

Comparison between the Movement Detection Systems Underlying the Optomotor and the Landing Response in the Housefly

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Abstract. Flies evaluate movement within their visual field in order to control the course of flight and to elicit landing manoeuvres. Although the motor output of the two types of responses is quite different, both systems can be compared with respect to the underlying movement detection systems. For a quantitative comparison, both responses were measured during tethered flight under identical conditions. The stimulus was a sinusoidal periodic pattern of vertical stripes presented bilaterally in the fronto-lateral eye region of the fly. To release the landing response, the pattern was moved on either side from front to back. The latency of the response depends on the stimulus conditions and was measured by means of an infrared light-beam that was interrupted whenever the fly lifted its forelegs to assume a preprogrammed landing posture (Borst and Bahde 1986). As an optomotor stimulus the pattern moved on one side from front to back and on the other side in the opposite direction. The induced turning tendency was measured by a torque meter (Götz 1964). The response values which will be compared are the inverse latencies of the landing response and the amplitude of the yaw torque.

1. Optomotor course-control is more sensitive to pattern movement at small spatial wavelengths (10° and 20°) than the landing response (Fig. 1a and b). This suggests that elementary movement detectors (EMDs, Buchner 1976) with large detection base (the distance between interacting visual elements) contribute more strongly to the landing than to the optomotor system.

2. The optimum contrast frequencies of the different responses obtained at a comparatively high pattern contrast of about 0.6 was found to be between 1 and 10 Hz for the optomotor response, and around 20 Hz for the landing response (Fig. 2a and b). This discrepancy can be explained by the fact that the optomotor response was tested under stationary conditions (several seconds of stimulation) while for the landing response transient response characteristics of the

movement detectors have to be taken into account (landing occurs under these conditions within less than 100 ms after onset of the movement stimulus). To test the landing system under more stationary conditions, the pattern contrast had to be reduced to low values. This led to latencies of several seconds. Then the optimum of the landing response is around 4 Hz. This is in the optimum range of the optomotor course-control response. The result suggests the same filter time constants for the movement detectors of both systems.

3. The dependence of both responses on the position and the size of the pattern was examined. The landing response has its optimum sensitivity more ventrally than the optomotor response (Fig. 3a and b). Both response amplitudes increase with the size of the pattern in a similar progression (Fig. 3c and d).

In first approximation, the present results are compatible with the assumption of a common set of movement detectors for both the optomotor course-control and the landing system. Movement detectors with different sampling bases and at different positions in the visual field seem to contribute with different gain to both responses. Accordingly, the control systems underlying both behaviors are likely to be independent already at the level of spatial integration of the detector output.

Introduction

The optomotor and the landing response of flies are both behaviors which require the processing of movement in the visual field. The optomotor response consists in a turning reaction which counteracts involuntary rotation of the fly. The landing response is a stereotyped sequence of leg movements which occurs when the fly is approaching a visual target (Borst 1986). An attempt is made in the present paper to compare

the entirely different responses with respect to the underlying movement detection systems.

The optomotor turning reaction of insects has been studied extensively on different species (*Apis*: Kunze 1961; *Chlorophanus*: Reichardt 1961; *Drosophila*: Götz 1972; Buchner 1984; *Musca*: Fermi and Reichardt 1963). Referring to this Hassenstein and Reichardt (1956) proposed a mechanism by which movement information can be extracted from the signals coming from two visual elements: one of the signals is delayed by a low-pass filter and is subsequently multiplied with the instantaneous signal from a second visual element (correlation-type of movement detection). This local process of movement detection is thought to take place in so-called elementary movement detectors (EMDs, Buchner 1976) the outputs of which are spatially integrated by large field elements. Neuronal correlates of the latter have been found in the posterior part of the third optic ganglion of the fly, the lobula plate (Hausen 1981, 1982, 1984). There is good evidence that some of these neurons control the optomotor turning reaction studied before at the behavioral level (Hausen 1981; Hausen and Wehrhahn 1983; Wehrhahn 1985).

The landing response is another example of a visually induced behavior which is driven by movement (Braitenberg and Taddei Ferretti 1966): a front-to-back movement presented to both eyes leads to a fixed pattern of leg extension which is assumed to prevent freely flying animals from crashlanding. This behavior has recently been shown to be highly stereotyped: The latency of the onset seems to be the only parameter which decreases gradually with increasing stimulus strength (Borst 1986). The model proposed to account for this stimulus-response relationship implies some kind of temporal integration of the instantaneous output signal of a movement detection system. Whenever this integrated signal reaches a given threshold landing is initiated. All behavioral data available so far are in full agreement with the assumption that the movement detection process underlying the landing response is also of the correlation-type (Borst and Bahde 1986). The interesting question arising in this context is, whether or not the landing and the optomotor turning response use the same movement detection system (Taddei Ferretti and Perez de Talens 1973; Eckert and Hamdorf 1983; Borst and Bahde 1987).

There are at least three characteristics of a correlation-type of movement detection systems which can be determined experimentally: 1) The *sampling base* which corresponds to the angular distance between the two input elements of the elementary movement detector. Together with the acceptance angle of the visual elements it determines the dependence of the response on the spatial wavelength of a

pattern (Götz 1965). 2) The *time-constant* of the detector filter. It determines the dynamic range in which the detector is operative. If a periodic grating is moved with a constant velocity the time-constant is reflected by the contrast frequency (i.e. the number of grating periods per second which pass a single visual element) of optimum response. 3) The *spatial integration* of the output signals of EMDs in the different areas of the visual field. This process should be reflected by a) the strength of the response induced in these areas and b) the dependence of the response on the size of the pattern.

Although the optomotor response of the housefly has already been studied in some of the aspects mentioned above (McCann and McGinitie 1965; Reichardt 1966; Eckert 1973; Geiger and Poggio 1975; Reichardt et al. 1983), a reexamination has been necessary for comparison with the available data on the landing response since the stimulus conditions differed in many respects. The results of Pick and Buchner (1979) emphasize the importance of this point as they have shown that the wavelength dependence of the optomotor response of the housefly depends strongly on the mean luminance of the pattern. Therefore the optomotor and the landing response have been studied under the same conditions of mean luminance, spectral composition, contrast and spatial parameters of the stimulus. Both types of responses will be compared in the following.

Material and Methods

Animals: all experiments were performed with female houseflies *Musca domestica* from the laboratory stock. They were between 2 to 30 days old. Some days before the experiment, a small triangle cardboard was glued with wax to their head and thorax and the ocelli were covered. Until tested, flies were free to fly around in a cage containing food and water.

Experimental Set-Up: flies were placed between two monitors (Tektronix 608) which cover about 20% of the total visual field. The stimulated areas were reaching from 16° to 90° in horizontal direction from the frontal body axis and from -32° to +32° in the vertical direction from the equatorial plane of each eye. The pattern was produced by an image synthesizer (Picasso, Innisfree Inc.). Its intensity was sinusoidally modulated along its horizontal axis with adjustable wavelength and contrast. The spatial wavelengths tested did not fit into the display (74°) exactly once or multiple times. Thus the movement stimulus included also a slight modulation of the overall light intensity. All assertions of spatial wavelengths in this paper indicate the maximum angular extent of a pattern period seen by the fly. The spatial phase of the pattern

was set randomly. In all experiments the mean luminance I of the monitors was 10 cd/m^2 . In addition to the light coming from the monitors, flies were diffusely illuminated dorsally by a DC halogen lamp. To release the landing response, the pattern was moved on either side from front to back. To induce optomotor course-control responses the pattern was moved on one side from front to back and on the other side in the opposite direction. These different stimulus conditions are likely not to affect the conclusions drawn in the paper. So far no pronounced differences have been found in the spatial and temporal characteristics of movement detectors for front-to-back and back-to-front motion (Götz and Wenking 1973; Hausen 1982). To vary position and the size of the pattern parts of the monitor screens were covered with black cardboard. The landing response of the fly was detected by a light-beam that was interrupted by the fly's prothoracic legs when it performed its typical landing response (Borst 1986). The output of the detector unit was displayed on an oscilloscope to determine the latency of the response. For measuring the fly's turning reaction around its vertical axis it was attached with its cardboard to a torque meter (Götz 1964).

Experimental Procedure: in the landing paradigm the fly was given a maximum of 10 s to react. Every fly was tested for each stimulus parameter 10 times. Parameters were varied in a random order to prevent experimental results from being biased by time effects. The optomotor reaction was recorded for each stimulus parameter 8 times with the following time schedule: 8 s clockwise rotation – 2 s rest – 8 s counterclockwise rotation – 2 s rest.

Data Evaluation: The latencies of the landing responses obtained under a particular stimulus condition were averaged. From those mean values, the average response of different flies (Figs. 1b, 2b, 3b and d) was evaluated by averaging the reciprocal values of their mean latencies which reflect the strength of the stimulus. The optomotor responses were proceeded by a Nicolet signal averager (Model 527). The response values given in Figs. 1a, 2a, 3a and c refer to the mean difference between the response amplitude during clockwise and counterclockwise rotation. For calculating the components of the spectrum of spatial frequencies in the responses of the flies (inset of Fig. 1a and b) the original data were transformed into the spatial frequency dimension and were complemented between $2\Delta\phi$ and $1\Delta\phi$ (for details see: Buchner 1976).

Results

As mentioned before there are three characteristics of a movement detection system of the correlation type

which can be determined experimentally. 1) the sampling base which determines, together with the acceptance angle of the visual element, the dependence of the response on the spatial wavelength of the pattern, 2) the time constant of the filter which determines the optimum contrast frequency of the reaction when the fly is stimulated with a periodic grating moving at a constant velocity, and 3) the way by which elementary movement detectors in different parts of the visual field are combined: these spatial integrative properties are reflected in the dependence of the response on the location and the size of the pattern.

The Wavelength Dependence

The spatial wavelength of the sine-pattern was varied between 5° and 80° , while all other parameters of the pattern were held constant: the contrast frequency was 1 Hz, the contrast was 0.6 and the mean luminance was 10 cd/m^2 . As can be seen in Fig. 1a, the optomotor response reaches its plateau value between 10° and 20° and stays at this level up to 80° . Interestingly negative responses indicating spatial periods below twice the angular distance between interacting visual elements could not be obtained in the range between 2° and 4° . The Fourier transform of these data (inset of Fig. 1a) suggests that movement detectors using once and twice the interommatidial angle as the sampling base contribute about equally to this response. Those with a sampling base larger than 3 times the interommatidial angle seem to have no importance for the reaction under the stimulus conditions indicated above. Quite a different situation has been found for the landing response (Fig. 1b, data as in Borst and Bahde 1986). Here the wavelength dependence is nearly zero up to 10° , peaks between 30° and 60° and falls off again at higher wavelengths. As for the optomotor response no negative reactions, i.e. landing responses to bilateral back-to-front movement, could be observed at small wavelengths. The Fourier transform (inset of Fig. 1b) reveals that the main contribution to the landing response comes from movement detectors comprising several interommatidial angles as the sampling base. When the landing response is tested at higher contrast frequencies (data shown in: Borst and Bahde 1986) the reaction becomes slightly more sensitive for smaller wavelengths, but is still significantly different from the optomotor response measured under the same conditions.

The Contrast Frequency Dependence

As the optomotor response is known to be sensitive even at very low contrast frequencies, we tested the reaction of *Musca* for a wide range of contrast

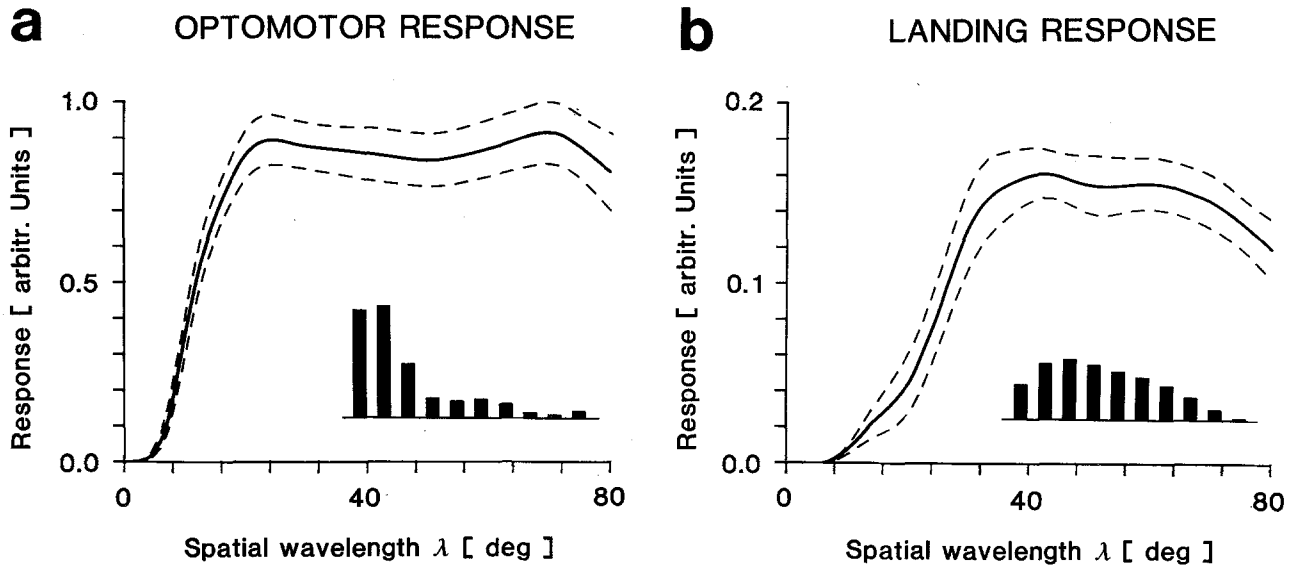


Fig. 1 a, b. Dependence of the optomotor (a) and the landing (b) responses on the spatial wavelength of a periodic pattern (contrast frequency = 1 Hz, pattern contrast $C=0.6$). Graphs are smoothed data values. The landing response is given in units proportional to the inverse latency of the reaction (1 arbitr. unit = 50 ms). At small wavelengths the optomotor response is more sensitive than the landing response. The insets show the first 10 components of the Fourier transform of the spatial frequency dependence. These are equivalent to the relative amount by which elementary movement detectors (EMDs) with a sampling base equal to 1, 2, ..., 10 times the interommatidial angle contribute to this response. The different wavelength dependence of both reactions is reflected in a stronger contribution of EMDs with a large sampling base to the landing than to the optomotor response. Means and SEMs (dotted line) of 15 flies. Number of measurements per fly per stimulus parameter: $n=8$ (optomotor response), $n=10$ (landing response)

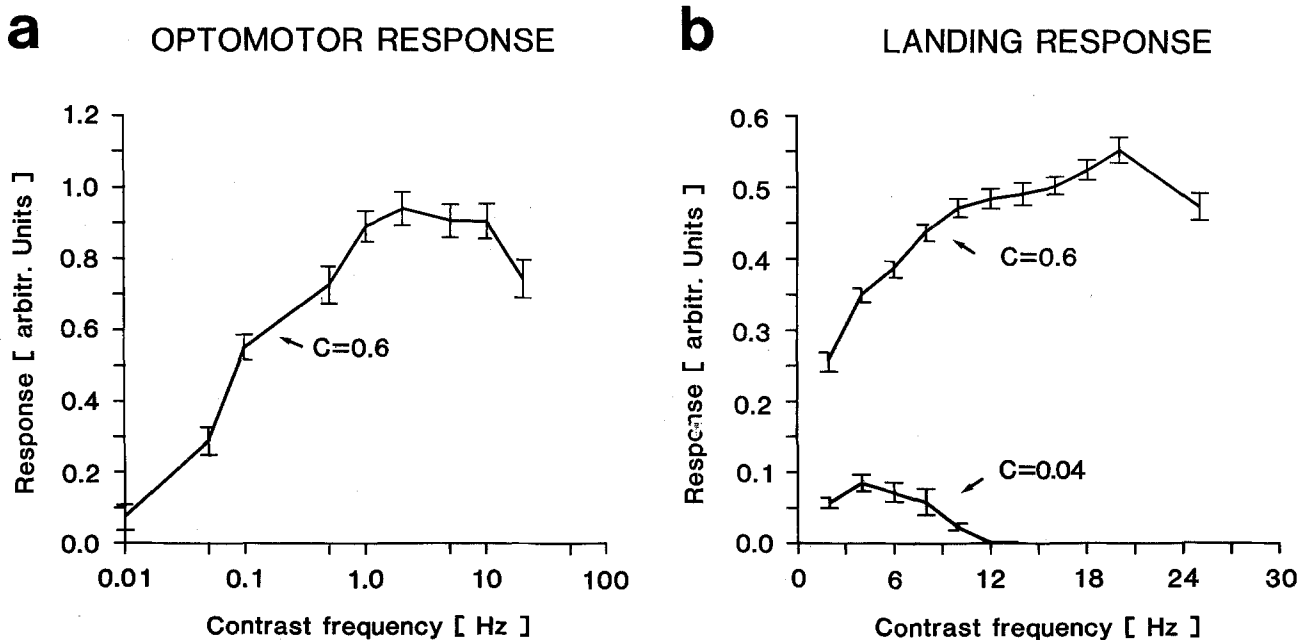


Fig. 2 a, b. Contrast frequency dependence of the optomotor (a) and the landing (b) responses (spatial wavelength $\lambda=30^\circ$, pattern contrast $C=0.6$). The landing response is given in units proportional to the inverse latency of the reaction (1 arbitr. unit = 50 ms). With high pattern contrasts ($C=0.6$) the contrast frequency optimum of the optomotor response is between 1 and 10 Hz, that of the landing response is around 20 Hz (minimum latency of less than 100 ms). If the pattern contrast is reduced, the latencies of the landing response are prolonged up to several 100 ms and even seconds. Under these conditions the landing response (second graph in b, $C=0.04$) has its contrast frequency optimum in the same range as the optomotor response. Note that the x-axis in a has a logarithmic scale, while in b it is linear. Means and SEMs of 15 (optomotor response) and 9 (landing response) flies. Number of measurements per fly per stimulus parameter: $n=8$ (optomotor response), $n=10$ (landing response)

frequencies reaching from 0.01 Hz up to 25 Hz. The response shown in Fig. 2a for a pattern contrast $C = 0.6$ has its optimum between 1 and 10 Hz. The landing response can hardly be elicited at contrast frequencies below 1 Hz (Borst and Bahde 1986). Therefore it was only tested between 1 and 25 Hz. At high pattern contrasts ($C = 0.6$), the optimum response was found around 20 Hz (Fig. 2b, data as in Borst and Bahde 1986). However, the contrast frequency optimum could be shown to depend on the pattern contrast: the higher the pattern contrast the higher was the optimal contrast frequency (Borst and Bahde 1986). In order to compare the landing with the optomotor response the transitory response characteristics of the movement detection system have to be taken into account: during the initial response phase the movement detector output follows the contrast frequency of the pattern almost independently of the time-constant of the filter, while in its stationary phase the output depends on both the contrast frequency and the time-constant of the filter. Thus early transitory output of the detector does not reflect the signal delay due to the filter characteristics. Using high pattern contrasts the landing response occurs within less than 100 ms after the onset of the stimulus. A filter time constant can therefore hardly be extracted from these data. To solve this problem the pattern contrast was reduced to low values ($C = 0.04$). Under these stimulus conditions the latencies were prolonged to several 100 ms and even seconds. Then transitory responses can be neglected and the system is in its stationary phase. This allows now a comparison with the respective data of the optomotor response. The second data graph in Fig. 2b was measured at a pattern contrast of $C = 0.04$. It shows a contrast frequency optimum between 2 and 10 Hz which is nearly the same as observed for the optomotor response at contrast $C = 0.6$. This suggests that both movement detection systems use a filter with the same time constant.

The Dependence on the Position and Size of the Pattern

Both the optomotor and the landing response were tested at two different contrasts ($C = 0.6$ and $C = 0.16$) of a pattern with reduced vertical extent of 13° . The spatial wavelength was 20° and the pattern was moved with a contrast frequency of 2 Hz in all of these experiments. The pattern was presented in 5 different positions between -26° and 26° with respect to the equator of the fly's eye. As can be seen in Fig. 3a, the optomotor response is strongest when the pattern is positioned symmetrically to the equator (position 3). This optimum is only slightly indicated at high pattern contrasts probably due to saturation effects but is more expressed at low contrasts. The sensitivity in the dorsal

and the ventral part of the eye is symmetrical with respect to the equator. The landing response shows its sensitivity optimum at pattern position 2 which reaches from about -19° to -6° ventrally of the equator (Fig. 3b). Again this optimum can be better seen when low pattern contrasts were used. Moreover the sensitivity distribution in case of the landing response is symmetrical to the optimum (position 2). Using the same parameters as in the experiments just described the dependence of the response on the size of the pattern was tested. When the vertical extent of the pattern was increased from 13° to 64° in steps of 13° , the optomotor as well as the landing response increased (Fig. 3c and d). At low pattern contrasts these responses were roughly the sum of the responses to the single patterns tested before (compare Fig. 3c with 3a and Fig. 3d with 3b). At high pattern contrasts they were significantly diminished: in case of the optomotor response one would expect a value of about 3 arbitrary units for pattern size 5, instead of the value of about 1 found in the experiment. For the landing reaction the corresponding value should be around 2 instead of 0.8 arbitrary units.

Discussion

The optomotor and the landing response have been measured under identical conditions for different stimulus parameters such as mean luminance, contrast and the spatial characteristics of the pattern. The results will be discussed in the following in order to decide whether or not the two responses can be attributed to the same movement detection system.

The Sampling Base

The optomotor response is more sensitive to small spatial wavelengths (between 10° and 20°) than is the landing response (Fig. 1a and b). Similar results have been obtained by Heisenberg and Buchner (1977) for the landing response of *Drosophila*. So far the spatial wavelength dependence of the landing response of *Musca* has not been tested. Several data are available for the optomotor response of *Musca* (Eckert 1973; McCann and MacGinitie 1965; Geiger and Poggio 1975; Pick and Buchner 1979). Using high luminance conditions all these studies found an inversion of the optomotor response between 2° and 4° hinting at a sampling base of a single interommatidial angle. Pick and Buchner (1979) showed that this wavelength dependence is a function of the mean luminance: low mean luminance conditions lead to a stronger participation of movement detectors with large sampling bases. It should be noted that also for the optomotor response there exists, most probably, no uniform class of elementary movement detectors but rather sets of

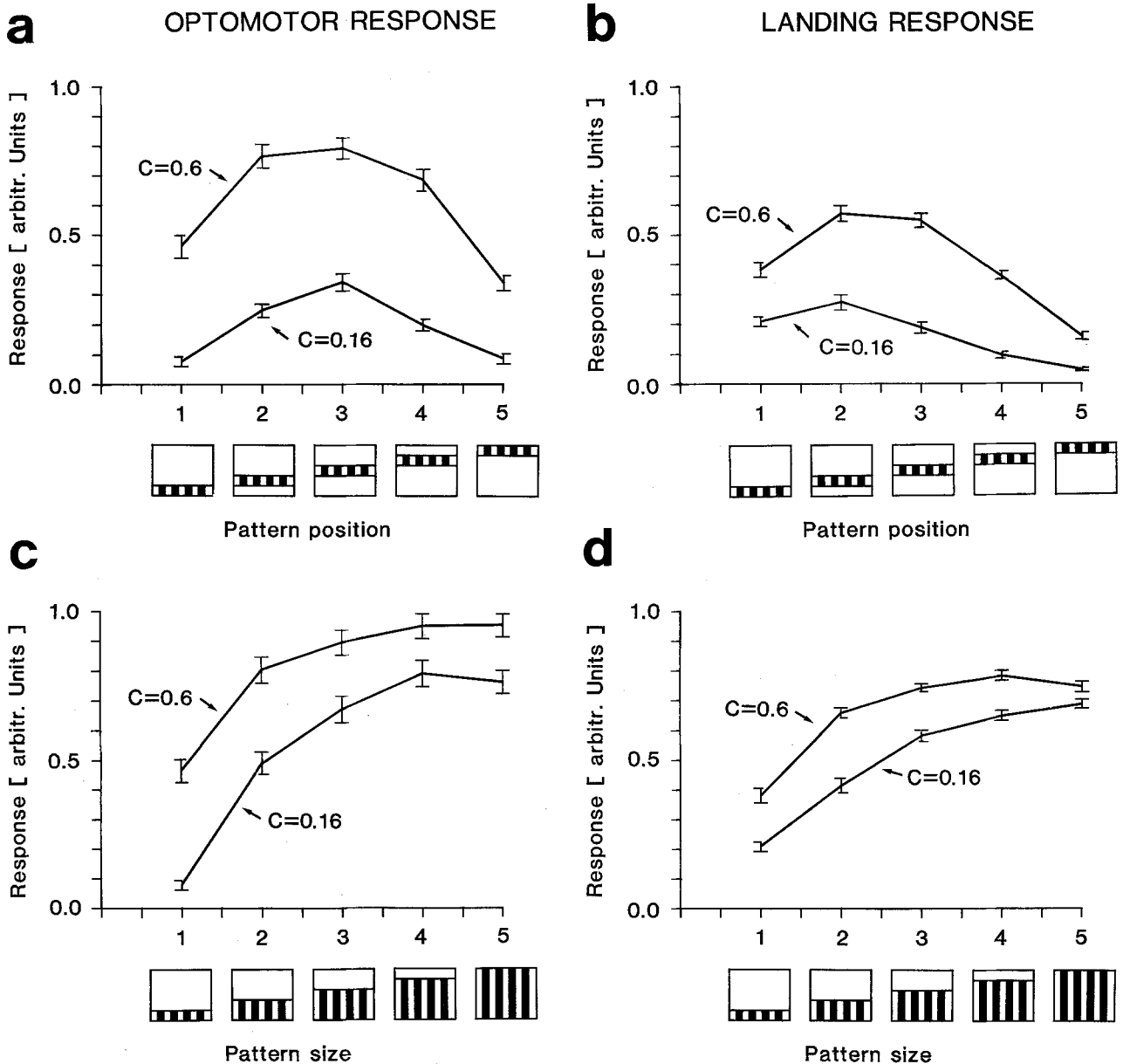


Fig. 3a-d. Dependence of the optomotor (a, c) and the landing (b, d) responses on the position and the size of the pattern (spatial wavelength $\lambda = 20^\circ$, pattern contrast $C = 0.6$ and 0.16). The landing response is given in units proportional to the inverse latency of the reaction (1 arbitr. unit = 50 ms). In a and b the pattern had a vertical extent of 13° and its position was shifted from -26° to $+26^\circ$ with respect to the equator of the fly's eye. In c and d the vertical extent of the pattern was increased from 13° to 64° in steps of 13° . The landing response shows a sensitivity optimum which seems to be more ventrally than the optimum for the optomotor response (compare a with b, especially for $C = 0.16$). If the pattern size is increased, both the optomotor and the landing response increases. At low pattern contrasts the increase seems to be proportional to the number of stimulated visual elements (compare with Fig. 3a and b). At high pattern contrast the responses to combined patterns are significantly lower than the sum of the responses to their constituents. Means and SEMs from 20 (optomotor response) and 15 (landing response) flies. Number of measurements per fly per stimulus parameter: $n = 8$ (optomotor response), $n = 10$ (landing response)

detectors with different sampling bases which contribute different amounts to the overall responses. The luminance conditions of the present study are between the two extreme values of 100 and 0.003 cd/cm^2 chosen by Pick and Buchner (1979). The Fourier analysis of our data reveals that movement detectors with sam-

pling bases once or twice the interommatidial angle contribute with about an equal strength to the response, whereas interactions of a wider extent do not seem to play a significant role in this behavior (inset of Fig. 1a). The wavelength dependence of the landing response was tested for horizontal movement only.

Fourier analysis of the respective data revealed a strong contribution of movement detectors having a sampling bases of several times the interommatidial angle (inset of Fig. 1b). It has been shown that the preferred direction of pattern motion for the landing response differs in different parts of the visual field (Wehrhahn et al. 1981; Eckert and Hamdorf 1983). If the orientation of the corresponding elementary movement detectors is indeed different from the horizontal direction in the more dorsal and ventral regions of the eye, then the contribution of wide-angle interactions to the landing response is even stronger than is expressed by our data: the real detection bases are the computed detection base in Fig. 1b, divided by the cosine of the angle subtended by the orientation of any participating elementary movement detector and the horizontal direction.

The Time-Constant

Under stationary conditions the optimum contrast frequency of the optomotor response was determined to be between 1 and 10 Hz (Fig. 2a). This is in accordance with previous findings on the optomotor response of *Musca* (McCann and MacGinitie 1965; Reichardt 1966) and *Calliphora* (Wehrhahn 1985). The contrast frequency optima of the tangential cells of the lobula plate also fall in this range (Eckert 1980; Hausen 1981, 1982, 1984; Wehrhahn 1985). However a filter time constant can not be calculated from these data because no significant differences of the responses can be found between 1 and 10 Hz. Assuming a second order low-pass filter this sets the range for the time constant between 9 and 90 ms. When the landing response was tested under quasi-stationary conditions (long latencies, obtained with low pattern contrasts) its optimum contrast frequency was found to be in the same range as the one of the optomotor response (compare Fig. 2a with 2b ($C=0.04$)). This suggests that both movement detection systems use lowpass filters with about the same time-constant.

The Spatial Integration

Using horizontal pattern movement in the frontolateral part of the visual field the optomotor response showed an optimal sensitivity at the equator of the eye (Fig. 3a). This is in accordance with previous results of McCann and MacGinitie (1965). The receptive field organization also has been measured for many of the lobula plate tangential cells (Eckert 1980; Hausen 1982; Wehrhahn 1985). They are likely to control the turning reactions of the fly as an ensemble. Thus the receptive field of a single type of cell cannot be compared with the behavioral response of the whole

animal. In contrast to the optomotor response the optimum sensitivity of the landing response seems to be below the equator (Fig. 3b). Although the values at position 2 and 3 ($C=0.16$) are not significantly different neither for the optomotor nor for the landing responses, the peak values can be assigned with sufficient accuracy if the decline on either side is taken into account. Differences between the detector fields used for optomotor course-control and landing behavior are already known from measurements in the most frontal eye region: there the landing response can be elicited by horizontal as well as vertical pattern movement (Wehrhahn et al. 1981; Eckert and Hamdorf 1983). Both the optomotor and the landing response increase with the size of the stimulated eye region (Fig. 3a and d). This has already been found for the optomotor response using oscillating stimuli (Reichardt et al. 1983). We tried to decide whether in case of the landing response a similar gain control mechanism can be found as has been postulated and found for the optomotor turning response as well as for lobula plate tangential cells (Hausen 1982; Egelhaaf 1985). Unfortunately this can not be decided on the basis of the present data: in both cases (Fig. 3c and d) the responses almost represent the sum of the responses to the 13° - components of the patterns at low contrast ($C=0.16$). At high pattern contrast the responses are significantly lower than the corresponding sum of the responses to the parts of the patterns. This can be due to either a gain control mechanism or simply to a saturation phenomenon.

General Conclusion

It has been shown in an earlier study (Borst and Bahde 1986) that the movement detection system underlying the landing response is likely to use the same type of elementary movement detectors as the optomotor system. The present investigation shows similar properties of the movement detectors and their low-pass filters in the control systems for course-control and landing. Whether or not these elementary units are identical on the structural level cannot be decided by behavioral investigations. The landing and the optomotor response have been found to differ with respect to wavelength of the visual stimulus and its position within the visual field. Both results suggest different application of elementary movement detectors in the two control systems for optomotor course-control and landing. Movement detectors with different sampling bases and different location in the visual field are not equally used by the two systems: At least the integration of the detector outputs seem to require separate neuronal networks for course-control and landing.

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