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optomotor-blind^{H31} – a *Drosophila* Mutant of the Lobula Plate Giant Neurons

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Summary. In the *Drosophila* mutant *optomotor-blind*^{H31} (*omb*^{H31}), previously isolated for its defects in the optomotor turning response, the visual giant neurons of the lobula plate are missing or significantly reduced. In particular, fibres homologous to the H- and V-cells of *Calliphora* as well as two fibres (M-cells) in the middle plane of the plate are affected.

Optomotor turning reactions in flight and in the walking mode are strongly reduced in *omb*^{H31}. Also pattern induced orientation is disturbed. In flight this behavior is thought to be controlled by 3 parameters: the response to the position of the pattern, the response to the direction of motion of the pattern and the spontaneous torque fluctuations of the fly. All of these are reduced in the mutant.

Two other visual reactions, the optomotor thrust response and the movement-stimulated landing response can readily be elicited. Although *omb*^{H31} and wild type differ in certain properties of these responses preliminary experiments indicate that in both cases the response strength is not significantly reduced by the mutation.

These findings confirm the rôle of the H-cells in optomotor turning reactions but question the suggestions based on anatomical and electrophysiological results from big flies that the V-cells are mediating the optomotor thrust response.

Introduction

In recent years the visual giant neurons in the lobula plate of flies have been extensively studied (e.g. Pierantoni, 1976; Dvorak et al., 1975; Hausen, 1976). Extra- and intracellular recording combined with subsequent staining of individual neurons has provided some hints as to the functional properties of these cells. It was proposed that a set of 3 neurons (H-cells) at the anterior surface of the lobula plate is part of the main pathway for the optomotor turning response and that a set of 8 or 9 staggered T-shaped neurons (V-cells) at the posterior surface constitutes the corresponding part in the pathway for the optomotor thrust response. We report here on a mutant of *Drosophila* which is severely impaired in both the optomotor turning response and the visual giant neurons of the lobula plate. This strain had been isolated in a screening experiment for mutants deficient in the optomotor turning response. Among a large number of such mutants this had been the only one with a normal electroretinogram suggesting a more central defect in the optomotor system (Heisenberg, 1972; Heisenberg and Götz, 1975).

Material and Methods

Stocks. Wild type *Drosophila melanogaster* "Berlin" and two mutants *omb*^{H31} and S100 derived from this stock by mutagenesis were used. The isolation of *omb*^{H31} in the optomotor maze has been described earlier (Heisenberg and Götz, 1975). The mutation was found after treatment with ethylmethanesulfonate and is associated with the X-chromosome. The X-chromosome of *omb*^{H31} carries a large inversion which very effectively suppresses crossing over. The break points of the inversion are close to 4C4-7 and 12D2-E1 according to a preliminary investigation of J.K. Lim (personal com. to W.D. Kaplan). Whether the phenotypic defects are related to this inversion or to an additional mutation is not known. Behavioral experiments were performed on 4–14 days old females while females and males of any age served for histology.

Histology. For silver stained preparations flies were fixed and stained according to the procedure of Holm and Blest (Blest, 1961). For 1 µm serial sections glutaraldehyde and subsequently OsO_4 were used as fixatives. Flies were embedded in Araldite, cut and stained by toluidine blue.

Behavioral Experiments. Most experimental procedures are described by Heisenberg and Götz (1975), Buchner (1976) and Heisenberg and Buchner (1977). Some experimental details are given in the legends to the figures. Pattern-induced flight orien-

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tation behavior was evaluated with a HP9825A calculator. In experiments in which the calculator alternately received data from the torque compensator and the ringpotentiometer reflecting stripe position it evaluated 20 such double measurements/s with a 15 ms delay after the position measurement (and a 35 ms delay after the torque measurement).

Pattern induced orientation of walking flies was measured in a circular arena ($\varnothing = 29$ cm, height from center of walking platform $\alpha = 64°$). The arena was built of a translucent plexiglas tube illuminated from behind by 4 circular 40 W fluorescent lamps. Flies with clipped wings were placed in the center of the arena and were scored when reaching one of 12 segments of a measuring circle ($\varnothing = 10$ cm). Each fly performed 10 runs. The stripe position relative to the walking platform (and to the observer) was changed after every second run in an arbitrary sequence. Prior to the experiment flies were adapted to about the light intensity of the arena.

Results

1. Anatomy of the Lobula Plate in Drosophila Wild Type

The general architecture of the lobula plate seems to be quite similar to that of big flies. Large diameter fibres are found in three parallel planes: on the frontal and caudal surfaces and midways between them. The three layers are maximally separated by ~10–15 µm. These large fibres run at about right angles to the mass of thin fibres which presumably constitute the lobula plate columns corresponding to the visual elements. Some of the giant fibres are up to 7 µm in diameter. (Fibres included in this account had to be at least ~2 µm in diameter for some length in order to stand out sufficiently against the background of thin fibres.) All the big fibres join into a very conspicuous horizontal bundle at the back of the brain ending on the protocerebral slope close to the oesophagus.

a) H-Cells. Like in *Musca*, *Phaenicia* and *Calliphora* the three fibres which lie on the frontal surface of the lobula plate are distinguished from each other by the domains of their arborizations (north, equatorial, south). In *Drosophila* these overlap considerably. They are slightly tilted in respect to the surface of the plate and are staggered like tiles on a roof. As judged by the planes of the fibre trunks they avoid direct contact with each other. The north- and equatorial fibres join the horizontal bundle where they leave the plate; the south-fibre joins it just laterally to the retractor muscle of the proboscis.

Immediately medially to the retractor the 3 H-cells leave the bundle, bend downward and split each into two branches, one going further down along the posterior slope, the other turning forward into the depth of the brain (Fig. 1a).

b) M-Fibres. In the middle plane of the lobula plate two fibres were found in reconstructions from 1 µm serial sections and in silver impregnations: a big equatorial fibre and a small south-fibre. The fibers join the bundle together with the corresponding H-cells but are lost in the bundle (Fig. 1b). Also in *Calliphora* the middle plane is occupied by a pair of large-field neurons which Hausen (1976) named V2 according to their physiological properties. It is possible that these are homologous to M-cells in *Drosophila*.

c) V-Cells. The most significant difference to the larger flies is found in the set of fibres at the caudal surface of the lobula plate. It is not clear as yet how many of these cells there are. Five of them can be easily identified in 1 µm-sections and in silver impregnations. A sixth one and possibly a seventh can be occasionally seen, but they are too small to be reliably detected.

Since the giant fibre bundle enters the lobula plate fairly high up and since in addition the lobula plate is tilted ventrally by ~20° the downward extending branches of the V-cells No. 1 and 2 are very prominent, covering ~3/4 of the height of the plate. All branches are nicely parallel to each other, those of cells No. 1 and 2 and of cells No. 4 and 5 being closer together than the others. The branches of cells No. 1, 2, and 3 are accompanied by satellite fibres. Since only short pieces of these were reconstructed they are omitted from Figure 1.

The upward extending branches are much smaller and less well oriented. It is clear from 1 µm serial sections and from a Golgi-impregnated V-cell that some of them have more than one upward extending branch. What distinguishes the V-cells of *Drosophila* from those of *Musca* and *Calliphora* is that several of these collaterals run parallel to the columns of the lobula plate to the frontal surface where they have arborizations in the plane of the H-cells. These branches end in a part of the lobula plate which presumably corresponds to the upper frontal part of the visual field. In addition we found a large branch of cell No. 2 which enters the middle plane of the plate and again fills the upper frontal part of the projection of the visual field; this region is spared by the M-fibres.

The V-cells have long horizontal extensions to the upper posterior slope. Close to the oesophagus they split into an ascending and a descending branch and end in a region where they meet some of the ocellar giant fibres and a branch of a huge fibre of the cervical connective. In the 1 µm-sections cut sagittally 6 fairly big fibre profiles are distinguished in the bundle of V-cells. Whether they all actually are V-

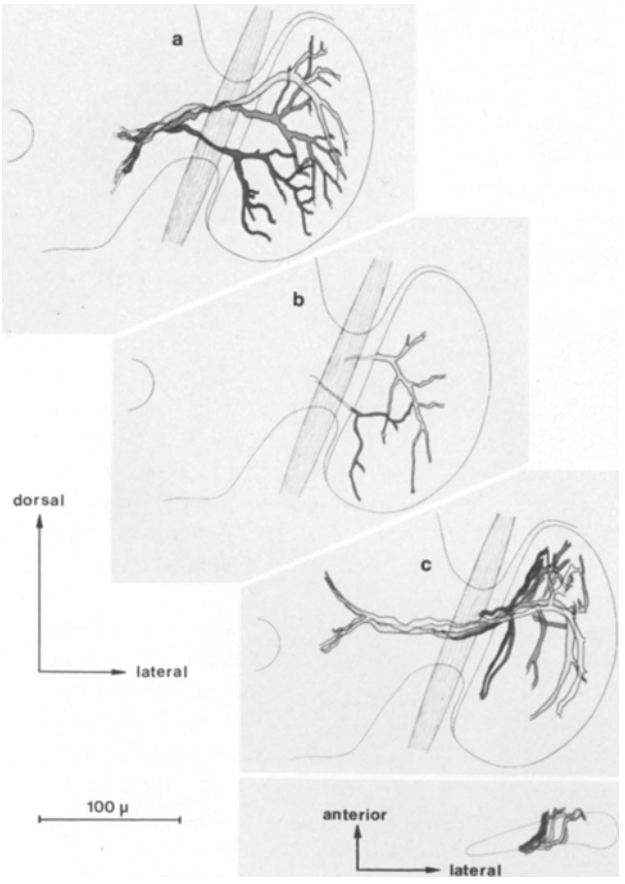


Fig. 1a–c. Reconstruction of visual giant neurons of the lobula plate from 1 µm serial sections. **a** H-cells; **b** M-cells; **c** V-cells (for details see text)

cells can not be determined with certainty since so far we can not follow all the individual cells through the whole length of the bundle (Fig. 1c).

2. Anatomy of the Lobula Plate of omb^{H31} (optomotor-blind^{H31})

In *omb*^{H31} the lobula plate is clearly visible and of about normal vertical and lateral extent. Only the thickness of the plate is reduced by about 30%. The thin fibres which run through the inner chiasma into the medulla and lobula seem to be normally developed. This does not exclude, that some small-field elements of the lobula plate might be missing.

From silver impregnations and 1 µm serial sections it is quite obvious that all three types of lobula plate giant fibres are very poorly developed in *omb*^{H31}. Expression of the genetic defect is very consistent (Table 1). Only one fly with fairly normal

Table 1. Regularity of anatomical defects in *omb*^{H31}. Silver impregnated paraffin preparations as well as 1 µm Araldite sections cut sagittally, frontally or horizontally are summarized

	H-cells	V-cells
Preparations in which fibres were absent or not identifiable as H- or V-cells:	49	54
Preparations in which fibres were tentatively identifiable but much smaller than in wild type	11	7
Preparations with large fibres, not safely distinguishable from those in wild type	1	–

visual giant fibres has been found so far. Sometimes bundles of tiny fibres are present at the position of the H-cells, often medium sized cells with arbitrary shapes are found. It is conceivable, however, that these small and medium sized fibres have little functional significance for the optomotor response. In the posterior slope of wild type just above the V-cells a tract of small fibres from the lobula and lobula plate is observed (posterior optic tract) which in part gives rise to the posterior commissure. This tract is present in *omb*^{H31} (Fig. 2a). Any fibres in *omb*^{H31} which might be homologous to the H- and V-cells in wild type and which are still visible in our preparations, have their axons in this bundle. Thus they may miss their proper postsynaptic neurons. At the position of the H- and V-cells on the posterior slope no fibres are seen even in animals with medium sized cells in the lobula plate.

Other giant fibres in *omb*^{H31} are well developed. The ocellar nerve fibres, the giant fibres of the central commissure, the giant fibres of the cervical connective and the large fibres of the lobula all seem to be present. The general morphology of the brain seems to be well preserved. In particular the major tracts connecting the lobula and medulla to the midbrain and to the optic lobes of the other side have been checked for further anatomical defects – with negative results.

However, various occasional anatomical defects have been observed in preparations of *omb*^{H31} brains. In one fly the two β-lobes of the corpora pedunculata were fused; in another one an errant fibre bundle from the inner chiasma went through the medulla to form a little lobe distal to the medulla; in a third fly the retinula cell axons formed a large chiasma over 10–15 cartridges in the vertical plain. These rare developemental errors seem to occur more frequently than in wild type – a property shared by several other visual mutants. It is typical for these somewhat random abnormalities, that they occur only unilaterally leaving the equivalent structure in the other half of the brain unaffected.

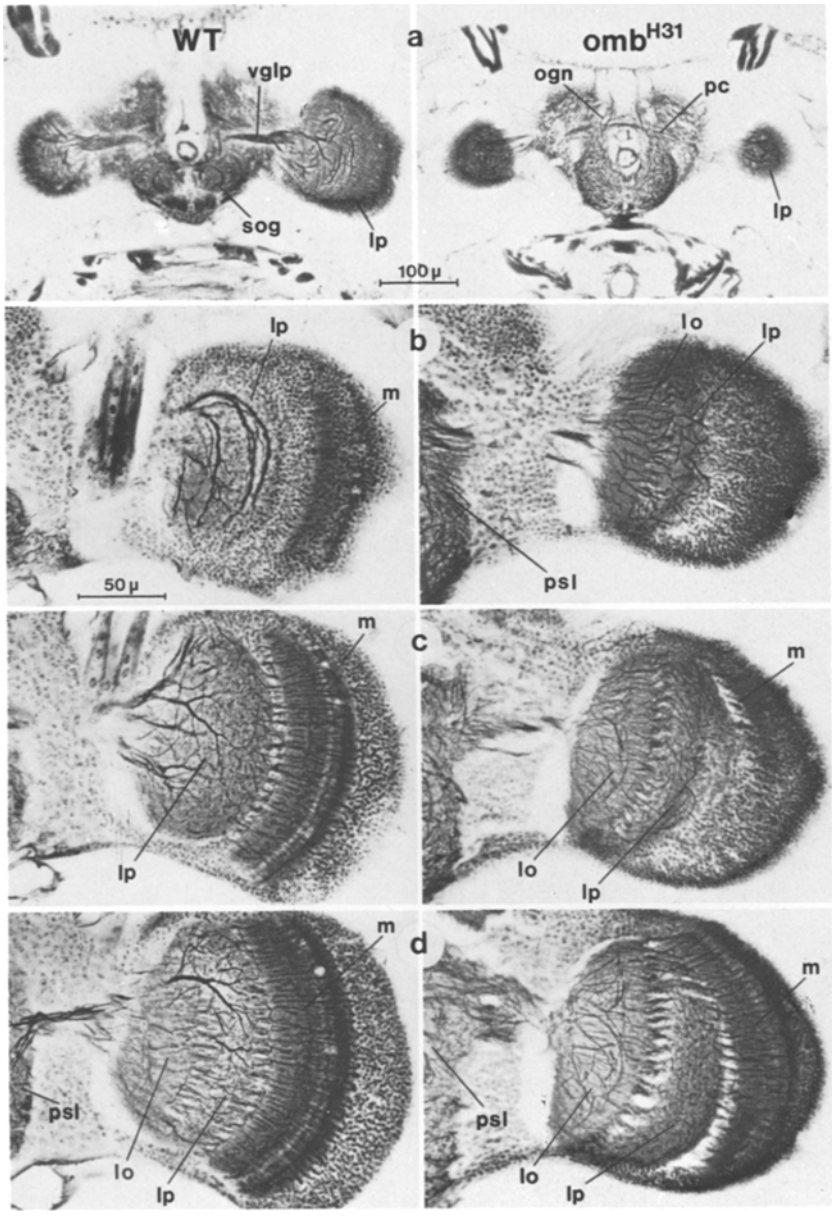


Fig. 2a–d. Silver stained frontal sections (10 µm) of the brain of *Drosophila* wild type (left) and *omb*^{H31} (right).
a Most caudal section of whole brain. Note the posterior commissure and the ocellar giant fibres in *omb*^{H31}.
b–d Three consecutive sections (from caudal to frontal) through right half of brain showing in wild type and *omb*^{H31} roughly the same parts of optic lobes (and posterior slope of central brain). Visual giant neurons of lobula plate (vglp); medulla (m); lobula (lo); lobula plate (lp); posterior slope (psl); posterior commissure (pc); ocellar giant neurons (ogn); suboesophageal ganglion (sog)

3. *Visual Behavior of omb*^{H31}

a) Optomotor Turning Responses

optomotor-blind^{H31} has been mentioned already in previous publications (Heisenberg, 1972; Heisenberg and Götz, 1975; Heisenberg and Buchner, 1977). It is one of the 5 mutants with defects in the high sensitivity system (HSS) of which optomotor turning responses to broad and narrow stripes were recorded by Heisenberg and Buchner (1977). The measurements with *omb*^{H31} which stem from 1973 showed that at high light intensity the optomotor turning response was reduced to about 50% of that of wild type. We recently repeated these measurements with the same experimental set up. The mutant responses are now about 10% of those of wild type (Fig. 4) and the HSS-defect can not be distinguished. The reason for this further reduction is not clear. Occasionally flies with a stronger optomotor turning response in the walking mode are still found but in our recent experiments no fly (out of 15) showed a response as big as those reported by Heisenberg and Buchner (1977).

Optomotor turning responses in flight are also strongly disturbed. Responses to saturating stimuli can be as much as 60% of the wild type response. But under non-saturating conditions the optomotor turn-

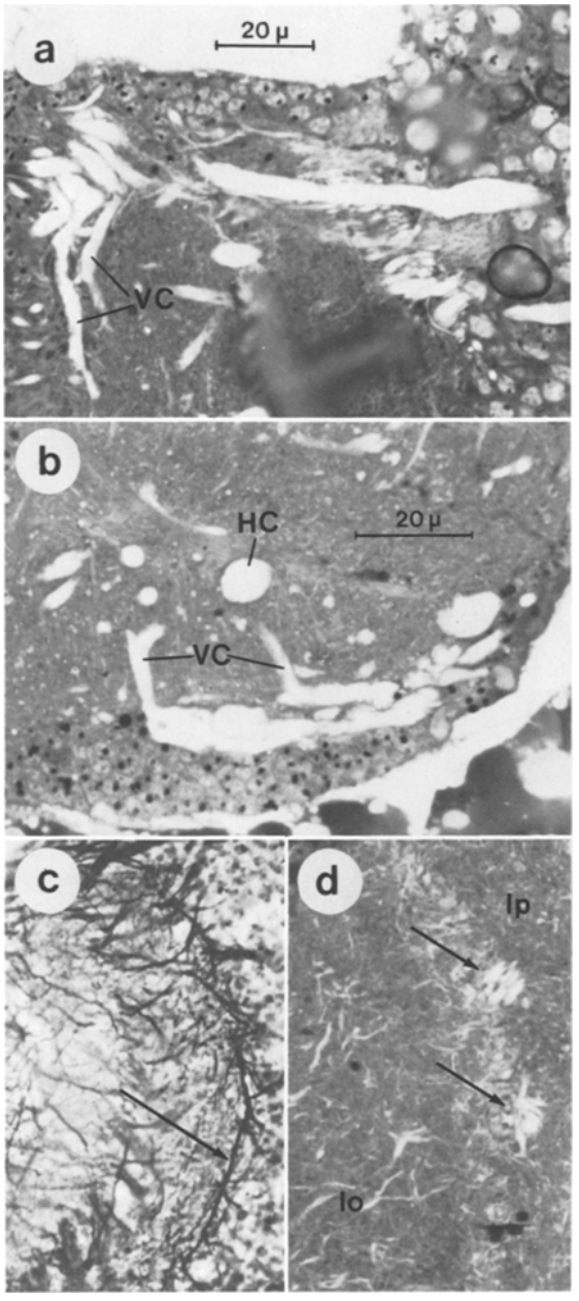


Fig. 3. a Frontal section through caudal part of lobula plate showing V-cells (VC) having upward and downward extending branches (1 µm Araldite, toluidine blue). **b** Horizontal section through lobula plate at a level where the bundle of V-cells enters the lobula plate. Note the two V-cells (VC) extending collaterals to frontal side of lobula plate (Araldite, toluidine blue). **c** Medium sized silver stained neuron (arrow) in lobula plate of *omb*^{H31}. The cell resembles V-cells (No 1 or 2) of wild type but is much thinner and smaller. **d** At the place of H-cells in wild type *omb*^{H31} flies sometimes have bundles of small fibres (arrows) which join the posterior tract. Lobula plate (lp); lobula (lo). (Araldite, toluidine blue)

ing response is reduced to less than 20%. In a striped drum (spatial wavelength $\lambda = 90°$; vertical pattern extension $\pm 40°$; pattern contrast $\Delta I/\bar{I} = 0.06$; average luminance $\bar{I} \cong 2\,cd/m^2$; variable contrast frequency $w/\lambda = 0.3$–10 cps) the average response of 7 wild type flies was 17 mdyn·cm while that of 6 *omb*^{H31} flies was 3.3 mdyn·cm. Since under these stimulus conditions some wild type flies gave maximum responses the ratio of 5 for wild type/mutant response is a low estimate. Thus optomotor turning responses seem to be roughly equally reduced in flight and in the walking mode. Since Buchner and Straub (unpublished; see below, 3c) found that the lattice of visual elements appears slightly blurred we also compared the optomotor turning response of *omb*^{H31} and wild type in flight at a narrow pattern wavelength ($\lambda = 6°$) for which the optical precision of the eye is critical. Under these conditions the mutant response was close to zero while that of wild was 18 mdyn·cm. Again this result is in disagreement with the 1973 observation of Heisenberg and Buchner (loc. cit.) that in walking *omb*^{H31} flies the optomotor turning response is about equally reduced at broad and narrow pattern wavelengths.

b) Pattern Induced Orientation Behavior

The position histogram for *omb*^{H31} in the basic closed loop experiment with one stripe was also measured by Heisenberg and Buchner (1977). The flies keep the main direction of flight towards the stripe (Fig. 5d). However, this result masks the marked differences in the performance of *omb*^{H31} and wild type. While wild type turns immediately towards the stripe *omb*^{H31} seems not to take any notice of it when the stripe is at a lateral position. Only when the fly happens to head into the direction of the stripe it keeps this direction thoroughly. Reichardt (1973) and Poggio and Reichardt (1973) described the closed loop behavior of *Musca* in the 1-stripe experiment by 3 parameters (in addition to the flight dynamics of the fly) which can be measured separately in open loop experiments: the torque response evoked by the position of the stripe ($D(\psi)$), the torque response to the direction of movement of the stripe ($r(\psi)\dot{\psi}$) and the torque "noise", $N(t)$, produced by the fly. We copied several of the experiments of Reichardt and Poggio (review, 1976) to measure these parameters in *Drosophila* wild type and *omb*^{H31}. Torque fluctuations are shown in Figure 5e, f as torque histograms. Under closed loop conditions in the 1-stripe-experiment torque fluctuations of *omb*^{H31} are about 60% of those in wild type.

Without any visual stimuli, however, wild type shows significantly more torque fluctuations than

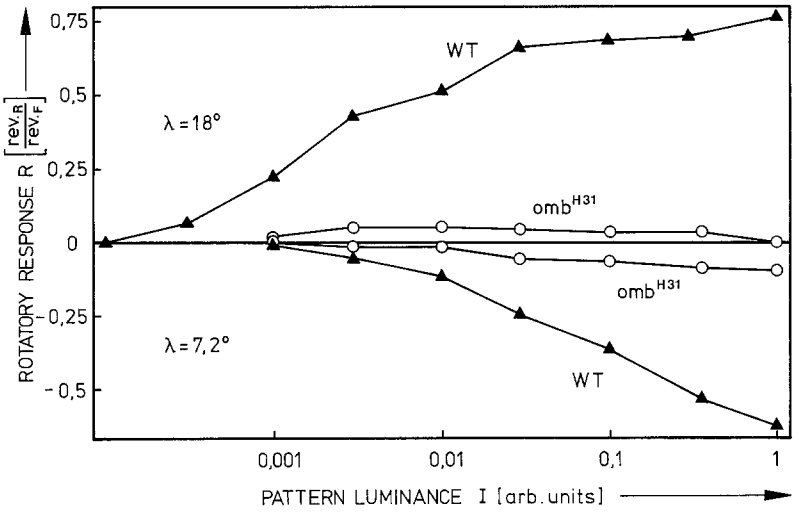


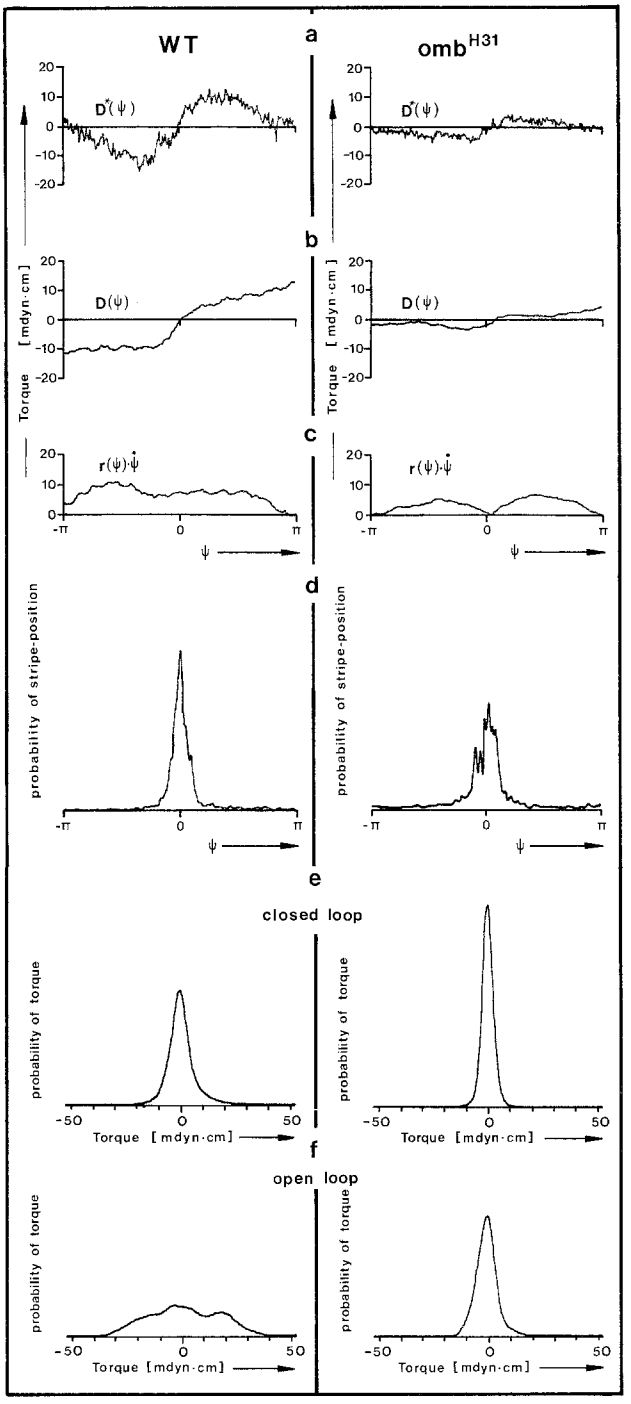
Fig. 4. Average optomotor turning reactions of WT and *omb*^{H31} flies as functions of pattern luminance. Flies walked on a styrofoam ball (Buchner, 1976) in the center of a striped drum with spatial wavelengths $\lambda_p = 7.2°$ and $\lambda_p = 18°$. The contrast frequency w/λ was kpt at 1 cps, the spectral wavelength of the pattern was $\lambda_I = 475$ nm (b.w. = 20 nm). Wild type curves are from single flies with 30–40 measurements at each pattern luminance. $\lambda_p = 18°$ curve for *omb*^{H31} shows mean response of 4 flies and 203 measurements at each pattern luminance; $\lambda_p = 7.2°$ curve is an average from 3 flies and 165 measurements at each pattern luminance. Standard errors of the means for the measurements on *omb*^{H31} are too small to be shown. Small mutant responses are not due to the particular spectral wavelength used here as recent experiments (from different context) have shown. Quotient rev.R/rev.F as defined by the recording technique (Buchner, 1976) represents turning tendency of the fly averaged over ~60 cm of forward walk

omb^{H31}. These extra fluctuations consist in part of the so called "torque spikes", a new visually controlled element of flight behavior in *Drosophila* which will be described in a separate publication. The reactions to the position, $D(\psi)$, and direction of movement, $r(\psi)\dot{\psi}$, of the stripe were measured simultaneously in an open loop experiment: The stripe was slowly moved around the fly first clockwise then counter-clockwise. For each position of the stripe the torque was recorded. If in such an experiment the responses for clockwise and counter-clockwise movement are added they represent $D(\psi)$, if they are subtracted they give a signal proportional to $r(\psi)$. The result for *Drosophila* wild type (Fig. 5b, c) is not too different from that for *Musca*. The details will again be discussed elsewhere. In this context it is sufficient to note that *omb*^{H31} shows very poor reactions to both, position and direction of movement of the stripe. Thus it appears that all 3 parameters (D, r, N) are strongly affected while the closed loop behavior recorded as the position histogram of the stripe is hardly changed.

In order to ensure that the torque response to *position* is really suppressed we recorded on a magnetic tape the torque of flies from an orientation-blind (but not movement-blind) mutant stock (laboratory name: S100; Heisenberg, unpublished) during a 1-stripe-closed loop experiment. We then used this recording (containing the movement response and numerous torque spikes) to turn the 1-stripe panorama in an open loop experiment with *omb*^{H31} and wild type. Again we measured torque as a function of position. Since with this type of motion of the stripe wild type shows a strong position response $(D^*(\psi))$ while the orientation-blind mutant does not (data not shown) we assumed this to be a fair test for the position response in *omb*^{H31}. As can be seen in Figure 5a, *omb*^{H31} again shows only a very weak response.

The severe visual defects of *omb*^{H31} can be demonstrated under partial closed-loop conditions. Wild type *Drosophila* tracks a randomly moving black stripe (for *Musca* see: Poggio and Reichardt, 1973) whereas *omb*^{H31} does not (for details: Heisenberg and Wolf, unpublished).

In contrast to pattern induced orientation during stationary flight the orientation response of freely walking *omb*^{H31} flies in a circular arena with a vertical black stripe gives a nearly flat histogram (Fig. 6). This is not surprising if the experimental procedure is considered. In the latter experiment flies are placed in the center of the arena from where they immediately start walking towards the periphery; the performance of the flies lasts a few seconds until they reach the measuring circle. Thus the flies normally do not "find" the direction of the stripe during this period.



c) Optomotor Thrust Response

Since in big flies some of the V-cells are known to respond to vertical movement we expected the optomotor thrust response to vertical movement also to be disturbed in the mutant. E. Buchner and C. Straub (unpublished) kindly measured this response in *omb*^{H31} and wild type flies. The experiment was similar to that described by Heisenberg and Buchner (1977). The result shows that with optimal pattern

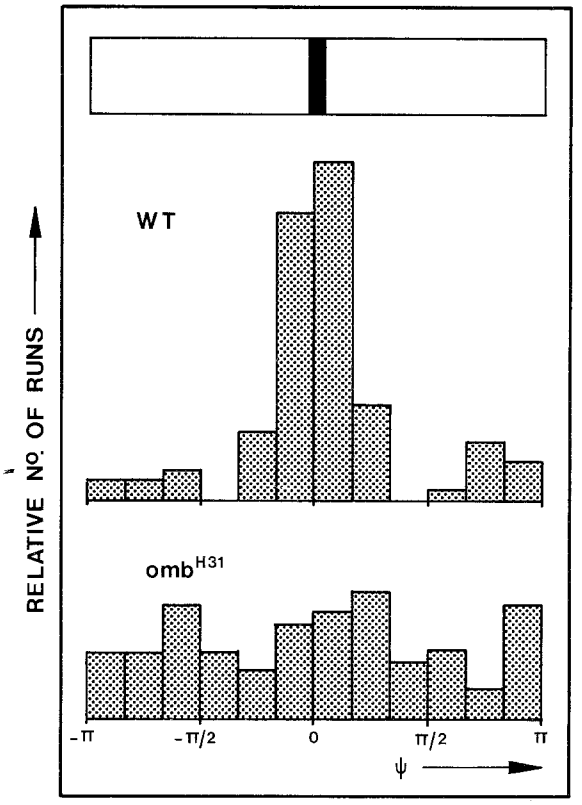


Fig. 6. Pattern induced orientation of walking *Drosophila* wild type and *omb*^{H31}. Pattern was a narrow vertical black bar (vertical extension +64°, width 10°, from center of arena). For experimental details see "Material and Methods"

Fig. 5a–f. Pattern induced flight orientation in wild type and *omb*^{H31}. **a–c** Torque responses to a narrow vertical black bar (vertical extension ±40°, width 3°) were decomposed into the response components to position, $D(\psi)$, and to direction of motion, $r(\psi)\dot{\psi}$ of the stripe. **a** Position response $D^*(\psi)$ to the stripe moving as previously recorded in a closed loop experiment with an orientation-blind fly. (With such flies the position histogram for the stripe is nearly flat.) **b** and **c** Simultaneously recorded responses to position, $D(\psi)$, and direction of motion, $r(\psi)\dot{\psi}$, of the stripe moving slowly (18°/s) alternately clockwise and counterclockwise around the fly. The direction of movement was reversed at $\psi = \pm 180°$. **d** Position histograms for stripe in closed loop experiments. **e** Torque histograms in an illuminated arena without pattern. **f** Torque histograms in closed loop experiments as shown in **d**. In **a** 22 4-min-experiments from 7 wildtype and 15 4-min-experiments from 5 *omb*^{H31} flies were averaged. **b** and **c** averaged responses from 40 clockwise and 40 counterclockwise rotations of the stripe in 10 independent experiments with 6 wild type and 7 *omb*^{H31} flies. **d** and **f** represent, for wildtype and *omb*^{H31} respectively, averages of 10 4-min-experiments taken from 5–8 flies. With few exceptions measurements on individual *omb*^{H31} flies are characteristically different from those on wild type (not shown)

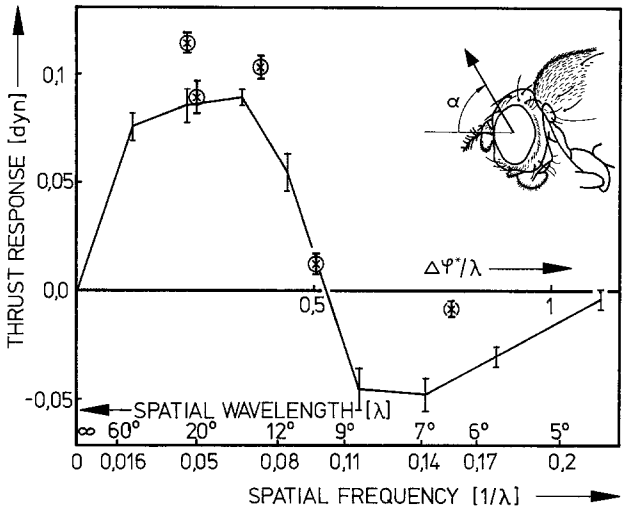


Fig. 7. Average direction-sensitive optomotor thrust responses as a function of spatial frequency ($1/\lambda$) of a moving sinusoidally modulated pattern presented to corresponding small lateral parts of the visual fields of both eyes. The pattern was moving upward back-to-front at an angle $\alpha = 60°$ to forward direction of the horizontal line of symmetry in the hexagonal array of visual elements. Pattern speed w adjusted to keep contrast frequency w/λ at 1.3 cps. Drawn curve: data from wild type; ⊛: data from *omb*^{H31}. Each point average of measurements with at least 5 flies. Vertical bars: standard errors of the means. Courtesy of E. Buchner and C. Straub, Max-Planck-Institut für biologische Kybernetik, Tübingen

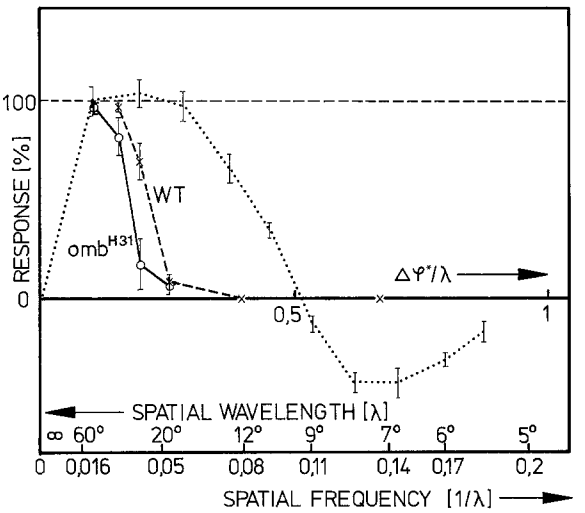


Fig. 8. Movement induced landing reactions fo wild type and *omb*^{H31} as functions of spatial frequency ($1/\lambda$). Data for wild type taken from Heisenberg and Buchner (1977). Dotted curve gives, for comparison, spatial frequency dependence of the optomotor turning response of walking *Drosophila* wild type. Note that a landing response was counted only if flies fully extended both front legs during the 3 s movement period. For experimental details see Heisenberg and Buchner (1977)

wavelengths of the movement stimulus the optomotor thrust response of the mutant is not reduced (Fig. 7). Even with small pattern contrast $\Delta I/\bar{I} = 0.035$ the mutant response does not fall below that of wild type (data not shown). Three of the flies which performed in this experiment were prepared for histology and impregnated with silver. In all 3 flies the V-cells were strongly reduced or absent.

Only at a narrow pattern wavelength ($\lambda = 1{,}5\,\Delta\phi$) the response of *omb*^{H31} is in fact significantly reduced (negative reactions in Fig. 7). This may correspond to the observation that the lattice of the visual elements is less clearly visible in *omb*^{H31} (Buchner and Straub, unpublished).

d) Landing Response

As previously reported (Heisenberg and Buchner, 1977) *Drosophila* like other Dipterans extends its legs for landing if it is stimulated by vertical stripes moving from front to back. The response characteristics differ somewhat from those of the optomotor turning response. For landing the optimal contrast frequency is higher and narrow stripes ($\lambda < 18°$) are not effective (Hengstenberg, unpublished; Heisenberg and Buchner, 1977). Since this directionally sensitive movement response seems to involve a separate pathway from that of the optomotor response we measured it in *omb*^{H31} (Fig. 8). The landing response can be reliably stimulated in nearly every *omb*^{H31} fly by front-to-back movement of vertical stripes. The dependence upon pattern wavelength is very similar to that in wild type. The slight shift of the curve to longer wavelengths is most likely due to the fact that some *omb*^{H31} flies do not fully extend their legs although they clearly respond to the stimulus.

Discussion

This initial account of the neuroanatomical abnormalities and their behavioral correlates of the mutant *omb*^{H31} is bound to be incomplete in many respects. The conclusions to be drawn have to remain tentative for a number of reasons: First of all we have no way to tell so far whether the pathway of the visual giant neurons is completely blocked or whether small cells are present in *omb*^{H31} which partially perform the same functions. Secondly, we also do not know to what extent the rest of the brain and in particular the lobula and other large field neurons in the lobula plate are affected. This is an inherent difficulty of the mutant approach which can be only gradually diminished.

The main conclusion one would like to draw is that some of the visual giant fibres of the lobula plate (presumably the H-cells) are indeed a step in the pathway of the optomotor turning response. In fact, electrophysiological experiments on the larger flies have shown that the H-cells are most responsive to horizontal movement around the fly (Dvorak et al., 1975; Hausen, 1976). Thus they are good candidates for mediating optomotor turning responses. The present result is an argument in favor of this assumption.

The second result to be discussed is the finding that in pattern induced flight orientation all three parameters which are thought to determine this behavior are reduced in the mutant. This could be interpreted as indicating that some of the visual giant fibres in fact mediate the torque response to the *direction of motion* as well as to the *position* of an object and that the neural signals eliciting torque spikes also travel via these cells. In this case the activity of the visual giant fibres would be directly correlated with the torque for pattern induced flight-orientation. The highly variable nature of the $D(\psi)$-function (Geiger, 1975; Heisenberg and Wolf, unpublished) may be an argument against this view. An alternative interpretation would be that the visual giant fibres have merely an influence on the torque response to stripe position and the generation of torque spikes. The presence or absence of torque spikes in the walking mode of wild type may help to distinguish between these alternatives.

Reichardt (1973) and Poggio and Reichardt (1973) have developed a phenomenological theory which quantitatively describes pattern induced flight orientation behavior in *Musca*. The finding that omb^{H31} can still very well keep its course towards an object although all 3 parameters thought to govern this behavior are strongly affected, might provide a critical test for the theory. Qualitatively this result is not in conflict with the simple conceptual model underlying the theory since for the orientation behavior the reduction in torque fluctuations will compensate the reduction of the position dependent torque response. This, in fact, appears as a confirmation of the model. The formalism, however, seems not to be directly applicable to *Drosophila* without modifications. Under open loop conditions the frequency and polarity of the torque spikes depend upon the position and direction of movement of the stripe. In omb^{H31} the reduction in torque fluctuations is mainly due to the lack of torque spikes. Thus, while the spikes seem not to be essential for keeping the stripe in the frontal position they do contribute to $D(\psi)$ functions of wild type. This will be considered in more detail elsewhere. It should be emphasized here that although conceived to account for behavior of wild type *Musca* the theory has proved to be very useful also for the description of the visual defects in this *Drosophila* mutant.

From the result that the optomotor turning response (and also pattern induced orientation behavior) are disturbed in flight and in the walking mode we may further conclude that the flight response and the walking response to horizontal movement are both mediated by visual giant fibres of the lobula plate (presumably the H-cells). This suggests that up to the visual giant neurons the pathway for the optomotor turning response is the same in flight and in the walking mode.

One major difference between optomotor responses of flying and walking flies lies in the fact that only 2–5% of the stimulus strength leading to a maximum response in the walking mode is sufficient to give the maximum response in flight (Götz, 1964; Götz and Wenking, 1973). This "amplification" (or "clipping" as one wishes to name it) should occur on the efferent side of the visual giant fibres if the above conclusion is correct. Indeed, since the full reduction of the optomotor flight response in the mutant can only be measured with weak stimuli the neural defect should occur prior to this "amplification".

The normal optomotor thrust response of omb^{H31} using large pattern wavelengths for stimulation is the most surprising result of this account. What it tells us is that we are still missing the main behavioral functions in which the V-cells are involved. Even if these cells were mediating the optomotor thrust response there should be something to this response for which the normal conspicuous size of these cells mattered. Considering the effect of the reduction of the H-cells on the optomotor turning response it is more likely that the V-cells mediate some other function, possibly a turning response around the fly's longitudinal axis (Srinivasan, 1977).

The reduced thrust response at the narrow pattern wavelength $\lambda = 1.5 \Delta\phi$ in contrast to the normal response at $\lambda = 4 \Delta\phi$ points towards an additional disturbance of the optics in the mutant. It can hardly be explained as a defect at the level of the V-cells. An impairment of the optical properties of the eyes is actually observed as a slightly blurred appearance of the lattice of visual elements (Buchner and Straub, unpublished) and might indicate an increased $\Delta\rho$ or an imprecision in the alignment of optical axes. It may be caused by the reduced volume of the lobula plate. Similar disturbances show up in other pieces of visual behavior as well, e.g. the remaining optomotor turning responses (see above).

In the search for behavioral functions of the V-cells it is worth while to look once more at the anatomy. The V-cells are properly aligned in the

lobula plate along its caudal surface. It is only in the region corresponding to the upper frontal part of the visual field that they send collaterals to the frontal plane of the lobula plate, the domain of the H-cells. If these different planes of the lobula plate reflect the projections of differently oriented elementary movement detectors (EMDs) this feature of the V-cells may serve as a guide to finding their behavioral involvement.

The last conclusion we would like to draw from the above results is that the movement-stimulated landing response as we measure it in our experiment is mediated by a pathway in the brain which is different from that of the optomotor turning responses and, that the visual giant fibres of the lobula plate are not an essential part in it. The previous observations that the movement stimulated landing response differs in its dependence upon pattern speed and pattern wavelength from the optomotor turning response indicated already a different pathway but did not necessarily exclude the involvement of the H-cells. Our result should, however, be taken with caution: Since the triggering of the landing response is to some extent an all-or-none event it is conceivable (though unlikely) that the visual giant fibres are a non-critical link in the response chain and that even a considerable reduction of their size would have little effect on the triggering threshold.

The above results about the functional rôle of the visual giant neurons of the lobula plate must be compared with recent experiments of Blondeau (1977) who evoked stereotypic course control reactions of *Calliphora* by electrically stimulating the lobula plate. As expected from the specificities of the respective giant neurons stimulation at the frontal margin of the plate caused torque responses while in the middle it caused roll and at the caudal margin thrust and lift. Stimulation of the caudal surface of the plate at positions corresponding to fronto-ventral and latero-ventral parts of the visual field also frequently elicited landing responses. This result seems to disagree with our finding that the movement-elicited landing response and the optomotor thrust response to vertical movement in the mutant omb^{H31} are nearly undisturbed. However, if one considers that most of the large field neurons of the lobula plate which have been characterized by the injection of procion yellow in big flies would not be detected with our histological techniques one is free to assume such cells to be still present in omb^{H31}, the more so, since many of them have their axons in the posterior commissure which is well intact in the mutant.

Evidently a lot more is to be found out about the neuroanatomy, visual behavior and genetics of omb^{H31}. Some of the conclusions may have to be modified eventually. Nevertheless, omb^{H31} corroborates our hope that the mutant approach will be usefull in correlating behavior with its corresponding neural structures and functions.

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