

## Landing Reaction of *Musca domestica*, III: Dependence on the Luminous Characteristics of the Stimulus

Cloe Taddei-Ferretti

Laboratorio di Cibernetica del C.N.R., Arco Felice, Napoli, Italy,

and

Antonio Fernandez Perez de Talens

Laboratorio di Fisiologia Clinica del C.N.R., Pisa, Italy

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1. The house fly shows landing reaction to an expanding visual stimulus or to a decrement of the environmental light level. The quantitative relationship between the dependence of landing reaction on expansion and on light level decrement is analyzed.

2. The different properties of the reactions at different light levels may be correlated with the two visual systems in Diptera and may be explained by the existence of an altering mechanism that weighs stimuli for landing reaction at low illumination levels.

3. The landing reaction resembles the optomotor reaction with respect to the influence of the contrast of the stimulating pattern. The landing reaction appears to be invariant to the phase relations between the spatial components of the periodic patterns used in the present experiments.

### Introduction

During the investigations on the motion perception of Insects, it has been fruitful and of great interest the analysis of the optomotor turning reaction (see, *f. i.*, Hassenstein, 1951; Hassenstein and Reichardt, 1956; Kunze, 1961; Fermi and Reichardt, 1963; Götz, 1964; Thorson, 1964; McCann and MacGinitie, 1965; Kirschfeld, 1972), *i. e.* the evoked response of the animal of following a movement relative to itself occurring in its visual field, for the feasibility of this response to be observed, reproduced and quantified and to offer the possibility to analyze the functional principle of input output relationships. The same can be said about the study of different Insect's optomotor reactions to different types of moving stimuli: The thrust optomotor reaction, *i. e.* the variation of the forward thrust exerted by an Insect during flight, can be obtained by movements perceived in opportune directions that are concordant on the two eyes (Götz, 1968, 1969); the approach reaction can be elicited by the velocity, relative to the fly, of a still object on a distant background perceived by a flying Insect (Reichardt and Wenking, 1969; Reichardt, 1973); the escape response is due to the approach of an object (Goodman, 1960; Taddei and Fer-

nandez, 1971, 1972 a, b; Fernandez and Taddei, 1973). As Insects are capable of perceiving other complex dynamic patterns, it is of interest to analyze the so called landing reaction, that is presented by a flying Insect as it approaches a surface on which it is going to land (Hyzer, 1962): At a definite distance from the surface, it lifts its first pair of legs to both sides of the head and extends the last pair backward and remains in such a position until it has made contact with the surface; this is an all-or none reaction. Previous works on the landing reaction (Goodman, 1960, 1964; Braitenberg and Taddei, 1966) proved that there are at least two different visual stimuli for landing: The "expansion" of a pattern on the visual field of the Insect's compound eye and the variation in the total luminous flux from the seen pattern, a decrement of which elicits a reaction of the Insect. Neurons which are brightness detectors and movement detectors and fibres which respond to movement and to luminance variation are known in Arthropods (Burt and Catton, 1960; Horridge *et al.*, 1965; Wiersma, 1967; Palka, 1967; McCann and Dill, 1969; Mimura, 1971; Rowell, 1971; Wiersma and York, 1972). Generally, systems that produce expanding stimuli involve a change of total luminous flux, thus preventing separate analysis of the influences of the two stimuli. In previous investigations (Braitenberg and Taddei, 1966; Taddei and Fernandez, 1967; Fernandez and Taddei, 1970; Cogshall, 1971,

Requests for reprints should be sent to Dr. Cloe Taddei-Ferretti, Laboratorio di Cibernetica del C.N.R., 80072 Arco Felice, Napoli, Italy, Via Toiano 2.



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1972) the two visual stimuli have been separated under particular experimental conditions and the dependence of the landing reaction on the first of them has already been analysed in *Musca domestica*. The same experimental conditions of Braitenberg and Taddei, 1966 are imposed in present analysis on dependence of the landing reaction on the luminous characteristics of the stimuli.

### Methods

Simulation of pattern expansions or contractions without variation of the total luminous flux were produced by rotating an opaque disk on which were drawn  $2n$  arithmetic spirals of pitch  $p$ , uniformly dephased among themselves. The stripes between two neighbouring spirals were alternately painted black and white. The rotation of the disk produced the movement of black and white wavefronts in the radial directions. This pattern was presented to the fly flying at a fixed spatial point with its head fixed in respect to the thorax (Taddei and Fernandez, 1967). The fly was facing the center of the disk. The velocity of rotation of the disk could be varied with a potentiometer. Illumination of the disk was obtained from the light of a Philips Projector bulb of 220 V and 60 W placed at a distance of approximately 40 cm to the disk. To avoid stroboscopic effects, the bulb was powered by a direct current SELO generator. Illumination of the disk in the range of 10 lux to 1500 lux was thus obtained by the operator manually, varying the D.C. voltage by means of a potentiometer. The stability of the electric system was such to assure a very fine reproducibility of the luminous flux values. We have not taken into account the response latency, that in other Insects has been observed to be inversely related to the stimulus intensity (Cogshall, 1972), cause the very little values of this parameter in *Musca*.

### Quantitative Relationships between the Dependence of the Landing Reaction on Perceived Pattern Expansion speed and on Changes in Light Level

Let us give: The illumination level, measured as the illuminance on the stimulating disk,  $I$  [lux], while during each experiment the distance of the fly from the disk will be unchanged; the fly-disk distance,  $d$ ; the radial expansion speed,  $V_R$  [cm/sec], of the wavefronts of the stimulating white and

black pattern; the angle,  $\alpha$ , which is function of time and is formed by the fly's long axis and the straight line joining the center of the fly's head and a moving wavefront; the perceived radial expansion speed of these wavefronts,  $V_P = (V_R/d) \cos^2 \alpha$  (Taddei and Fernandez, 1972 b); as  $\alpha$  does not depend on illuminance  $I$ , we will briefly identify  $V_P$  with its central value, i. e.  $V_P = V_R/d$  [rad sec<sup>-1</sup>]; the spatial wavelength of the pattern in the radial direction,  $L = p/n$ ; the contrast frequency,  $V_P/\arctan(L/d)$ ; the interommatidic angle,  $\Delta\varphi$ ; the receptor acceptance angle,  $\Delta\varphi$ .

It has been previously shown (Goodman, 1960; Braitenberg and Taddei, 1966) that, for the values attained, if for definite values of the state parameters  $I$ ,  $V_R$  and  $d$ , the fly does not react, it is possible to obtain the reaction by an increase of  $V_P$  (by increasing  $V_R$  or, with subthreshold  $V_R > 0$ , by decreasing  $d$ ) or by a decrease of  $I$  (with subthreshold  $V_P \geq 0$ ). The sign of this light effect on landing reaction is opposite to that on dark activation (Büchner, 1972). Note that, for each stimulating disk, each value of  $V_P$  implies definite values of the times,  $T_1 = \Delta\varphi/V_P$  necessary for a stimulus (a definite  $\Delta I$ ) to pass from one ommatidium to the adjacent (i. e., to stimulate a movement detector of the Reichardt's model),  $T_2 = (\arctan(L/2d))/V_P$  necessary for two successive stimuli (two  $\Delta I$  of opposite sign)

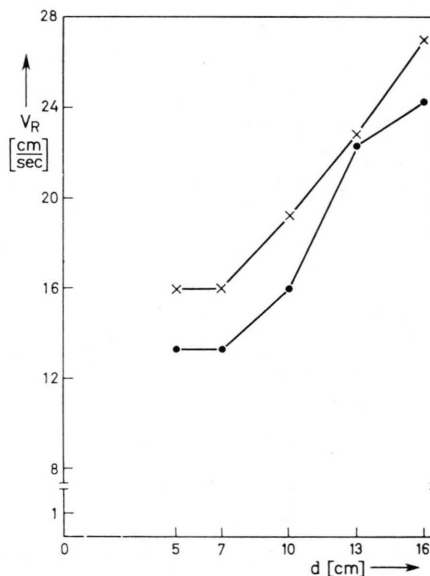


Fig. 1. Dependence of radial expansion speed  $V_R$  [cm/sec] of the stimulating pattern necessary for landing reaction on fly-stimulus distance  $d$  [cm], for two values of illumination level (●)  $I = 50$  lux, (×)  $I = 500$  lux.

to reach an ommatidium, and  $T_3 = f(\Delta Q/V_P)$  necessary for a stimulus to be completely fulfilled over an ommatidium; analogously, each value of the

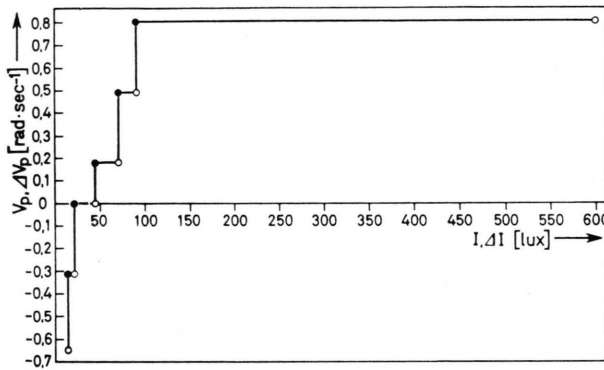


Fig. 2. On (●) and off (○) states of the landing reaction obtained respectively by decrements of the illumination level  $I$  [lux] and by decrements of the perceived radial expansion speed  $V_P$  [rad sec<sup>-1</sup>] of the stimulating pattern.

speed of the decrease of  $I$  implies a value of  $T_3$  (in this case,  $T_3$  = the time employed to obtain such  $\Delta I$ ). The effect of the two parameters,  $+\Delta V_P$  and

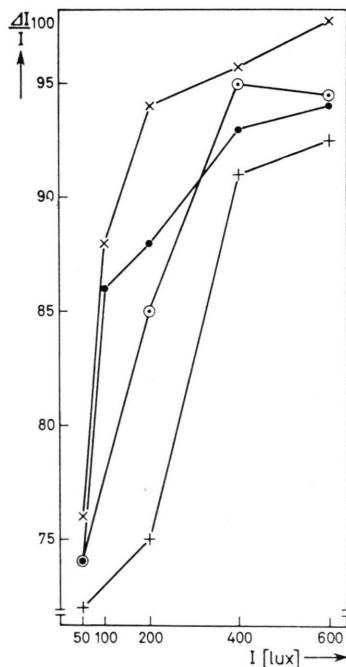


Fig. 3. Dependence of the percentage decrements  $(\Delta I/I) \cdot 100$  of the illumination necessary for landing reaction on the initial value of illumination level  $I$  [lux]; subthreshold perceived radial expansion speed of the stimulating pattern: (+)  $V_P = 0.495$  rad sec<sup>-1</sup>, (●)  $V_P = 0.0185$  rad sec<sup>-1</sup>, (•)  $V_P = 0$  rad sec<sup>-1</sup>, (×)  $V_P = 0.33$  rad sec<sup>-1</sup>, (○)  $V_P = 0.185$  rad sec<sup>-1</sup>.

$-\Delta I$ , combine in an interactive way (Taddei and Fernandez, 1967, 1971): For example a contraction, to which corresponds a negative value of  $V_P$ , may stop a previous reaction caused by a previous decrement in illumination level.

The results of observation on the behaviour of flies adapted for 10 min to two light levels ( $I = 50$  lux and 500 lux) show that the threshold for reaction was lower at the lower of the two illumi-

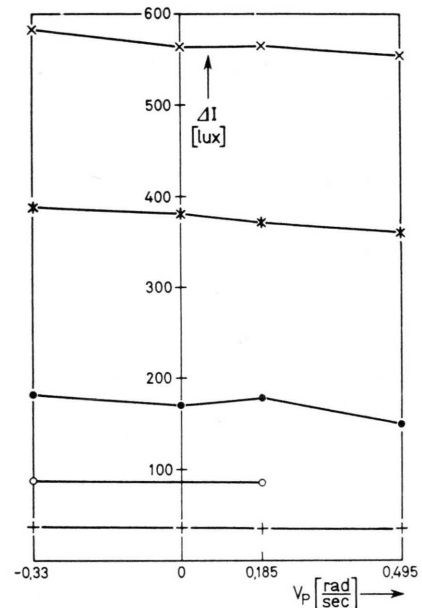


Fig. 4. Dependence of the decrements  $\Delta I$  [lux] of the illumination necessary for landing reaction on the subthreshold perceived radial expansion speed  $V_P$  [rad/sec] of the stimulating pattern; initial value of illumination level: (+)  $I = 50$  lux, (○)  $I = 100$  lux, (●)  $I = 200$  lux, (★)  $I = 400$  lux, (×)  $I = 600$  lux.

nances (Fig. 1). Then, in order to investigate the interaction of reaction dependence on  $V_P$  and on  $\Delta I$ , the values of a sequence of alternate decrements of  $V_P$  and  $I$  necessary to alternate periods of reaction (on) with others of reaction absence (off) were recorded (see example, Fig. 2). Such records were obtained under various experimental conditions: Increasing or decreasing  $V_P$  (with constant  $d$ ) and  $I$  and subsequently beginning at lower or at higher levels of  $I$ , beginning from an on reaction state or from an off reaction state; note that one can begin from negative values of  $V_P$  only if one has just reached that condition through a  $V_P$  decrement. As landing reaction depends (Goodman, 1960) both on the total decrease of  $I$ ,  $\Delta I$ , and on the speed of

this decrease,  $\Delta I/\Delta t$ , it should be noted here that there was no bias between the actual measurement to be made and the human accuracy in turning the helipot to change  $I$ . To obtain comparable data, all the experiments were realized with the same stimulating disk. The curve of Fig. 2 represents four relationships: The dependence of  $\Delta I$  on  $V_P$ , of  $\Delta I$  on  $I$ , of  $\Delta V_P$  on  $I$  and of  $\Delta V_P$  on  $V_P$ ; with each change of the reaction state from "on" to "off" and vice versa, the values of  $\Delta I$  or  $\Delta V_P$  were determined with  $I$  and  $V_P$  as the independent variables.

The first two of these four dependencies were then experimentally found in a direct way: With  $d$  fixed, the decrements of  $I$  necessary to obtain landing reaction depending on the initial value of  $I$  ( $V_P$  fixed in the range  $0.495 \text{ rad sec}^{-1} > V_P > -0.33 \text{ rad sec}^{-1}$ ) and on  $V_P$  ( $I$  fixed in the range  $50 \text{ lux} < I < 600 \text{ lux}$ ) were respectively measured (Fig. 3 and Fig. 4). These figures show a dependence of the decrements of light level required for their detection, with respect to landing reaction, on the initial value of illuminance and on the intensity of subthreshold velocity of the expanding stimulus. It can be seen that the decrement of light level necessary to obtain reaction increases with the initial illuminance and that it decreases with the increase of subthreshold  $V_P$ , although very slowly. It is to be noted that at higher  $I$  higher  $\Delta I/I$  were needed although, due to the relationship between speed in turning the helipot and variation of the luminous flux of the bulb, at higher  $I$  the  $\Delta I$  were obtained with higher decrement speed ( $\Delta I/\Delta t \cong 2.4, 1.7, 0.95, 0.45, 0.25$  in arbitrary units respectively for  $I = 600, 400, 200, 100, 50 \text{ lux}$ ), *i.e.* although, according to Goodman, 1960, lower  $\Delta I$  were expected to be needed: this fact indicates a real dependence of the  $\Delta I$  needed to elicit landing reaction on the initial level of  $I$ . Instead, higher  $\Delta I/I$  were needed at the lowest  $I$  for the honey bee light intensity discrimination in the phototactic attractivity of two luminous screens of different brightness (Labhart, 1972). The last two relationships, that is the dependence of  $\Delta V_P$  on  $I$  and  $\Delta V_P$  on  $V_P$ , are without meaning in this context since, as it has been previously stated (Braitenberg and Taddei, 1966), the threshold value  $V_{Pt}$  is such that for  $V_P > V_{Pt}$  the fly reacts and for  $V_P < V_{Pt}$  the fly does not react. Then the value of  $V_P$  should always be the difference between the initial value of  $V_P$  and the threshold value for the reaction  $V_{Pt}$  at this illuminance and for the

adaptation attained. Instead information could be obtained from a curve showing the dependence of the threshold expansion speed  $V_{Pt}$  on the illuminance  $I$ . Such a curve has been experimentally found in which for each value of  $I$ , *i.e.* for a 10 min adaptation of the fly to this value of  $I$ , the value of  $V_{Pt}$  necessary for the landing reaction is determined (Fig. 5). The shape of the curve does not change

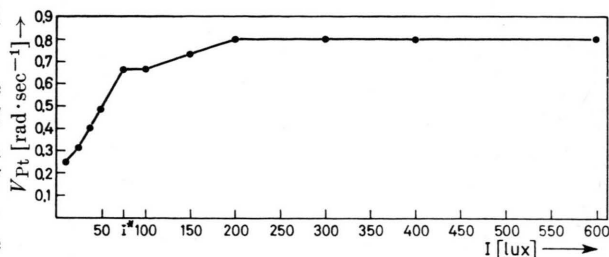


Fig. 5. Dependence of threshold perceived radial expansion speed  $V_{Pt}$  [rad sec<sup>-1</sup>] of the stimulating pattern necessary for landing reaction on the illumination level  $I$  [lux];  $I^*$  = value of  $I$  to which corresponds an abrupt change in the variation of  $V_{Pt}$  on  $I$ .

qualitatively for individual flies. The curve in Fig. 5 shows that, in the tested range, the  $V_{Pt}$  necessary for the landing reaction increases with light intensity, that is the threshold for the stimulus is lower at lower than at higher illuminances. This fact is not in contrast with the increase of contrast sensitivity to moving striped pattern with illumination when the pattern is used to elicit an optomotor response (Hecht and Wolf, 1929), since the used stimuli are largely above the visual acuity limit. The variation of  $V_{Pt}$  and that of the difference between the thrust exerted by fixed flying flies in darkness and in light as a function of  $I$  (Buchner, 1972) are of the same sense. Fig. 5 shows three kinds of variation of  $V_{Pt}$  with  $I$ : For very low values of  $I$ , up to  $I^*$  which corresponds approximately to 15–75 lux,  $V_{Pt}$  increases quickly with  $I$ ; then abruptly the increases of  $V_{Pt}$  abates until, at approximately 170–240 lux, the curve gradually begins to reflect a saturation, that is to an increase of  $I$  there corresponds no increase of  $V_{Pt}$ .

The finding, that for every tested fly one finds a value  $I^*$  of  $I$  that clearly discriminates two variations of the stimulating pattern's  $V_{Pt}$  with respect to  $I$ , may reflect a correspondence with the two visual systems of Diptera which have different anatomical and physiological (Trujillo-Cenóz and Melamed, 1966; Braitenberg, 1967; Langer, 1967; Kirsch-



feld, 1965, 1967, 1969 a, 1969 b; Kirschfeld and Reichardt, 1970; Eckert, 1971; McCann and Arnett, 1972) characteristics. The first visual system consists of single units, each composed of six peripheral sensory cells that are placed in six different positions (No. 1 to 6 of Dietrich, 1909, order) of six different ommatidia which are close to an ommatidium 0; the six positions and the six ommatidia are arranged in an asymmetric scheme (Braitenberg, 1967); the axes of the six sensory cells of a single unit are parallel to each other and parallel also to the axes of sensory cells 7 and 8 of the ommatidium 0; the six short fibers of each single unit meet in a cartridge of the lamina ganglionaris, where they end (see also Vigier, 1908). Each unit of the second visual system consists of the two central sensory cells of each ommatidium (No. 7 and 8 of Dietrich, 1909, order) with their long fibers running directly to the medulla. The size of the visual field of a single unit of the first system is larger than that of the second; thus a unit of the first system conveys a higher light flux; it is also protected against strong illumination by a pigment migration mechanism (Kirschfeld and Franceschini, 1969) in sensory cells 1 to 6 which reduces the light flux in the rhabdomeres at high light intensity levels, and appears to be specialized for low light intensities; on the other hand the second system, which has almost no pigment migration mechanism and is specialized for high light intensities, has a higher contrast transfer for similar patterns (Kirschfeld and Franceschini, 1968). Thus it is feasible that difference in behaviour of the fly at low and high light levels (at  $I < I^+$  and  $I > I^+$ ) is associated with the alternate predominant use of the low or the high light level visual system. We conclude that the probability of the occurrence of the fly's landing reaction depends on  $\Delta I$ , on  $I$  and on  $V_P$ . Its dependence on  $I$  has three successive monotonic forms shown in Fig. 5: The first one may be associated with the predominance of the visual system 1–to–6 (low  $I$  levels, *i.e.*  $I < I^+$ ), the second one with the predominance of the visual system 7–and–8 (high  $I$  levels, *i.e.*  $I > I^+$ ), the third one with the saturation of the system (at higher  $I$  levels). Some considerations about the facilitation of the landing reaction by some factors influencing  $V_P$ , such as geometrical characteristics of the stimulus, and about its dependence on some anatomical features of the fly's eye are reported in Fernandez and Tad-

dei, 1970. Present findings indicate that when the fly is in a state corresponding to the predominant use of the first visual system it has quite a different behaviour, in the sense that threshold for all-or-none landing reaction is lowered much more rapidly with a decrease in light intensity, than when the second system is used. We may interpret these results by proposing an alerting mechanism that weights stimuli for landing by its sensitivity to light intensity and that functions when the high illumination level visual system defaults.

### Dependence of the Landing Reaction on the Stimulating Pattern Black Percentage

The intensity of the light flux from the rotating disk may be also varied, without changing the environmental illumination, by varying the width of the black strip relative to the white one, that is by shifting non uniformly the already uniformly de-phased spirals among themselves, thus changing the percentage of the total area covered by black (black percentage, B%). More details about the spirals can be found in Taddei and Fernandez, 1967. In a set of disks with painted spirals of 8 cm pitch, the black percentage of the pattern was varied and the reflectance percentage  $\varrho\%$  of each disk was tested, being  $\varrho\% = (\text{luminance of the disk} / \text{luminous flux of the bulb}) \cdot 100$ ; as the relative positions of bulb, disk and fly's eye are never varied during each experiment, nor the disk area, we can measure  $\varrho\%$  as  $(\text{illuminance at the fly's eye position} / \text{illuminance on the disk}) \cdot 100$ . The ratio between the experimental and the theoretical value of  $\varrho\%$  of the whole disk was calculated for various values of B% (having calculated the theoretical  $\varrho\%$  taking into account the B% of each disk with painted spirals and the experimental values of illuminance at the fly's eye position when a total white or total black disk reflected the light). The value of this ratio never differs more than  $\pm 3\%$  from the value 1 over the entire range of B%, demonstrating that our disks were accurately prepared and that then the results of experiments performed with them could not be attributed to the disk inaccuracy.

Fig. 6 shows the dependence of the threshold perceived radial expansion speed  $V_{Pt}$  of the stimulating pattern on the black percentage of the stimulating pattern. When a higher value of  $V_{Pt}$  is needed, the threshold for landing reaction is raised; in that

sense it could be said that the trend of the curve expressing the variation of the inverse of  $V_{Pt}$  on B% indicates the trend of the variation of the easiness of the occurrence of landing reaction on B%. The curve of the variation of  $1/V_{Pt}$  on B% shows two

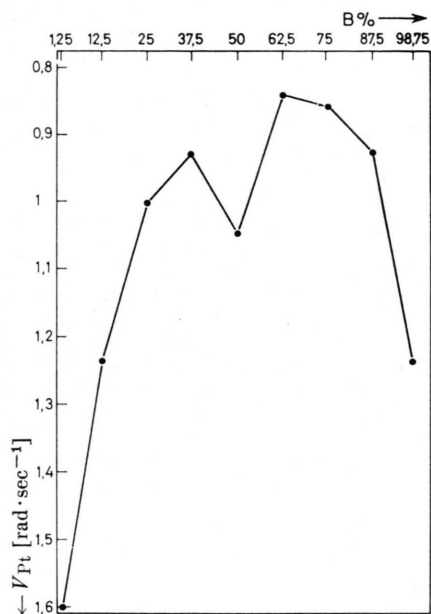


Fig. 6. Dependence of the threshold perceived radial expansion speed  $V_{Pt}$  [rad sec<sup>-1</sup>] of the stimulating pattern necessary for landing reaction on the black percentage B% of a set of disks with spirals of 8 cm pitch; fly-stimulus distance  $d=17$  cm.

relative maxima. It should be noted that the curve is not symmetric with respect to the value corresponding to a total area of the stimulating disk one half black and one half white, *i. e.* a pattern and its photographic negative do not have the same power for stimulating landing. The patterns with higher total contents of black are more efficient than the symmetric ones with higher contents of white. These results are independent of the pitch of the set of spirals used. We may explain the two characteristics of the experimental curve in Fig. 6 by testing the hypothesis that the mechanisms underlying the optomotor and landing reactions are in some respect the same. It has been experimentally established (Hassenstein, 1959; Reichardt and Varjú, 1959; Reichardt, 1962) that the optomotor reaction depends on: a. The perceived contrast of the stimulating pattern, b. its Fourier spectrum. Thus we will now consider the dependence of the landing reaction on such two parameters.

a. Perceived contrast of the stimulating pattern. We will first interpret the asymmetry of the experimental curve. The finding that stimulating patterns with higher contents of black are more efficient than the symmetric whiter ones appears clear since, being the contrast  $c = (I_M - I_m) / 2\bar{I}$  with  $I_M$  = maximum intensity,  $I_m$  = minimum intensity,  $\bar{I}$  = mean intensity, when B% increases  $\bar{I}$  decreases. In fact, repeating the experiments outlined in Fig. 6. varying the illumination in order to maintain a constant mean intensity of light reflected by the pattern and perceived by the fly, the asymmetry of the curve was found to decrease. The asymmetry decreases also if the total contrast of each pattern is decreased, that is if a dark-grey light-grey pattern (*f. i.*  $\rho_b\% = 15$  and  $\rho_w\% = 40$  rather than  $\rho_b\% = 5$  and  $\rho_w\% = 50$ , where  $\rho_b\%$  and  $\rho_w\%$  are respectively the reflectance percentage of black and white stripes) is used; further explanations of this finding can be found in Taddei and Fernandez, 1973. The higher efficiency of blacker patterns is in agreement with data on the increment of contrast sensitivity of the locust compound eye, measured by rotation of radial striped patterns, using patterns in which black stripes were wider than the white ones (Burr and Catton, 1969). Our result is also in agreement with data showing that a higher percent of landing responses is obtained when a black pattern on a white background rather than a white pattern on a black background is brought towards the fly (Table 2 of Goodman, 1960). Also Kunze (1961) found that the bee's optomotor reaction increased with the decrease of the level of  $\bar{I}$  if the difference  $\Delta I$  between stripes and background of a rotating cylinder was held constant (gray stripes better on a black background than on a white one, for the same  $\Delta I$ ).

To measure the transferred contrast of used patterns we must consider an Insect's ommatidium to be acting as a Gaussian transducer (Götz, 1964; McCann and MacGinitie, 1965; Vowles, 1966), as stated also experimentally (Laughlin and Horridge, 1971); the angular sensitivity of the ommatidium can be separated into a product of the angular sensitivity of the dioptric apparatus and the angular sensitivity of the rhodome (Snyder, 1972). Such a transducer weights the intensities of light depending on the direction from which the rays arrive from different parts of the seen pattern, thus resulting in a dependence of the perceived pattern contrast on the black percentage of the pattern. In Tad-

dei and Fernandez, 1973, we have applied a method of calculation by which, considering the ommatidium as a Gaussian transducer, one obtains the values of the contrast of a striped white and black infinite pattern as perceived by the ommatidium depending on the black percentage of this pattern. We may apply such considerations to the experiments reported here since, while the visual field of an ommatidium is very small, the arcs of the spirals seen by each ommatidium can be considered as straight lines. One finds then that the curve expressing the dependence of the perceived contrast on the black percentage of the pattern is in itself asymmetric. We should keep in mind also that the optomotor reaction is a quadratic function of the perceived contrast of the stimulating pattern (Hassenstein, 1959; Reichardt, 1962). In Fig. 7 is represented the computer

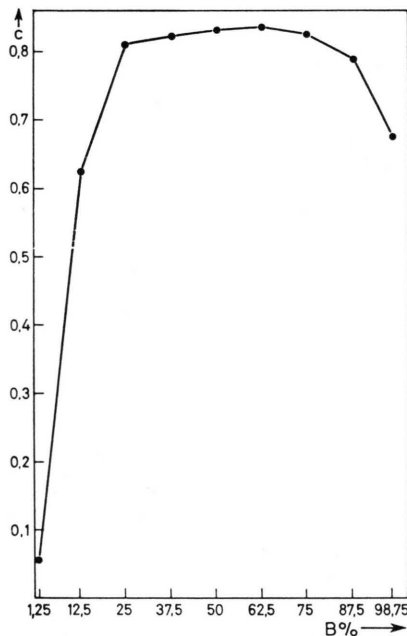


Fig. 7. Dependence of the computer evaluated perceived contrast  $c$  of the pattern on the black percentage  $B\%$  of a set of patterns with spirals of 8 cm pitch, reflectance percentage of the black zone  $Q_b\% = 5$ , and of the white zones  $Q_w\% = 50$ , seen by an ommatidium with opening angle  $\Delta\varphi = 1.8^\circ$  at a distance  $d = 17$  cm.

calculated curve of the perceived contrast of the pattern for various values of pattern  $B\%$ , where  $Q_w\% = 50$ ,  $Q_b\% = 5$ ,  $d = 17$  cm, receptor opening angle  $\Delta\varphi = 1.8^\circ$ . Note that the curve is asymmetric, in the same sense of the curve expressing the variation of  $1/V_{Pt}$  with  $B\%$ .

**b. Fourier spectrum of the stimulating pattern.** We will now examine the two relative maxima of the experimental curve expressing the dependence of  $1/V_{Pt}$  on  $B\%$  with respect to the characteristics of the Fourier spectrum of the stimulating pattern. Each periodic function  $f(x)$  with period  $L$  can be expanded into a Fourier series

$$f(x) = \sum_{n=-\infty}^{+\infty} a_n e^{in\omega_0 x} \quad \text{with} \quad \omega_0 = \frac{2\pi}{L},$$

where the coefficients  $a_n$  are

$$a_n = \frac{1}{L} \int_{-L/2}^{L/2} f(x) e^{-in\omega_0 x} dx,$$

representing the amplitude of the  $n^{\text{th}}$  harmonic component of  $f(x)$  having pulsation  $n\omega_0$ . In the case of a periodic succession of identical rectangular pulses of period  $L$ , amplitude  $E$  and duration  $w$  (Fig. 8 a), the application of such formulae yields

$$a_n = E \frac{w}{L} \left[ \sin \frac{n\pi w}{L} / \frac{n\pi w}{L} \right].$$

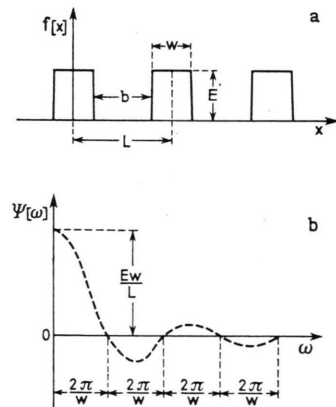


Fig. 8. a. The stimulating waveform made by a periodically repeated pulse of intensity  $E$ , full period  $L$ , ON period  $w$ , and OFF period  $b$ . b. Envelope of the corresponding Fourier spectrum  $\psi(\omega) = E \frac{w}{L} \frac{\sin \omega}{\omega}$ ; discrete lines representing spec-

trum coefficients are defined as  $a_n = \psi \left( \frac{n\pi w}{L} \right)$ .

This Fourier spectrum shows an envelope of the form  $\sin z/z$  (Fig. 8 b) which is that of an harmonic oscillation of decreasing amplitude.  $a_0$  corresponds to pattern average intensity. We will next multiply each  $a_n$  for the factor

$$\exp \left[ -\frac{\pi^2}{4 \ln 2} \frac{\Delta\varphi^2}{\arctan^2 \frac{L}{n d}} \right]$$

which reflects the contrast transfer properties of the ommatidium for the  $n$ -th Fourier component of the periodic stimulus, Götz (1964). Hassenstein (1959) introduced the finding that the *Chlorophanus* optomotor response to a moving pattern is the sum of the responses to each Fourier component of the pattern involved in the stimulation and that relative phases of the components have no influence on the optomotor reaction, *i.e.* the Insect is phase blind

with respect to optomotor reaction; Reichardt and Varjú (1959) found that the amplitude of the optomotor response is a quadratic form of the Fourier coefficients of the stimulating pattern, *i.e.* the response is independent of the sign of the Fourier coefficients. The model for movement perception, deduced from the analysis of *Chlorophanus* behaviour, is found to apply also to the *Musca* and *Drosophila* optomotor behaviour. In Fig. 9 are re-

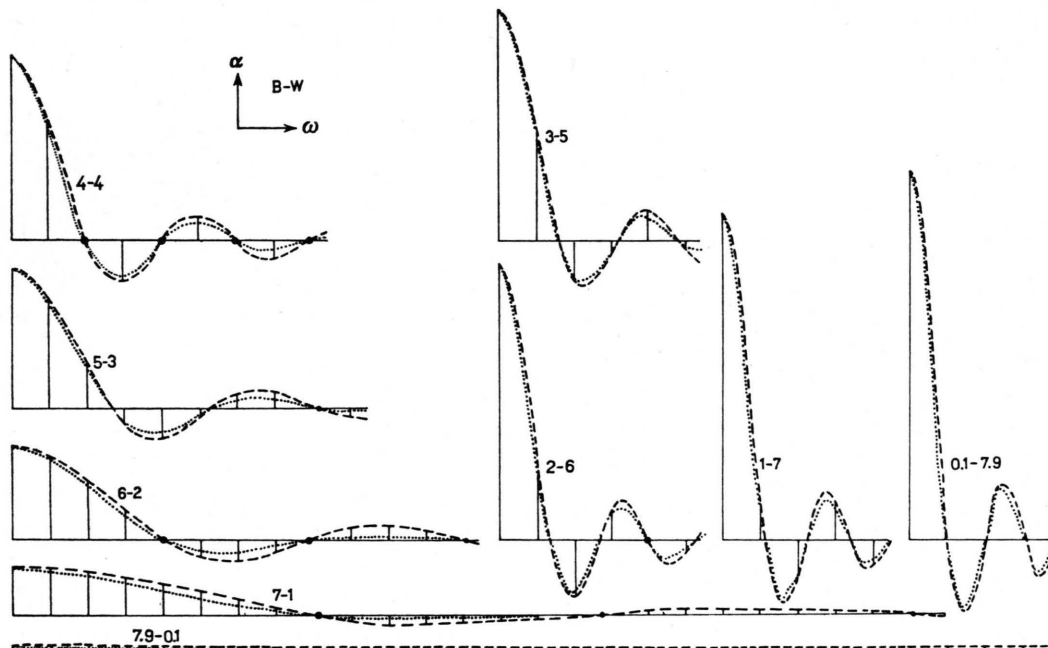


Fig. 9. The first Fourier coefficients,  $\alpha$ , for each of the used disks;  $B$  = width of the black stripes;  $W$  = width of the white stripes; (—) envelope of  $\alpha_n$ ; (···) envelope of  $\alpha_n \exp \left[ -\frac{\pi^2}{4 \ln 2} \frac{\Delta Q^2}{\arctan^2(L/n d)} \right]$ , being  $\Delta Q = 1.8^\circ$ ,  $L = 8$ ,  $d = 17$ .

ported the first Fourier coefficients,  $\alpha$ , for each of the used disks. The sum of the absolute values of the first 160 computer calculated Fourier coefficients of the pattern is then presented, for various values of pattern B%, in Fig. 10. This represents a very close approximation of the original function. The curve presents two maxima of identical value.

Then, by computer multiplication of the squares of the values of the curve of Fig. 7 and the corresponding values of the curve of Fig. 10, we obtained Fig. 11 curve, which shows the complete dependence on pattern B% of the two factors considered under points a. and b. on which the optomotor reaction depends. In the given hypothesis that the mechanisms underlying the optomotor and the

landing reactions are equal, the curve of Fig. 11 represents also the theoretical dependence on pattern B% of two factors on which the landing reaction depends. The curve in Fig. 11 conforms well with experimental data on the dependence of the inverse of the threshold perceived radical expansion speed,  $1/V_{Pt}$ , on the stimulating pattern black percentage, B%, indicating the variation of the easiness of the occurrence of landing reaction on B% (inverse of the curve of Fig. 6). Thus it appears that really the landing reaction, like the optomotor reaction, depends on both the square of the perceived contrast and on the sum of the absolute values of the Fourier coefficients of the stimulating pattern and, as a consequence, that really there is a close



similarity between mechanisms underlying optomotor and landing reactions. Such a result means also that, in so far as it concerns landing reaction,

the house-fly is indifferent to  $180^\circ$  phase shifts of the Fourier coefficients of the stimulating pattern. This result, considered under the above similarity,

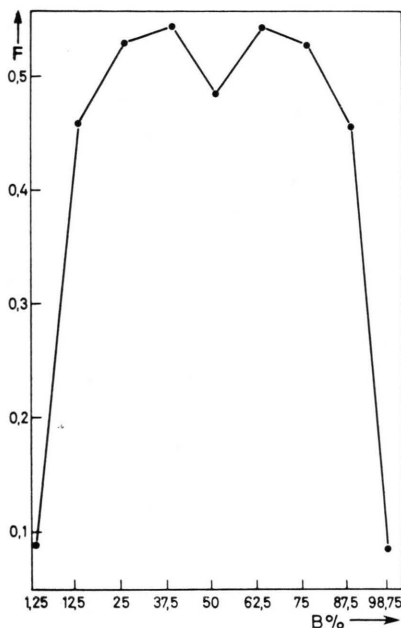


Fig. 10. Dependence of the computer evaluated sum  $F$  of the absolute values of the first 160 Fourier coefficients, each one multiplied for  $\exp \left[ -\frac{\pi^2}{4 \ln 2} \frac{\Delta \varphi^2}{\arctan(L/n d)} \right]$ , of the stimulating pattern on the black percentage  $B\%$  of a set of patterns with spirals of 8 cm pitch.

let us generalize saying that, as in the optomotor response theory, also in so far as it concerns landing reaction the house-fly appears to be phase blind.

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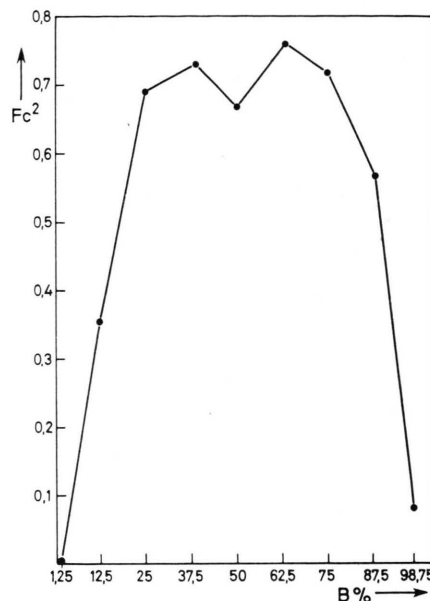


Fig. 11. Computer evaluated curve showing the dependence of both the square of the perceived contrast  $c^2$  of the stimulus and the sum  $F$  of the absolute values of Fourier coefficients of the stimulus, obtained from Figs. 7 and 10, on the black percentage  $B\%$  of a set of patterns with spirals of 8 cm pitch.

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Contrary to the rules of this journal, the references of the present contribution are listed in alphabetical order.

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