coordinate 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. φ refers to the relative phase between figure and ground oscillation. "Progressive" and "regressive" motion refer to horizontal motion from front-to-back and back-to-front, respectively.

2 Animals

The behavioural experiments were carried out with wild type female blowflies, *Calliphora erythrocephala* (Meig.) or houseflies, *Musca domestica* (L.). The electrophysiological experiments were performed with *Calliphora*. All animals were obtained 2–10 days post eclosion from laboratory cultures of the institute.

3 Behavioural Analysis

The flies were prepared as described by Fermi and Reichardt (1963). Under light carbon dioxide anesthesia the head of the animals was fixed to the thorax with a mixture of wax and collophonium. A piece of cardboard was fixed to the wax just above the frontal part of the thorax. The ocelli were covered with the same mixture of collophonium and wax. The test flies were suspended from a torque compensator which prevented both rotatory and translatory movements of the animal and allowed direct measurement of the instantaneous yaw torque generated by the fly (e.g. Fermi and Reichardt, 1963; Götz, 1964). The torque response was directly inspected on an oscilloscope screen, stored and further processed by a signal averager and finally plotted with a $X-Y$ recorder.

The stimulation was almost identical to that used in previous behavioural figure-ground discrimination experiments (Reichardt et al., 1983). The animals were positioned in the centre of two concentric cylindrical patterns, their diameters amounting to 80 mm and 72 mm, respectively. While the horizontal angular extent of the outer cylinder was 360°, the inner panorama consisted of only a cylinder segment of variable width. The height of both cylinders amounted to 50 mm which corresponds in the vertical direction to an angular extent of the stimulus of about $\pm 32°$ as seen by the fly. The outer cylinder ("ground") consisted of translucent white perspex and was covered with a statistical pattern of black and transparent pixels ("Julesz pattern"; see e.g. Fig. 2.4-1 in Julesz, 1971). The segment of the inner cylinder ("figure") was opaque and covered with a "Julesz pattern" of black and white pixels. The side length of all pixels was 2.51 mm corresponding to an angular subtense of $3.6° \times 3.6°$ for pixels in the middle of the cylinder. The two cylinders were illuminated by three direct current driven fluorescent ring bulbs. The average luminance of the figure and background texture were about $155\,cd \cdot m^{-1}$ and $460\,cd \cdot m^{-1}$, respectively. The contrast of the black pixels amounted to 77% for the figure and about 90% for the ground. The stimulation programmes used in the different experiments will be described in the result section.

4 Electrophysiology

The preparation follows the routine for intracellular recording in the fly optic lobes developed previously (Hausen, 1976). The animals were briefly anesthesized with carbon dioxide and mounted ventral side up with a mixture of wax and collophonium on a small piece of glas. The legs were amputated and the wounds sealed with a wax-collophonium mixture. The head was tilted about 30° ventrally and waxed to the thorax. A small hole was cut in the occipital cuticle to gain access to the lobula complex. The musculus retractor haustelli, the neck muscles and the pulsatile organs were dissected away in order to reduce movements of the preparation. Furthermore, the proboscis was cut near its base, the wound sealed with the wax-collophonium mixture and the oesophagus pulled caudad and fixed to the thorax. The tracheal system was left intact in all experiments where extracellular recordings were done. For some of the intracellular recording experiments, however, it was necessary to remove single tracheal branches when overlaying the brain areas to be recorded from.

The animals were adjusted to the centre of the stimulation device using the symmetry of the deep pseudopupil of both eyes (Franceschini and Kirschfeld, 1971). During an experiment a

small constant flow of oxygen saturated with vapour was released from a glass capillary about 10 mm above the fly's head. The fly was supplied with Ringer solution from a reservoir in a microsyringe fitted via a thin silicon-tube to the holder of the indifferent electrode. Its composition was as follows: 7.5 g NaCl; 0.14 g $NaHCO_2$; 0.35 g KCl; 0.21 g $CaCl_2$; 2.5 g glucose in 1 l distilled water; pH = 7.0, buffered with 0.04 M Sørensen phosphate buffer (Case, 1957; Hausen, 1976).

Extracellular recordings were carried out with tungsten electrodes which were sharpened by electrolytic etching in a solution of 71 g $NaNO_2$ and 34 g KOH in 100 ml distilled water (Levick, 1972; Hausen, 1982a) and insulated with lacquer (Insl X). Their tips were electrolytically coated with platinum in a solution of 1 g $H_2[Pt(Cl)_6]$ and 2 mg lead acetate in 100 ml distilled water (Plating current: 0.2 μA, ≈ 10 s).

For intracellular recordings, glass micropipettes were pulled with a modified MC 753 Moving Coil Electrode Puller (Campden Instruments, London). When filled with 2 M potassium acetate solution, the electrodes had resistances of 50–100 MΩ. Recorded signals were amplified using standard electrophysiological equipment. Together with the electronically encoded stimulus parameters they were permanently stored on magnetic tape. The data could be averaged with a signal averager and subsequently plotted on a $X-Y$ recorder. Spike rates were determined with an electronic counter.

To allow direct comparison of the behavioural and electrophysiological results the stimulation device was almost identical to that used in the behavioural experiments, except the ground panorama was opened behind the fly in order to allow access to the animal's brain with the electrode. The cylindrical ground panorama reached from $-120° \leqq \psi \leqq +120°$. The figure could be placed at variable positions. The diameters of the figure and ground cylinders were 70 mm and 66 mm, respectively. Their height amounted to 50 mm. This corresponds to a vertical angular extent of the stimulus of about ±35°, when the fly was suspended in the middle of the cylinder. The side length of one pixel of the Julesz patterns covering figure and ground was about 1.83 mm which corresponds to an angular width of 3° × 3° along the equator of the fly's eye. The mean luminance of figure and background was 185.5 cd · m^{-1} and 1537 cd · m^{-1} respectively. The contrast of the black pixels amounted to 67% for the figure and 95% for the ground. Control experiments in which figure and ground were homogeneously illuminated from above revealed that these differences in mean luminance and contrast do not affect the conclusions derived in this study.

5 Computer Simulations

The computer simulations were carried out with a Hewlett-Packard 86 computer. The programmes were written in BASIC and the results plotted on a Hewlett Packard 7225 B Plotter.

Results

1 Constraints Imposed on the Neuronal Networks Underlying Figure-Ground Discrimination

The characteristic properties of figure-ground discrimination behaviour impose specific constraints on the organization of the underlying neuronal network. In the first step of this analysis these constraints will be specified with respect to the response properties of the presumed output cells of this network. They will be formulated in terms of the model circuitry originally proposed to underly figure-ground discrimination (Poggio et al., 1981; Reichardt et al., 1983; see Fig. 2). However, a second model circuit proposed by Reichardt et al. (1983) as well as further alternative network (see Appendix) lead to virtually the same predictions for the response properties of the output cells despite different underlying operations. In the subsequent electrophysiological analysis (Sect. 3, Egelhaaf, 1985a) these model predictions will be used as criteria for establishing neurones in the fly's brain as output cells of the network underlying figure-ground discrimination. The conclusions drawn in this chapter are partly based on previous behavioural studies, partly, however, on behavioural response characteristics which have not been addressed explicitly so far.

1.1 Spatial Integration Properties

The torque response generated by the fly was found to be independent of the angular horizontal extent of the textured stimulus when averaged over a large sample of flies; in contrast, it was found to increase with increasing velocity of the stimulus (see Fig. 7 in Reichardt et al., 1983). This finding led to the proposal of a specific gain control mechanism that operates on the number of excited detector channels (Reichardt et al., 1983). In terms of the model shown in Fig. 2 the gain control mechanism is due to saturation of the pool cells (S_R and S_L in Fig. 2), shunting inhibition of the elementary movement detectors and non-linear synaptic transmission between movement detectors and the output cells of the circuit (X_R and X_L in Fig. 2). This mechanism implies that the output cells of the neuronal network underlying figure-ground discrimination should be equipped with the same spatial integration properties as found at the behavioural level.

1.2 Heterolateral Interactions

The neuronal networks evaluating relative motion of figure and ground in the corresponding visual ganglia of both optic lobes do not operate independently. This has been inferred from the outcome of various behavioural experiments (Reichardt et al., 1983). These experiments could only be explained on the basis of the model circuitry shown in Fig. 2, if the presumed large-field pool cells on both sides of the brain (S_R and S_L in Fig. 2) were functionally coupled. Moreover, these presumed pool cells were concluded to be sensitive to motion in either horizontal direction. If the circuitry were realized in the fly's brain in essentially this form, the response of its output elements to ipsilateral motion should be significantly reduced by simultaneous motion of another textured stimulus in front of

the contralateral eye. This inhibitory influence should be independent of the direction of motion of the contralateral stimulus.

1.3 Variability of Figure-Ground Discrimination Behaviour

1.3.1 Response Induced by Progressive Figure Motion. Even on superficial inspection it becomes obvious that the responses to relative motion of figure and ground are rather variable. During simultaneous oscillation of an extended background and a small figure in front of one of the eyes (phase: $\varphi = 90°$ or 270°) a sharp peak in the torque response may be generated. It is induced at a specific phase of the stimulation period, i.e. when the ground reverses its direction of motion, while the figure still moves progressively (Reichardt et al., 1983). In unrestrained flies it would lead to turning towards the position of the oscillating figure. This response peak is the most characteristic signature of the reaction to relative motion and represents an especially sensitive indicator for the variability of figure-ground discrimination behaviour.

The extent of variation of the amplitude of this response peak is illustrated in Fig. 3. After several cycles of synchronous oscillation of a binocular ground and a small figure positioned in front of the right eye their relative phase was switched to $\varphi = 90°$ (see bottom trace in Fig. 3). Torque signals with positive or negative sign mean that the fly tries to turn to the right or left, respectively. One end of the range of behavioural variability is characterized by torque responses to relative movement which do not provide an indication that the figure has been detected. The example of Fig. 3a shows almost no shift of the mean torque signal nor any obvious influence on its time-course, when figure and ground are oscillated with a phase shift of $\varphi = 90°$. In the example shown in Fig. 3b the response peak under consideration is still small in amplitude but can be discovered easily in the overall waveform (see arrow in Fig. 3b). It is much more pronounced in Fig. 3c and already larger than the response to synchronous oscillation of figure and ground, whereas with an amplitude of almost 7×10^{-8} Nm, the response peaks in Fig. 3d approach the upper limit found for this response component in the present study. The shift of the mean torque signal increases correspondingly in the different examples of Fig. 3.

A possible explanation at the neuronal level for the variability observed in figure-ground discrimination behaviour has been proposed by Reichardt et al. (1983). It is based on the presumed sigmoidal transmission characteristic of the synapses between the elementary movement detectors and the output cells (X-cells in Fig. 2) of the model circuitry. Different

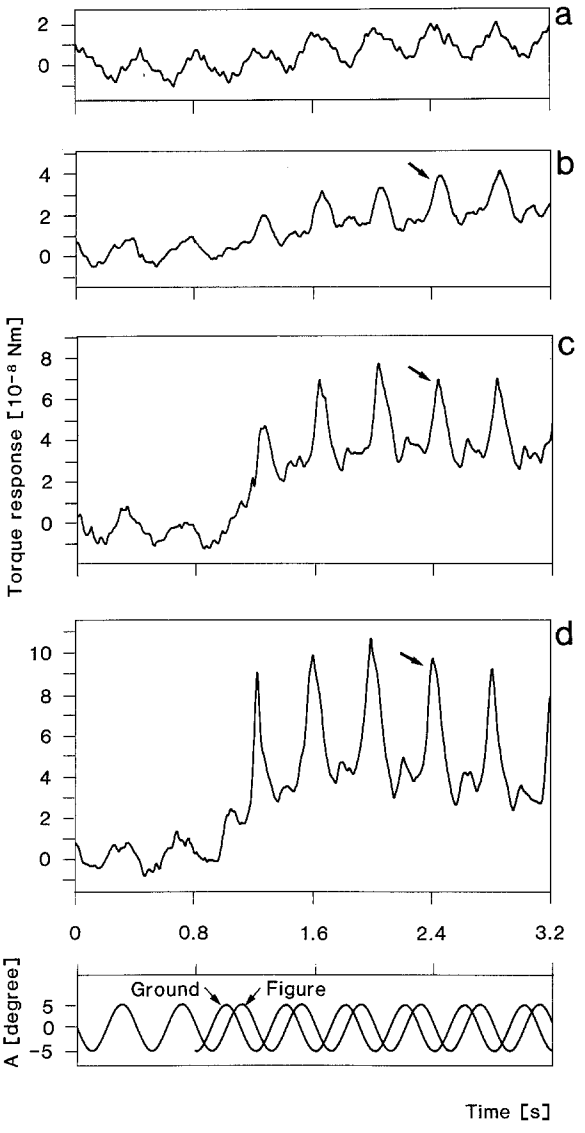

Fig. 3a–d. The range of typical torque response profiles observed in *Musca* in behavioural figure-ground discrimination experiments. A textured stripe of 7.2° angular width was oscillated sinusoidally about an angular position of $\psi = 30°$ in front of a 360° textured background. Figure and ground oscillated with a frequency of 2.5 Hz and an amplitude of $\pm 5°$. The bottom traces indicate the deviation of figure and ground from their mean positions. With respect to the right eye, movements from $-5°$ to $+5°$ are progressive movements, whereas movements from $+5°$ to $-5°$ are regressive movements. Positive and negative torques represent turning tendencies to the right and left side, respectively. As demonstrated in the bottom traces, figure and ground moved synchronously in the beginning and were set to a relative phase of $\varphi = 90°$ at time 0.8 s. Each plotted response curve represents the average of 50 sweeps with a single fly. The curves in **a–d** were obtained with four different flies. Since the curves in **a–d** were measured under identical stimulus conditions, they illustrate the range of variability found during relative motion of figure and ground in both the shift of the mean torque response as well as in the amplitude of the characteristic response peak which is induced when the ground reverses its direction of motion while the figure still moves progressively (see arrows)

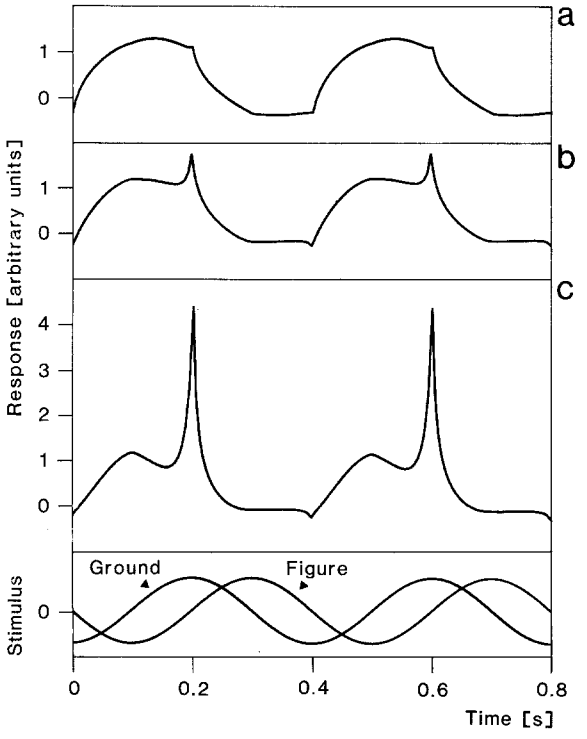

Fig. 4a–c. Predicted response profiles to relative motion of the right output cell of the neuronal network proposed to underly figure-ground discrimination. The plotted curves represent computed responses of the X_R-cell of the model circuitry shown in Fig. 2 [Eq. (1b)]. The characteristic response peak induced by progressive figure motion increases in size, if the exponent n describing the non-linear synaptic transmission characteristic at the synapses to the X-cell increases ($n=1$ in **a**; $n=1.5$ in **b**; $n=2.5$ in **c**). Variation in this parameter, therefore, represents a possibility to account for the corresponding response component at the behavioural level. All other parameters of simulation are the same in **a–c**: number of channels stimulated by the ground: 52; number of channels stimulated by the figure: 8; these channels are stimulated by either the figure or the ground; shunting inhibition coefficient: $\beta=0.05$; the exponent approximating the saturation of the S-cells: $q=0.5$; relative phase between figure and ground: $\varphi=90°$ as is indicated in the bottom trace; amplification factor for the progressive movement detector channels: $g_p=1$; amplification factor for the regressive channels: $g_r=0.3$

values of n in the model equation [Eq. (1b)] correspond to a different operating range on the pre-postsynaptic transmission characteristic and, as a consequence, lead to response peaks of different amplitude during relative motion in the behavioural response.

If this hypothesis were correct, the variability found in the time course of figure-ground discrimination should already be reflected in the output cells of the underlying neuronal network. Figure 4 illustrates the range of variability of their response to relative motion with a phase-shift of 90° which has to be predicted on the basis of the model circuitry shown in Fig. 2. These response profiles of the model output cell will be compared with the response properties of its potential neuronal counterpart in the fly's brain (Sect. 3.1.3; Egelhaaf, 1985a).

1.3.2 Response Induced by Regressive Figure Motion. An additional behavioural response characteristic which remained unnoticed so far is illustrated in the sample records shown in Fig. 5. They were obtained from subsequent measurements of a single test-fly under the same stimulus conditions as the torque reactions displayed in Fig. 3. After switching the relative phase between figure and ground from $\varphi=0°$ to $\varphi=90°$, distinct response peaks are induced in the

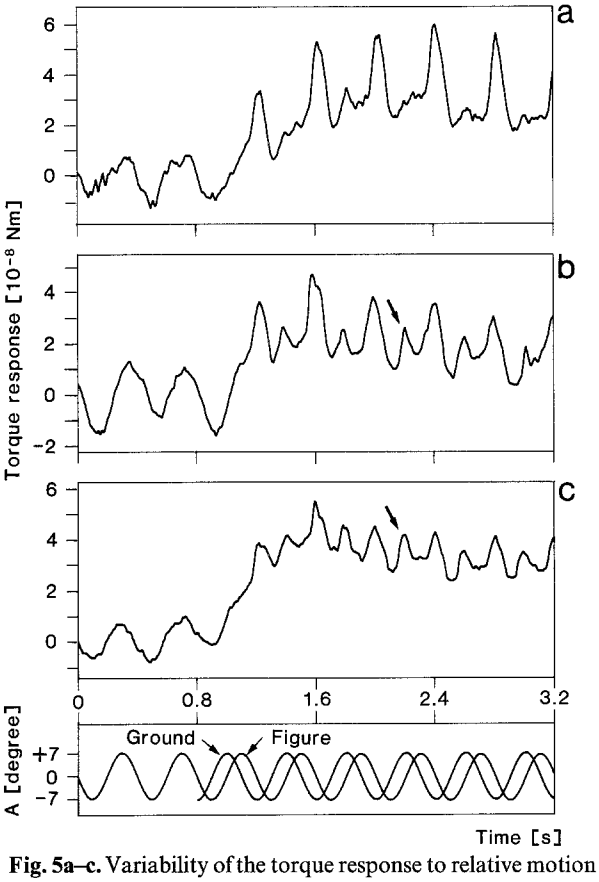

Fig. 5a–c. Variability of the torque response to relative motion of figure and ground in *Musca*. The experimental conditions were the same as in the experiments of Fig. 3 except the oscillation amplitude amounted to ±7°. The plotted response curves in **a–c** were obtained in subsequent measurements with a single test fly and represent the average of 100 sweeps each. The examples were chosen to illustrate the range of variability found in the amplitude of the response peak which can be elicited when the ground reverses its direction of motion while the figure still moves regressively. One of these response peaks is marked by an arrow in **b** and **c**, respectively. This characteristic response peak is rarely as pronounced as in **c**. It is usually much smaller than the corresponding response peak induced by progressive figure motion **b** or cannot be detected at all **a**

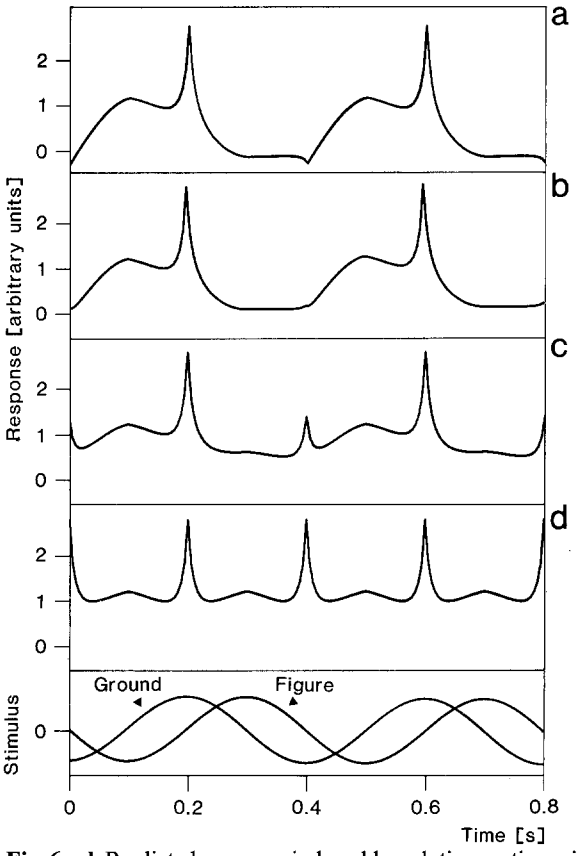

Fig. 6a–d. Predicted response induced by relative motion with a phase shift of $\varphi = 90°$ in the right output cell of the neuronal network proposed to underly figure-ground discrimination. The plotted curves represent the computed response of the X_R-cell in the model circuitry shown in Fig. 2 [Eq. (1b)]. In the different examples in **a–d** the amplification factor for the regressive movement detector channels is varied in both magnitude and sign: $g_r = 0.3$ in **a**; $g_r = -0.2$ in **b**; $g_r = -0.7$ in **c**; $g_r = -1$ in **d**. $g_r > 0$ leads to hyperpolarization of the cell by the regressive channels, $g_r < 0$ to depolarization. During relative movement $g_r < 0$ leads to a characteristic peak in the response of the cell which is induced when the ground reverses its direction of motion while the figure still moves regressively. It is phase-shifted by 180° to the corresponding response peak induced by progressive figure motion. For $g_r = -1$ and $g_p = 1$ both peaks have the same amplitude (g_p: amplification factor of the progressive channels). Variation in g_r represents a possibility to account for the variability in the corresponding response component in the behavioural data. All other parameters of the simulation are as in Fig. 4, except of n which amounts to 2

example shown in Fig. 5a, when the ground reverses its direction of motion while the figure still moves progressively. Hence, this record is very similar to the examples shown in Fig. 3. However, in the two other examples shown in Fig. 5 an additional type of response peak can be detected. One of them is marked by an arrow in Fig. 5b and c, respectively. This response peak is induced when the ground reverses its direction of motion, while the figure still moves regressively. This means that during regressive figure motion the fly tries to turn towards the position of the figure rather than in its direction of motion. Whereas in Fig. 5b this response peak has a smaller size than the response peak induced by progressive figure movement, the amplitudes of both types of response peaks are almost the same in Fig. 5c. They are displaced relative to each other by 180°. There is much variability with respect to the expression of this second response peak. It is usually small and often fuses with the subsequent response plateau, if it can be detected at all. Extreme examples with both response peaks of about the same size occur only rarely. Hence it is not much surprising that this response peak induced by regressive figure motion has not been found in the previous, studies on figure-ground discrimination. However, it should be noted that even in the original records of Reichardt et al. (1983, Fig. 3a and b) indications of response peaks can be detected which are phase-shifted with respect to the peaks evoked by progressive figure motion by approximately 180°.

Formally, the response peak elicited by regressive figure motion can be obtained on the basis of the figure-ground discrimination model shown in Fig. 2 by reversing the sign of synaptic transmission of the regressive channels to the output cells of the network (cell X in Fig. 2). This is illustrated in the computer simulations shown in Fig. 6 for the right output cell during stimulation by relative motion of figure and ground ($\varphi = 90°$). The amplification factor for the progressive channels was chosen to 1.0 in all computer simulations of Fig. 6. The amplification factor for the regressive channels amounted to 0.3 in Fig. 6a as in Fig. 4 and all computer simulations shown in the previous studies (Reichardt et al., 1983). Its sign is reversed in Fig. 6b–d. With an increasing amplification factor for the regressive channels the response peak induced by regressive figure motion increases (Figs. 6b, c). It reaches the same amplitude as the other response peak for an amplification factor of -1.0 (Fig. 6d). If the neuronal network underlying figure-ground discrimination were implemented in the fly's brain in the form shown in Fig. 2, its output cell should occasionally show a depolarizing response to regressive figure motion, as well as reflect the variability found in the expression of this response component at the behavioural level.

2 Calliphora and Musca do not Differ in Figure-Ground Discrimination Behaviour

For technical reasons all electrophysiological figure-ground discrimination experiments were carried out with the blowfly *Calliphora* rather than the much smaller housefly *Musca*. On the other hand, almost all behavioural studies were based on either *Musca* (Reichardt and Poggio, 1979; Reichardt et al., 1983) or

Drosophila (Bülthoff, 1981). The major reason why only few behavioural figure-ground discrimination experiments were done on *Calliphora* is their moderate readiness to fly fixed at a torque compensator in still air (see also Hengstenberg, 1983).

When doing behavioural and electrophysiological experiments with different, although related species the data obtained at both levels of analysis cannot be related directly to each other, unless it can be shown in control experiments that the species do not differ with respect to their behavioural and electrophysiological properties. In their initial attempt to relate the figure-ground discrimination behaviour to its actual underlying neuronal basis Reichardt et al. (1983) failed to demonstrate this correspondence. In *Calliphora* they could not find the characteristic peaks in the behavioural response to relative oscillatory motion of figure and ground with a phase shift of 90° typical for *Musca*.

Therefore, it was necessary to reinvestigate figure-ground discrimination of *Calliphora* in further behavioural experiments. Careful inspection of the new data revealed that, in contrast to the findings of Reichardt et al. (1983), *Calliphora* does not differ from *Musca* with respect to figure-ground discrimination behaviour. Also in *Calliphora* there is much variability in the response to relative motion both within the population of test flies as well as in the behaviour of a given fly when it is tested at different times. There are *Calliphorae* which do neither reveal any shift of the mean torque signal nor any obvious influence on the time-course of the response when the relative phase between the oscillating figure and the ground is switched from $\varphi = 0°$ to $\varphi = 90°$ (Fig. 7a). The other end of the range of variability found in *Calliphora* figure-ground discrimination behaviour is characterized by a pronounced shift of the mean torque response as well as by the conspicious response peak at $\varphi = 90°$ (Fig. 7c). It is, thus, virtually indistinguishable from the "typical" figure-ground discrimination behaviour of *Musca* as described by Reichardt et al. (1983). The example of Fig. 7b is intermediate between the examples shown in Fig. 7a and c. This variability in combination with the relatively small number of flies tested might have been the reason why no *Calliphorae* showing pronounced figure-ground discrimination were found in the earlier study of Reichardt et al. (1983).

In conclusion, these results provide clear evidence that *Calliphora* does not differ from *Musca* in any obvious way with respect to its reaction to relative motion between figure and ground. As a consequence the electrophysiological data on *Calliphora* can be related directly to the behavioural results obtained with *Musca*. Hence, the conditions for the organization of the neuronal network underlying figure-ground discrimination as derived in the previous section can serve as the conceptual framework for an electrophysiological analysis.

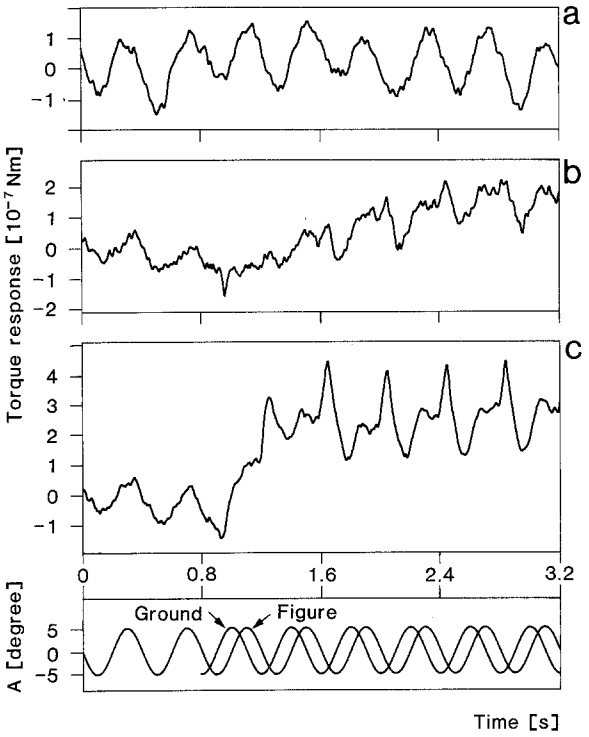

Fig. 7a–c. Variability in the dynamics of the torque response of *Calliphora* to relative motion of figure and ground. The experimental conditions were the same as in the experiments of Fig. 3. The different response curves in **a–c** were obtained with a single fly in subsequent experiments and represent the average of 100 sweeps each. Since *Calliphora* can generate during relative motion a shift of the mean torque signal as well as the characteristic response peak due to progressive figure motion, it does not differ from *Musca* with respect to figure-ground discrimination behaviour

3 Figure-Ground Discrimination and the Neuronal Network Controlling the Optomotor Response: A Reinterpretation

In the behavioural experiments on both figure-ground discrimination Sects. 1 and 2; Reichardt et al., 1983) as well as on the optomotor reaction (e.g. Fermi and Reichardt, 1963; McCann and MacGinitie, 1965; Götz, 1964, 1968) the yaw torque generated by the fly was chosen as the measure for the strength and time course of the reaction. Although the goals of both types of visually guided behaviour – fixation and tracking vs. stabilization of the flight course – are different, this poses the question for the relationship between their underlying control systems.

There is good evidence that optomotor yaw torque generation is controlled by an intricate network of

large-field tangential neurones of the lobula plate (see Fig. 1) with the three Horizontal Cells as its output elements (for review, see Hausen, 1981, 1984). The Horizontal Cells are selectively sensitive to ipsilateral front-to-back motion. They make direct synaptic contact in the ipsilateral posterior optic foci of the ventrolateral protocerebrum with descending neurones (see Fig. 1) which are thought to project directly to the motor control centres in the thoracic ganglia.

Since the network of "optomotor neurones" with the Horizontal Cells as its output elements is certainly stimulated massively under conditions of relative motion between figure and ground, it is suggested that it does not only control yaw torque generation in the optomotor reaction but plays also a critical role in figure-ground discrimination. Because of the apparent similarity between their behavioural data on *Calliphora* and the functional properties of the Horizontal Cells the hypothesis was initially put forward by Reichardt et al. (1983) that the neuronal network underlying the optomotor response might be sufficient to explain also figure-ground discrimination. In particular, the large Horizontal Cells were tentatively proposed to correspond to the output elements (X-cells in Fig. 2) of the model circuitry proposed to underly figure-ground discrimination. New behavioural data, however, and, first of all, the finding that *Calliphora* does not differ from *Musca* with respect to figure-ground discrimination (see Sect. 2) make it necessary to reexamine this hypothesis.

3.1 Are the Optomotor Neurones Sufficient for Figure-Ground Discrimination?

The optomotor neurones differ in their response properties from the presumed output cells of the neuronal circuitry underlying figure-ground discrimination. These differences pertain to their spatial integration properties, the heterolateral interactions in their input circuitry and the range of variability of their response.

3.1.1 The Spatial Integration Properties. The spatial integration properties of the Equatorial Horizontal Cell were analyzed in great detail by Hausen (1981, 1982b) for the vertical extent of the cell's receptive field. The corresponding behavioural experiments were done, however, with textured stimuli of variable horizontal width (Reichardt et al., 1983). In order to be capable of relating both levels of analysis the spatial integration properties of the optomotor neurones were reinvestigated under the same stimulus conditions as were employed in the behavioural analysis. For methodological reasons, the experiments aimed for a quantitative analysis were done with the

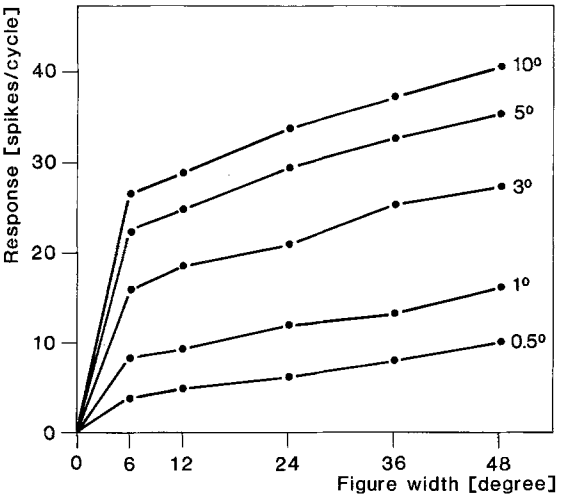

Fig. 8. Spatial integration properties of an optomotor neurone. Stimulus induced responses of the $H1$-cell are plotted as a function of the angular horizontal extent of a textured pattern. The pattern was oscillated sinusoidally with a constant frequency of 2.5 Hz about a mean position of $\psi = 30°$. The different response curves were obtained by varying the oscillation amplitude as is indicated at the right hand side of the figure. The individual data points were obtained from 8 different flies and represent the averaged spike response to 95 stimulation cycles. For a given oscillation amplitude the response does not depend linearly on figure width. After an initial sharp increase the response amplitude increases only slightly. The response curves are shifted to higher response levels for larger oscillation amplitudes

$H1$-neurone, a constituent member of the optomotor network (e.g. Hausen, 1981). There is, however, evidence from control experiments that the other optomotor neurones and, in particular, the Horizontal Cells possess qualitatively the same spatial integration properties as the $H1$-cell along the horizontal axis of the eye.

In Fig. 8, the response of the H1-neurone is plotted as a function of the angular horizontal extent of the oscillating figure; parameter is the oscillation amplitude. For a given oscillation amplitude the output of the cell increases less than proportionally with the figure width. The different response curves are shifted to higher response levels when the stimulus velocity is increased by increasing the oscillation amplitude (Fig. 8). In contrast to the behavioural reaction (see Sect. 1.1) the response of the neurone increases slightly with increasing figure width for all oscillation amplitudes. Thus, the network of optomotor neurones with the Horizontal Cells as its output elements differs in its spatial integration properties from the behavioural output. Since it is not sensitive enough to the motion of a small figure as compared with extended patterns, it is not sufficient to account for figure-ground discrimination.

3.1.2 Heterolateral Interactions. The consequences of the presumed heterolateral interactions in the figure-ground discrimination network for the response characteristics of its output elements (see Sect. 1.2) can be compared with the electrophysiologically analyzed response properties of the Horizontal Cells. The published data on their response to either monocular or binocular stimulation differ from the model predictions. Whereas the Horizontal Cells are excited by ispsilateral front-to-back motion, simultaneous contralateral motion in either direction does not alter significantly the response amplitude (see Fig. 1 in Hausen, 1982b). According to this, the hypothetical pool cells in the input circuitry of the Horizontal Cells in both halfs of the brain are not coupled, as has already been pointed out by Reichardt et al. (1983). Control of yaw torque in figure-ground discrimination, however, requires such a coupling. The heterolateral interactions in the input circuitry of the Horizontal Cells, therefore, do not comply with the constraints imposed by figure-ground discrimination behaviour on the underlying neuronal network.

3.1.3 Variability. Whereas there is a considerable amount of variability in the behavioural reaction to relative motion of figure and ground (Figs. 3, 5, and 7), there is no such variability in the response properties of the Horizontal Cells and the other optomotor neurones. Figure 9 shows the averaged response of the right Equatorial Horizontal Cell to both synchronous and relative motion of figure and ground (for comparable recordings, see Reichardt et al., 1983, Fig. 26). During synchronous motion of figure and ground the cell always shows qualitatively the same pattern of graded membrane potential changes. It responds to ipsilateral progressive and regressive motion with graded de- and hyperpolarizations, respectively (Fig. 9a). What is most obvious in the response to relative motion with a phase shift of 90° is that the response peak which is the characteristic signature of figure-ground discrimination behaviour (see Reichardt et al., 1983 and Sects. 1.3.1 and 2) is entirely lacking. This can be assumed to be an intrinsic property of the Horizontal Cells, since this response peak has never been observed in this cell type. Moreover, in long-time extracellular recordings of the *H*1-neurone, a constituent member of the optomotor network, no significant changes in the response pattern were observed. Furthermore, no Horizontal Cell was ever observed to become depolarized, at least occasionally, during ipsilateral regressive motion, as was predicted for an output cell of the neuronal network underlying figure-ground discrimination (see Sect. 1.3.2).

These results imply that the variability of the behavioural reaction cannot be explained by the

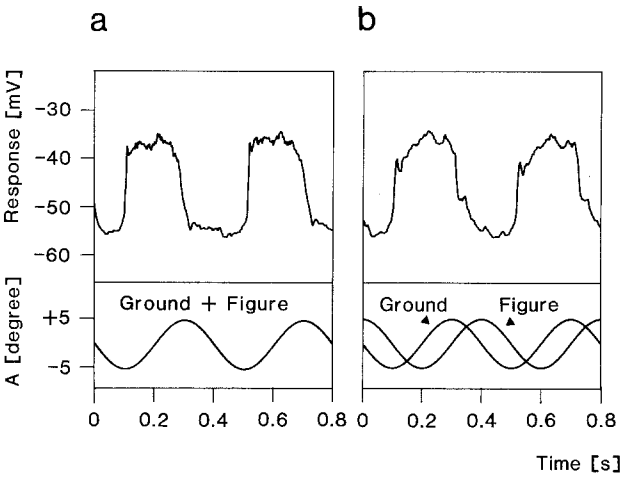

Fig. 9a and b. Responses of an Equatorial Horizontal Cell to synchronous **a** and relative motion of figure and ground with a phase shift of $\varphi = 90°$ **b**. A 12°-wide textured figure was positioned at $\psi = 30°$. An equally textured 240°-wide ground stimulated both eyes symmetrically. Oscillation frequency: 2.5 Hz; oscillation amplitude: $\pm 5°$. The recordings were obtained from the axon of the right Equatorial Horizontal Cell. Each recording represents a response average from 16 stimulation cycles. By comparing **a** and **b** it is obvious that the time course of the response is not much affected when figure and ground oscillate with a phase shift of 90° as compared to synchronous motion

response properties of the Horizontal Cells. Hence, the hypothesis proposed by Reichardt et al. (1983), that the variability of the behavioural reaction is due to shifting the operating range on the non-linear pre-postsynaptic transmission characteristic of the synapses between the elementary movement detectors and the output cells of the network (X_R, X_L in Fig. 2) has to be rejected. This provides further evidence that a second neuronal output system, in addition to the Horizontal Cells, is required to explain figure-ground discrimination.

3.2 Model Interpretation of the Horizontal Cell Response

Although the neurones supposed to control yaw torque in the optomotor reaction cannot explain figure-ground discrimination behaviour on their own, their main functional properties in the context of figure-ground discrimination can be interpreted in a similar way as has been done by Reichardt et al. (1983) in terms of the model circuits discussed in the Introduction and the Appendix. Figure 10 shows a model of the Horizontal Cells and their input circuitry as it can be derived from the original model proposed by Poggio et al. (1982; see also Fig. 2). There are two differences between the model circuit of Fig. 10 and the one proposed on the basis of the behavioural analysis for the output cells of the neuronal network underlying

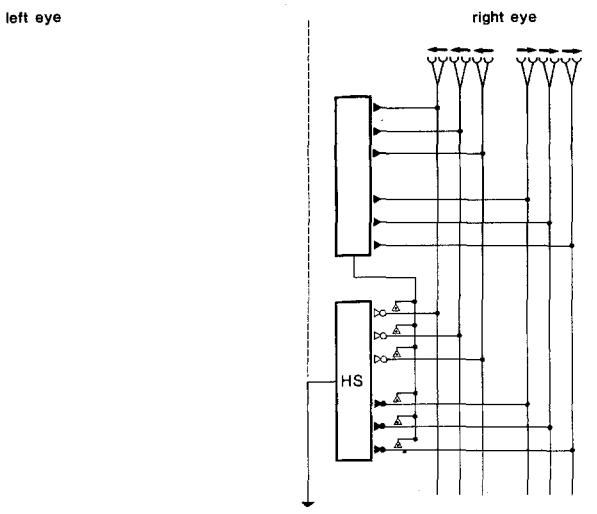

Fig. 10. Model of the Horizontal Cells and their input circuitry in terms of the model proposed to underly figure-ground discrimination (see Fig. 2). All symbols used are explained in the legend of Fig. 2. As the main topological difference to the original figure-ground discrimination model shown in Fig. 2, the presumed pool cells of both optic lobes in the input circuitry of the Horizontal Cells are not coupled. The simplifications made in this model are discussed in the text

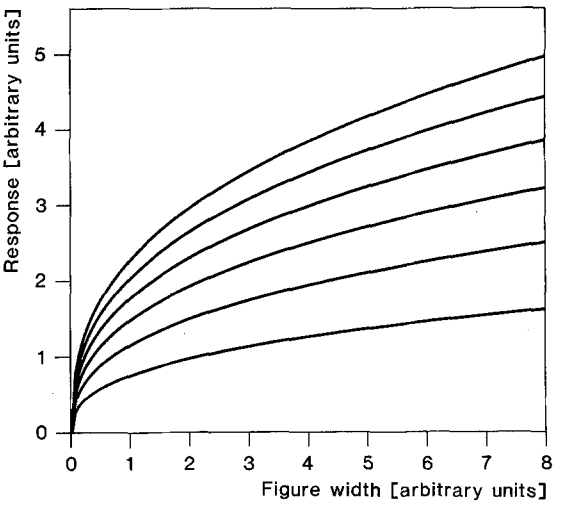

Fig. 11. Computer simulation of the spatial integration properties of an optomotor neurone. The response of the "HS"-cell of the model shown in Fig. 10 [Eq. (1b)] is plotted as a function of the number (N) of excited movement detector channels. N is assumed to be proportional to the figure width. The different curves represent different levels of channel detector output (w), which is assumed to be proportional to the pattern velocity. Parameter settings of this simulation: $n=1.25$, $q=0.5$, $\beta=0.05$; weighting factor for the progressive and regressive movement detector channels: $g_p=1$, $g_r=0.3$. If the parameter n characterizing the non-linear transmission characteristic of the synapses between the movement detector channels and the output cell of the network is chosen appropriately, the corresponding electrophysiological data on the optomotor neurones are fitted quite well

figure-ground discrimination. Firstly, the networks on both sides of the brain are assumed to operate independently; the proposed pool cells in the input circuitry of the Horizontal Cells are not coupled (see Sect. 3.1.2). Secondly, the exponent n in the model equation (Eq. 1) representing the non-linear transmission characteristic of the input synapses to the model Horizontal Cells has to be smaller ($n=1.25$) than is necessary to account for the behavioural reaction ($n=2$). The computer simulations shown in Fig. 11 illustrate that under these conditions the computed reaction of the cell depends in a similar way on figure width as the electrophysiologically determined cellular response (see Fig. 8). Figure 12 shows the simulated time course of the graded response of the Horizontal Cells to synchronous and relative motion of figure and ground ($\varphi=90°$). For the same parameter settings as used in the simulation of Fig. 11 the computed responses of the model cell fit the corresponding electrophysiological data satisfactorily. In particular, the characteristic response peak which was found to be the most prominent signature of figure-ground discrimination at the behavioural level is lacking in the response to relative motion of the model as well as the Horizontal Cells (compare Figs. 9 and 12). Hence, it can be concluded that the model circuitry of Fig. 10 is, in fact, sufficient to account for those functional properties of the Horizontal Cells which are important in the context of figure-ground discrimination. In one of the subsequent papers (Egelhaaf,

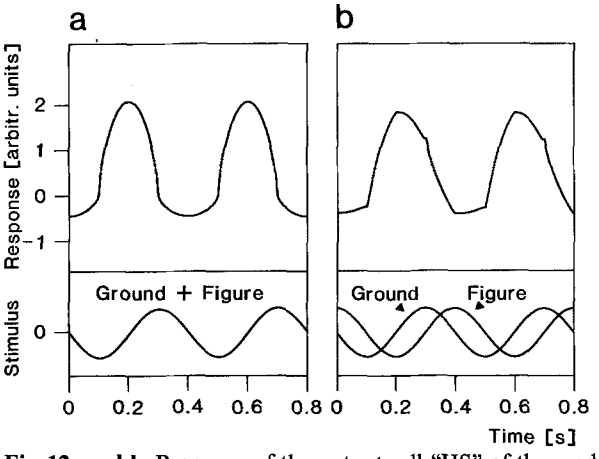

Fig. 12a and b. Response of the output cell "HS" of the model shown in Fig. 10 to synchronous **a** and relative motion of figure and ground with a phase shift of 90° **b**. As in Fig. 11 the parameter settings used in this computer simulation were chosen to account best for the functional properties of the optomotor neurones ($n=1.25$; $q=0.5$; $\beta=0.05$; other parameters as in Fig. 4). Under these conditions only the fine structure of the response is altered during stimulation with relative as compared with synchronous motion. Since the experimentally determined cellular responses (see Fig. 9) show delays with respect to the stimulus, the computed response curves are shifted for better comparison by the respective delays

1985b) this model will be used together with similar models for another functional class of cells, in order to simulate figure-ground discrimination behaviour.

It should be noted, however, that this model is in two ways a very simplified representation of the neuronal network as it is actually implemented in the fly's brain:

a) It accounts only for the graded potentials of the Horizontal Cells and does not make allowance for the small spike-like potentials which might be induced by contralateral regressive motion (Hausen, 1981, 1982a). However, the generation of graded changes of the membrane potential rather than regular spike trains is the prominent response mode of the Horizontal Cells to ipsilateral stimulation (Hausen, 1981, 1982a, b).

b) The organization of the input circuitry of the Horizontal Cells as proposed in the model of Fig. 10 is not based on direct experimental evidence, but is derived indirectly from their response characteristics. This model rather than the neurophysiologically established wiring of lobula plate tangential neurones (for review, see Hausen, 1981) was chosen for the computer simulations, since the latter network cannot account so far for the most important features of the Horizontal Cells in the context of figure-ground discrimination, namely their specific spatial integration properties.

Discussion

The present study on the neuronal basis of figure-ground discrimination by relative motion in the fly is based on behavioural and electrophysiological experiments, as well as on theoretical considerations. In a first attempt to bridge the gap between the behavioural and the neuronal level two alternative model circuitries have been proposed by Poggio et al. (1981) and Reichardt et al. (1983) as candidates for the principal organization of the neuronal network underlying figure-ground discrimination. A further alternative is put forward in this study (see Appendix). On the one hand, these model circuits are based on the detailed knowledge of figure-ground discrimination as it is revealed at the behavioural level. On the other hand, they were formulated in a way taking into account the hardware available in the fly's brain. On the basis of these models the functional properties of the presumed output cells of the neuronal network underlying figure-ground discrimination could be predicted. It should be noted that under the conditions tested so far all these alternative model networks lead to essentially the same predictions for the response properties of the output cells, irrespective of differences in their operations. Therefore, it is likely that on the basis of their response properties it cannot be resolved which alternative comes closer to the actual neuronal network implemented in the fly's brain.

Initially the three lobula plate Horizontal Cells, for long regarded as the output elements of the optomotor large-field course control system (e.g. Hausen, 1981; Hausen and Wehrhahn, 1983), have been proposed to correspond to the presumed output cells of the circuit underlying figure-ground discrimination (Reichardt et al., 1983). The predictions for the functional properties of the latter cell type have been compared with the electrophysiologically determined Horizontal Cell response: (1) The Horizontal Cells are not sensitive enough to motion of small objects as compared to large stimuli. (2) The heterolateral interactions within their input circuitry are not in accordance with the behaviour (see also Reichardt et al., 1983). (3) The variability found in the time course of certain components of figure-ground discrimination behaviour cannot fully be explained by the response properties of the Horizontal Cells. From the failure to demonstrate correspondence between model predictions and actual cellular response properties it has been concluded that additional output cells of the optic lobes with different functional properties are involved in the control of yaw torque generation.

One complication for the further analysis might arise from this conclusion. If the yaw torque is controlled by more than one neuronal system in a particular visual information processing task, the final behavioural output no longer represents any of the involved control systems unambiguously on its own. How can the functional properties of the individual neuronal subsystems be inferred from the common behavioural output in spite of this complication?

To begin with, it should be emphasized that this cannot be done by formally decomposing the visual responses to moving objects into a direction-sensitive and a direction-insensitive component. The direction-sensitive response component is given by half the difference, the direction-insensitive component by half the sum of the torque response to clockwise and counter-clockwise motion of the stimulus. Although this formal decomposition is always possible (at least if time-averaged responses are concerned) and has been applied widely in the phenomenological analysis of visual orientation behaviour of the fly (for review see Reichardt and Poggio, 1976; Poggio and Reichardt, 1976; Heisenberg and Wolf, 1984) there is no a priori reason why it should lead to isolation of the different control mechanisms as they are actually implemented at the underlying neuronal level.

A different strategy has, therefore, been adopted in this study. The functional properties of the additional control system can be predicted from the "deficits" of

the Horizontal Cells with respect to figure-ground discrimination, if one assumes that the different systems involved in yaw torque control interact linearly somewhere between the lobula plate and the final motor output. Although this represents only the most straightforward possibility, it can be justified in the subsequent studies (Egelhaaf, 1985a, b). On this basis the conditions for the presumed additional output cells of the neuronal network underlying figure-ground discrimination are as follows: (1) They should be more sensitive to motion of relatively small objects than to extended textured stimuli. (2) Specific heterolateral interactions are required in their input circuitry. Interpreted in terms of the model networks proposed to underly figure-ground discrimination, this means that the pool cells (*S*-cells in Figs. 2 and A.1) should be coupled and should not be selective for the direction of motion. (3) The sign of synaptic transmission of the regressive motion detectors should be variable and occasionally lead to depolarization of the output cells of the network. 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 system, one selectively sensitive to progressive, the other to regressive motion. (4) Their axonal projections should be appropriate for output elements of the optic lobes involved in the control of yaw torque generation. In the subsequent papers (Egelhaaf, 1985a, b) these conditions will be used as criteria in electrophysiological studies for establishing newly discovered neurones as likely output cells of the neuronal network underlying figure-ground discrimination.

More direct approaches to decompose the overall torque response into its physiologically significant components have been employed in recent studies. The contribution of the Horizontal Cells has been eliminated firstly, by genetic dissection in the *Drosophila* mutant optomotor-blind (Heisenberg et al., 1978; Götz, 1983; Bausenwein, 1984; Heisenberg and Wolf, 1984), secondly, by ablation with a laser microbeam of their precursor cells in the larval brain (Geiger and Nässel, 1981, 1982) and finally, by microsurgical lesion of their axons (Hausen and Wehrhahn, 1983; in prep.). Although all these studies were performed in a different conceptual frame, they are in agreement with the general conclusion drawn above that, apart from the Horizontal Cells, there must be an additional output system of the optic lobes involved in yaw torque control. Moreover, there emerge some interesting parallels between the conditions for the additional system and the torque response in flies devoid of functionally intact Horizontal Cells. Firstly, there is a direction-insensitive response component in both laser ablated (Geiger and Nässel, 1982) as well as microsurgically lesioned flies (Hausen and Wehrhahn, in prep.). Accordingly, monocular horizontal motion in either direction induces turning towards the stimulated side, although the response to regressive motion appears to be weaker. In particular the latter response component is reminiscent of the response peak which would lead in unrestrained flies to turning towards the figure and can occasionally be observed during relative motion when the figure moves regressively while the ground reverses its direction of motion (see Fig. 5). Secondly, Geiger and Nässel (1982) suppose that the additional yaw torque control system is most sensitive to small targets rather than to more extended stimuli. This is also suggested by the results on the mutant optomotor-blind which does not respond to wide-field stimulation but easily fixates a moving narrow stripe (Heisenberg and Wolf, 1984). These findings are quite in accordance with the conclusion drawn above. Thirdly, there is evidence from the data of Hausen and Wehrhahn (in preparation) that the additional system is inhibited by contralateral motion. Similar heterolateral inhibitory interactions had to be proposed to exist in the neuronal network underlying figure-ground discrimination. Cells which satisfy these conditions and might thus represent the additional output cells of the network underlying figure-ground discrimination will be analysed in the subsequent papers (Egelhaaf, 1985a, b).

Appendix

Another Alternative Cellular Model for Explaining Figure-Ground Discrimination

So far the main conditions for the output elements of the network underlying figure-ground discrimination have been derived in terms of the model circuitry originally proposed by Poggio et al. (1981) and further analysed by Reichardt et al. (1983). Reichardt et al. (1983) proposed an alternative network which relies, in contrast to their original model, on a recurrent pathway interacting with the individual movement detector channels prior to summation of the channel signals by the pool cells. This interaction is due to presynaptic shunting inhibition and, thus, of the same type as in the original model scheme. These alternative circuitries generate practically the same behavioural output, although their operations are mathematically different. This is also true for a further alternative which differs from the other models in that the inhibitory input mediated by the presumed large-field pool cells is directly on the output cells of the network (Fig. A.1a). The latter cell type, therefore, has to integrate at least three different kinds of input, i.e. retinotopic excitatory and inhibitory input which is distributed on the cell's entire dendritic tree as well as inhibitory input of the shunting type from the large-field pool cell. This input is placed in the simplest version of this postsynaptic shunting inhibition model on the axon just after convergence of the cell's main dendritic branches, as is shown schematically in Fig. A.1a. However, it could be distributed equally well over the entire dendritic tree.

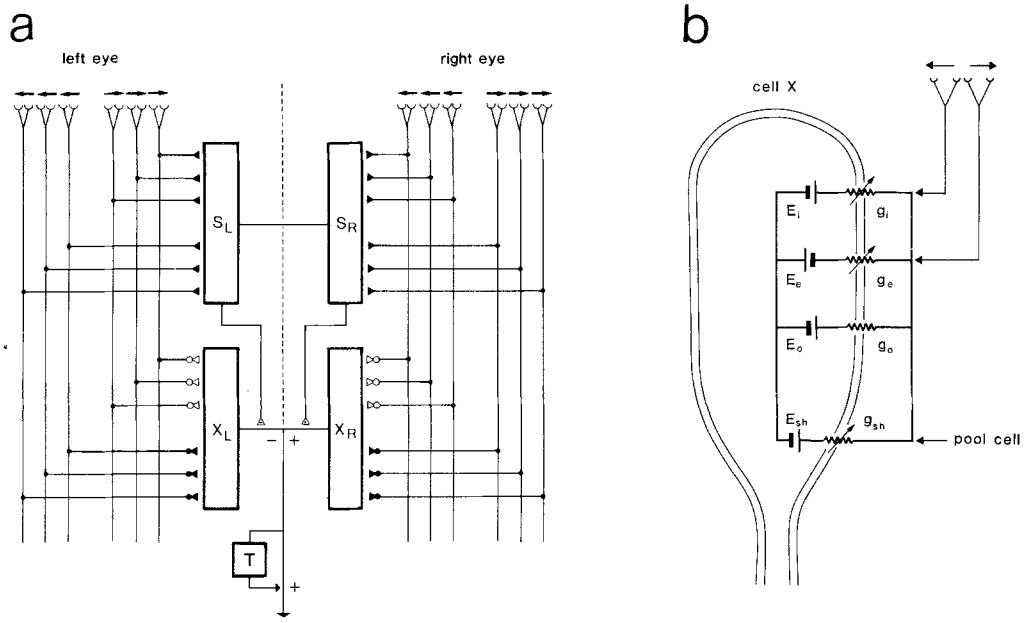

Fig. A.1a and b. An alternative model sufficient to explain figure-ground discrimination. **a** Outline of the network. It is topologically the same as the original one proposed by Poggio et al. (1981) and Reichardt et al. (1983) apart from the inhibitory input mediated by the pool cells *S*. It operates directly on the output cells *X* of the network (—◁). It is assumed to be of the shunting type. The other symbols are as explained in the legend of Fig. 2. **b** Biophysical mechanisms underlying the alternative model illustrated by its equivalent electrical circuit. The outline of the output cell *X* of the network of **a** is sketched schematically by the pair of thin parallel lines. It is assumed that the entire dendritic tree and at least the initial segment of the axon (bottom part of the diagram) are equipotential. The transfer resistances between the different sites of synaptic input, therefore, can be neglected and the entire excitatory and inhibitory retinotopic input resulting from progressive (——▶) and regressive (◀——) motion can be lumped together to a common excitatory and inhibitory input channel, respectively. These two inputs control the conductances g_e and g_i of different ionic channels with equilibrium potential $E_e > E_0$ and $E_i < E_0$, respectively. E_0 and g_0 are the resting potential and the resting conductance of the cell, respectively. The large-field pool cell *S* in the model network of **a** modulates via shunting inhibition the conductance g_{sh} with an equilibrium potential $E_{sh} = E_0$. For further explanations see text

A.1 Biophysical Mechanisms Underlying the Postsynaptic Shunting Inhibition Model

The equivalent electrical circuit of the output cell of the postsynaptic shunting inhibition model (*X*-cell in Fig. A.1a) is sketched in Fig. A.1b. This circuit simplifies the geometrical relations of the neurone since it is assumed, as a first approximation, that the entire dendritic tree and at least the initial segment of the axon are equipotential. Since under this condition the transfer resistances between the different sites of synaptic input can be neglected, the entire excitatory and inhibitory retinotopic input synapses can be lumped together to a common excitatory and inhibitory input channel, respectively. These two inputs control the conductances $g_e(t)$ and $g_i(t)$ of different ionic channels with equilibrium potential $E_e > E_0$, and $E_i < E_0$, respectively. E_0 is the resting potential of the cell. Shunting inhibition is mediated by modulating the conductance $g_{sh}(t)$ with an equilibrium potential $E_{sh} = E_0$. In order to simplify the calculations that follow the resting potential is set to $E_0 = 0$. Moreover, the membrane capacitance has been neglected. This means that the time changes of the input to the circuit are assumed to be slower than the membrane time constant. This does not seem to be too restrictive a condition in the present context, since membrane time constants smaller than 10 ms are common in other systems (Rall, 1977). If these conditions are satisfied, the circuit equation can be written as

$$V(t) = \frac{E_e g_e(t) + E_i g_i(t)}{g_0 + g_e(t) + g_i(t) + g_{sh}(t)}. \quad \text{(A.1)}$$

This equation defines a non-linear relation between the inputs $g_e(t)$, $g_i(t)$, $g_{sh}(t)$ and the membrane potential output $V(t)$. g_0 is the resting conductance of the cell. With adequately chosen input functions $g_e(t)$, $g_i(t)$, and $g_{sh}(t)$ this circuit can subserve figure-ground discrimination.

A.2 Derivation of the Model Equation

A signal $w_i(t)$ is generated in each movement detector which is, in a first approximation, proportional to pattern velocity. $w_i > 0$ and $w_i < 0$ stand for progressive and regressive motion, respectively. The output of the *X*-cell in Fig. A.1a can be derived from Eq. (A.1), if the different conductance inputs are related to the activity of the array of movement detectors. $g_e(t)$ and $g_i(t)$ in Eq. (A.1) corresponds to the retinotopic input of the progressive and regressive movement detectors, respectively. They may be lumped to a single expression

$$\sum_{i=1}^{N} |w_i(t)|^n \cdot \mathrm{sign}(w_i(t)),$$

since positive and negative values of w_i can be interpreted as the consequences of changes in g_e and g_i, respectively. N represents the number of movement detector channels. The exponent n approximates a nonlinear operation which transforms the presynaptic into the postsynaptic voltage. If the input via the synapses of the shunting type g_{sh} is omitted, it follows from

Eq. (A.1) for the output of the X-cell

$$\frac{\sum_{i=1}^{N} |w_i(t)|^n \cdot \operatorname{sign}(w_i(t))}{\beta + \sum_{i=1}^{N} |w_i(t)|^n}. \tag{A.2a}$$

β designates the resting conductance g_0 in Eq. (A.1). For $\beta \ll \sum_{i=1}^{N} |w_i|^n$ the response approaches a saturation level which can be interpreted in terms of Eq. (A.1) as the equilibrium potential of the corresponding conductance channel. In the simulations this has been arbitrarily chosen as 1 for the progressive channels and 0.3 for the regressive ones. This gain ratio comes close to the experimental findings on lobula plate tangential cells (e.g. Hausen, 1982b).

Decisive for the figure-ground discrimination capabilities of the network is the inhibitory input mediated by the large-field pool cell (S in Fig. A.1). The corresponding input conductance g_{sh} in Eq. A.1 can be equated with the expression

$$c\left(\sum_{i=1}^{N} |w_i(t)|\right)^m,$$

where

$$\sum_{i=1}^{N} |w_i(t)|$$

represents the output of the pool cell, m a non-linear transmission characteristic of the synapse and c a weighting factor for the shunting inhibition input. It should be emphasized that linear summation of the retinotopic input by the S-cell in Fig. A.1a represents only the most straightforward possibility and is not essential for the principal properties of the circuit. The S-cell can also be assumed to saturate, as is required for the figure-ground discrimination model shown in Fig. 2. This would only affect the admissable values of the parameter m.

The final output of the X-cell is given by the expression

$$y(t) = \frac{\sum_{i=1}^{N} |w_i(t)|^n \cdot \operatorname{sign}(w_i(t))}{\beta + \sum_{i=1}^{N} |w_i(t)|^n + c\left(\sum_{i=1}^{N} |w_i(t)|\right)^m}. \tag{A.3a}$$

This equation reduces to a simpler form, if $w_i(t) = w_j(t)$ for all i, j.

$$y(t) = \frac{N|w(t)|^n}{\beta + N|w(t)|^n + c(N|w(t)|)^m} \cdot \operatorname{sign}(w(t)). \tag{A.3b}$$

As in the original model of Reichardt et al. (1983) the behavioural output is given by adding to the output of the X_L and X_R cells their running time integral.

At first sight the Eqs. (A.3a) and (A.3b) look more complicated than the corresponding model equations of the original figure-ground discrimination model [see Eq. (1)]. The differences in both equations, however, do not pertain directly to figure-ground discrimination, but are mainly due to the saturation characteristics intrinsic in the X-cell of the present model. Both models become nearly equivalent, if in Eq. (A.3b) $N|w|^n + \beta \ll c(N|w|)^m$ and $c = 1$. This condition is satisfied as long as the cell operates in a range of its input-output characteristic well below the level of saturation. Moreover, the parameter m in Eq. (A.3) has to be related to the parameters q and n in Eq. (1) by the equation $m = q \cdot n$. Under these conditions the two alternative model circuitries can be expected to behave virtually identical. The output signal $y(t)$ becomes independent of N, if $m = 1$. For $m > 1$ the response amplitude decreases, for $m < 1$ it increases with increasing width of the stimulating pattern. In contrast to the original model version the spatial integration properties of the network shown in Fig. A.1 depend on only one model parameter (m). The parameters n and c only affect the waveform of the response and the operating range of the cell, respectively.

A.3 Performance of the Model

The performance of the postsynaptic shunting inhibition model will be analysed here with respect to the specific gain control

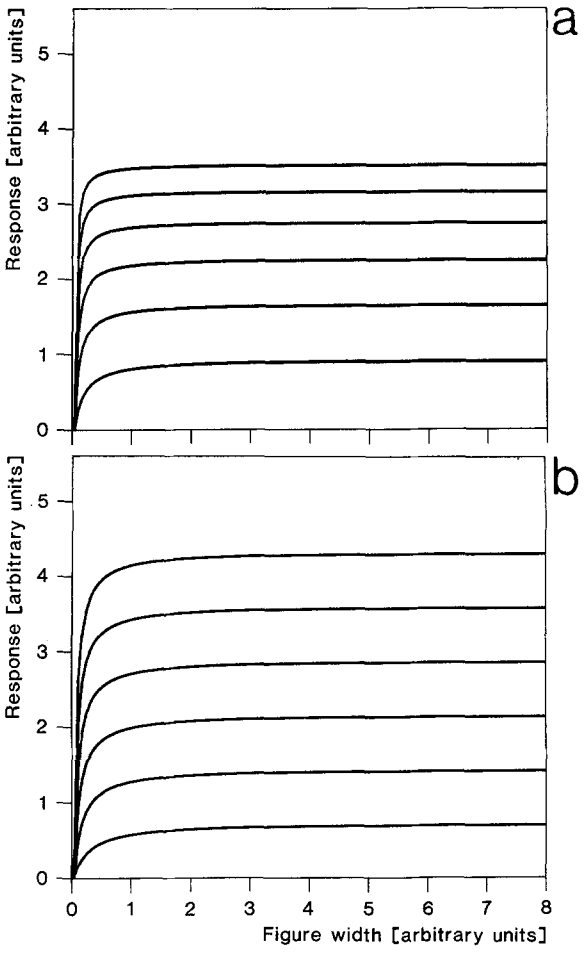

Fig. A.2a and b. Response of the model circuitries shown in Fig. A.1a **a** and Fig. 2 **b**, demonstrating the alternative gain control mechanisms that operate on the angular horizontal extent of the figure. Equations (A.3b) and (1b) were computed in **a** and **b**, respectively, as a function of the number (N) of excited movement detector channels. The different curves represent different levels of detector output (w), which is assumed to be proportional to the pattern velocity. w is increased in consecutive steps of constant increment. Parameter settings of the simulation shown in **a**: $n = 2$, $m = 1$, $\beta = 0.005$, $c = 1.5$. Parameter settings of the simulation shown in **b**: $n = 2$, $q = 0.5$, $\beta = 0.05$. For a given pattern velocity the response of both models becomes independent of N. Whereas the plateau levels of the different response curves are equidistant in **b**, their ratio is slightly less than 2 in **a** when the stimulus is doubled in amplitude

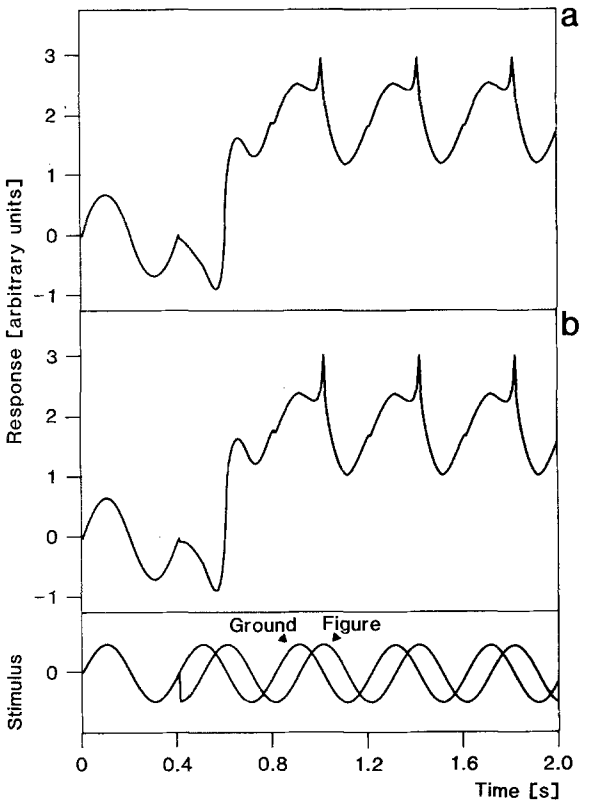

Fig. A.3a and b. Computer simulation of the behavioural response to synchronous motion of figure and ground as well as relative motion with a phase shift of 90° (see traces at the bottom of the diagram). **a** Simulation based on the model shown in Fig. A.1a. Parameter settings used: $n=2$; $m=1$; $\beta=0.005$; $c=1.5$. **b** Simulation based on the model shown in Fig. 2. Parameter settings used: $n=2$; $q=0.5$; $\beta=0.05$. The time constant of the running average amounted to 0.4 s. The number of channels stimulated by the ground (52) and by the figure (8), respectively, were the same in **a** and **b**. These simulations illustrate that there are only minor differences in the output of both model circuitries. They match the time course of the corresponding behavioural reaction equally well

characteristics observed in figure-ground discrimination behaviour and the typical time course of the response to relative motion of figure and ground with a phase shift of 90°.

Due to the theoretical considerations in Sect. A.2 the response becomes independent of figure width if m = 1 and the output cell of the network operates in the linear range of its input-output characteristic. The computer simulations of Eq. (A.3) show that this is true even when saturation phenomena become apparent. This is demonstrated in Fig. A.2, where the oscillation amplitude of the response to an oscillating figure is computed as a function of the figure's width. Parameter is the signal amplitude at the detector channel output which is assumed to be proportional to the velocity of the pattern. The response increases as the angular extent of the figure increases, but reaches quite soon a constant level. However, it depends strongly on the detector channel output. With increasing output one obtains response curves which approach higher and higher constant response levels. The output of the original model proposed by Reichardt et al. (1983) is very similar in this regard as is shown for comparison in Fig. A.2b. The responses of both alternative models differ, however, in one respect. Whereas the plateau levels of the different response curves corresponding to consecutive constant increments in the stimulus strength are equidistant in the original model, their distance decreases in the alternative model. This compression of the dynamic range in the alternative model is due to the saturation term in Eq. (A.3) and is closely matched by the corresponding behavioural measurements (see Fig. 7 in Reichardt et al., 1983).

In Fig. A.3 the characteristic time course of the reaction of both alternative models is compared for synchronous and relative motion ($\varphi=90°$) between a figure and a binocular ground. They are in good agreement with respect to their most prominent characteristics and match the time course of the corresponding behavioural reaction equally well (compare Fig. A.3 with Fig. 3a in Reichardt et al., 1983; see also Figs. 3 and 7). The correspondence of the output of both models is similarly striking for all other stimulus conditions. Therefore, they are both sufficient to account for figure-ground discrimination despite their different wiring schemes and underlying biophysical mechanisms.

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