Landing Reaction of *Musca domestica*, IV: A. Monocular and Binocular Vision; B. Relationships between Landing and Optomotor Reactions

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1. The behaviours of monocular and binocular flies are compared with respect to the landing reaction. It is found that landing reaction is elicited through different mechanisms by stimulating the zones of single or of double vision: Monocular stimulation in the field of single vision evokes reactions with both ipsilateral and contralateral legs; monocular stimulation in the field of double vision evokes reaction only with the ipsilateral legs.

2. The relationships between landing and optomotor reactions are analyzed. It is found that, a. When the fly is not free to turn itself, it may react to a lateral displacement in the visual field (optomotor stimulus) with a landing reaction; b. The threshold for landing evoked by an expansion in the visual field (landing stimulus) is much lower than the threshold for landing evoked by a lateral displacement; c. A horizontal lateral displacement in the visual field of an eye is adequate to evoke the landing reaction only if it is perceived in the direction from the front to the back of the eye; d. When the fly is free to turn itself, it can present both landing and optomotor reactions to a optomotor stimulus; e. When the fly is fixed at a point, landing reaction can be evoked also by an escape stimulus.

Introduction

The means by which Insects are capable of motion perception were formerly investigated by Hertz (1934 a, b), Graffon (1934) and Kalmus (1948). In a more recent period Hassenstein (1951), Hassenstein and Reichardt (1956), Reichardt and Varjú (1959), by interpreting behavioural data on the optomotor reaction of *Chlorophanus* that can be elicited by a lateral movement in the visual field, have constructed a model in which a minimum of two adjacent ommatidia, in front of each of which there appears in two successive moments a signal, consisting of a variation of the illuminance on the ommatidium, are required for the movement detector responsible for optomotor reaction. Fermi and Reichardt (1963) applied such a model to the behaviour of *Musca domestica*. In *Musca* at least two lines of sight spaced like the ommatidial axes of its neural-superposition eyes are required for a movement detector (Braitenberg, 1967), as found also experimentally by Kirschfeld (1972). In latest years a great movement of interest has involved the studies about the mechanisms undelying the motion detection by the compound eye and its processing by the central nervous system: Burtt and Catton (1954, 1966), Wallace (1959), Kunze (1961), Götz (1964, 1965, 1968, 1972), MacCann and Mac Ginitie (1965), Horridge (1966), Thorson (1966), Bishop and Keehn (1967), Wiersma and Yamaguchi (1967), Palka (1969), McCann and Foster (1971), Collett (1972), Kirschfeld (1972). Anatomical studies clarified the structure of the compound eye: Vigier (1908), Cajal (1909), Cajal and Sanchez (1915), Kuiper (1962), Vowles (1966), Trujillo-Cenóz and Melamed (1966), Braitenberg (1967), Kirschfeld (1967), Strausfeld and Blest (1970), Strausfeld (1970, 1971), Boschek (1970). More recently Braitenberg (1970, 1971 b, 1972), Strausfeld and Braitenberg (1970), Horridge and Meinertzhagen (1970) search for fibres which are the possible substrate for the correlation of visual inputs required for movement detection in Insects. Flying Insects are capable of perceiving more complex dynamic patterns and of extracting the features that are relevant to their control of flight and land-

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ing. It has been shown (Goodman, 1960, 1964; Braitenberg and Taddei, 1966) that an objects's "expansion" in the Insect's visual field, obtained for example by bringing the object toward the Insect, can evoke the all-or-none landing reaction (the Insect lifts its first pair of legs to both sides of the head and extends the last pair backward, preparing itself to land on the object's surface: Hyzer, 1962); no reaction is obtained with an object's "contraction".

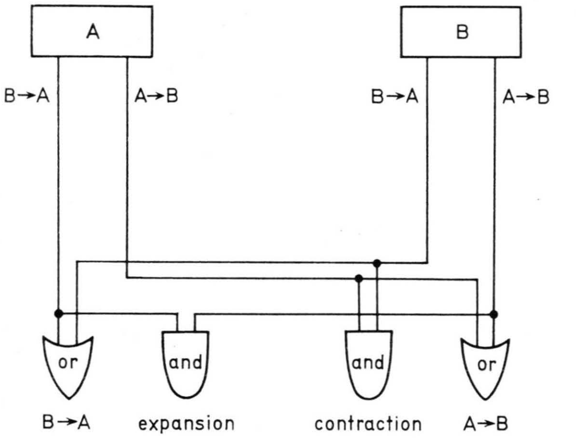

Fig. 1. A model which discriminates among expansion, contraction and lateral displacement.

A model that discriminates among expansion, contraction and lateral displacement in the visual field and that is so capable of control of both optomotor and landing reactions is shown in Fig. 1. If, limiting our consideration to one dimension, we take two Reichardt's movement detectors A and B on a straight line (Fig. 1), the perception of a unidimensional expansion consists in the detection in B of a movement in the direction from A to B and in A of a movement in the direction from B to A; conversely the perception of a unidimensional contraction consists in the detection in A of a movement in the direction from A to B and in B of a movement in the direction from B to A; the perception of a lateral displacement in the direction from A to B (or B to A) consists in the detection in A and/or in B of a movement in the direction from from A to B (or, respectively, B to A). Information for the system schematized in the model may be obtained from knowledge of the landing behaviour in the one-eyed fly. We will deal in the first part of this paper with monocularity and binocularity with respect to landing reaction, and in the second part with the relationships between the landing and optomotor reactions. Information about the way of action of visual stimuli for optomotor and landing reactions can be obtained by considering also their kinematic characteristics. The perceived angular velocity, ω, of the shifting image of a point P (moving with uniform rectilinear motion) on the fly's eye schematized as an hemisphere is a function of the angle, α, formed by the anterior part of the fly's long axis and the straight line joining P to the center of the two eyes at any time (Braitenberg, 1971 a; Taddei and Fernandez, 1972 a, b; Coggshall, 1972). The variation of ω with α, for different moving stimuli (such as the approach of an object to the Insect or vice versa, *i. e.* the "expansion" or "contraction" of the object being its distance from the Insect variable with time, the expansion or contraction or displacement of an object along a straight line the position of which respect to the Insect does not change with time), is given in Figs 2^{+}, 2^{++}, 2^{+++}.

Methods

Specimens of *Musca domestica* L. prepared in three ways have been used. 1. Two-eyed flies, with the head fixed in respect to the thorax by means of a bridge glued to the head and the thorax (Taddei and Fernandez, 1967), flying at a fixed spatial point. 2. One-eyed flies, head-thorax fixed, flying at a fixed spatial point, prepared by the following techniques: a. Covering the fly's eye with black wax, either covering also the three ocelli or leaving them uncovered; b. placing a cone of black paper on the fly's eye, glued with black wax and resin; c. surgically removing the fly's eye with a vibrating blade; generally the eye was cut off at the level of the second ganglium; in some cases the cornea of some ommatidia in peripheral zones remained attached to the skin, but separated from the lower nervous channels; the hemorrage was stopped by a small drop of glycerin; during the surgical operation, the fly was anaesthetized by vapours of ethyl ether. The experiments were performed several hours after the preparation of the flies, in order to permit their adaptation to monocular vision. 3. Two-eyed and one-eyed flies, head-thorax fixed, suspended by a 3.5 cm hair, *i. e.* free to fly in all directions.

The landing reaction was obtained by the following methods: A. Moving an object toward the fly or the fly toward an object, provoking in such a way both the perception of the movement of the periphery of the object relative to the background (and perceived ω's of all object's points as in Fig. 2^+ A) and the perception of a variation of the total light flux in the visual field, B. simulating the approach of an object without varying the total light flux by using a circular expanding pattern (see Fig. 2^+ B), *i. e.* by rotating a disk painted with white and black spirals and producing the movement of white and black wavefronts in the radial directions (Taddei and Fernandez, 1967, 1972 a), C. only diminishing the total light flux.

A stimulus will be said more effective, also in the case of the landing (as of each all-or-none) reaction, if it evokes the reaction under a greater number of experimental conditions.

Monocular and Binocular Vision

It was established (Goodman, 1960, with A., C. methods) that it is sufficient for a fly to have only one eye to land, *i. e.* that the landing reaction mechanism dees not depend on binocular vision. This finding is consistent with findings on optomotor reaction (Fermi and Reichardt, 1963; Götz, 1968). We confirmed Goodman's finding evoking landing reaction of monocular flies also by B. method.

Experiments were then performed, in which the reaction of the flies was evoked by moving a small vertical stick towards the flying fly from several directions. No difference in the behaviour of a binocular fly was observed if the stick was moved from the front or from the side of the fly. Instead, if monocular flies were used (30 were prepared in way 2 a, 30 in 2 b, 40 in 2 c), the reactions observed were as follows: If the object moves towards the fly α. from the side of the blind eye up to about 20° of the fly's plane of bilateral symmetry, there is no reaction; β. between -20° and $+20^\circ$ in front of the fly, there is reaction only or predominantly with the legs ipsilateral to the seeing eye; γ. over 20° of the fly's plane of bilateral symmetry, from the side of the seeing eye, the identical stimulus produces reaction with the legs of both sides. Since the fields of superposed vision of the two eyes nearly coincides with the zone in which an approaching object elicits a reaction of only the ipsilateral legs, the following tentative conclusions may be drown: if the fly sees the approaching object in the visual field of the only intact eye, *i. e.*, the object does not appear in the field of superposed vision of the intact eye, but only in its lateral vision field, it reacts with

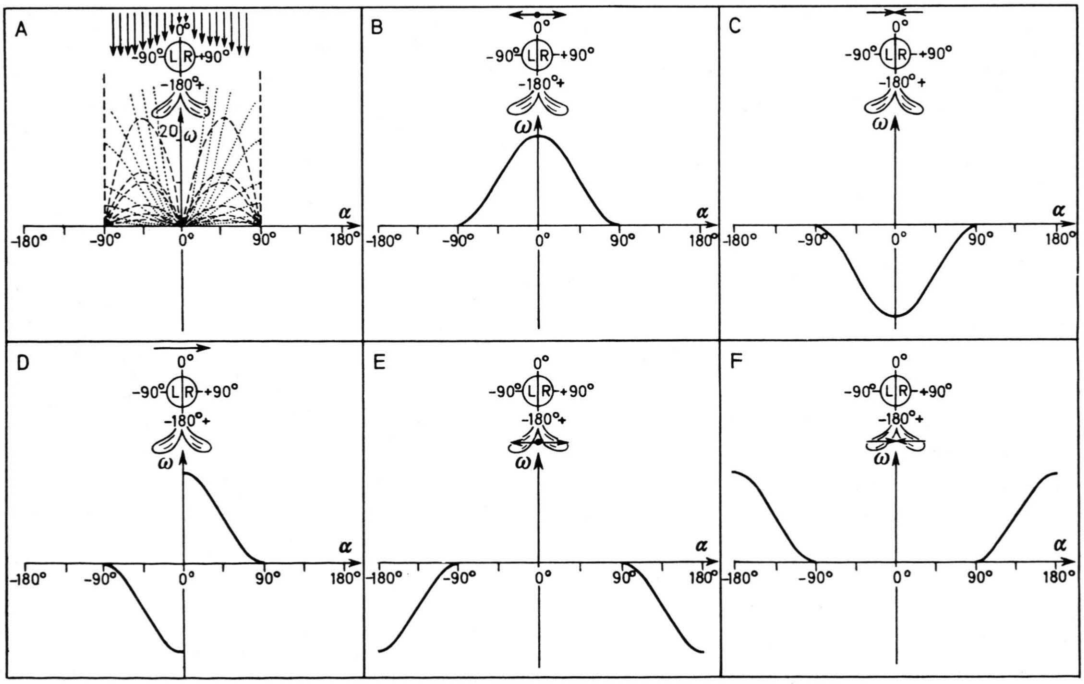

Fig. 2^+

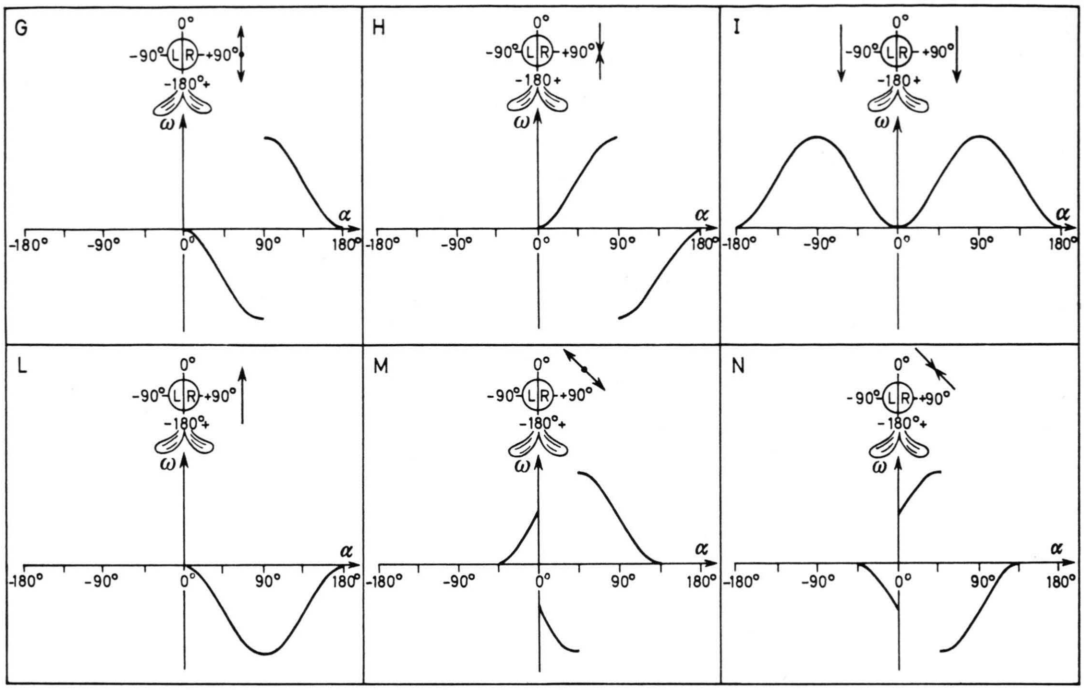

Fig. 2⁺⁺

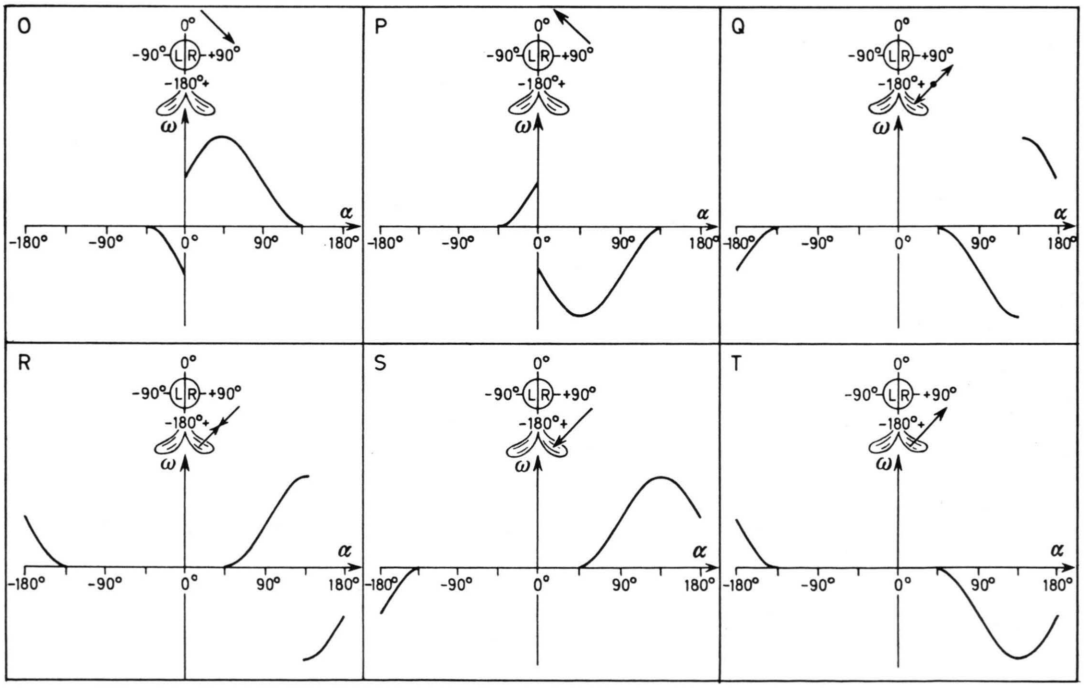

Fig. 2⁺⁺⁺

the legs of both sides; if instead the monocular fly sees the approaching object in the visual field of both the functional eye and the blind one, *i. e.*, in the field of superimposed vision of the intact eye, it reacts only, or higher, or faster with the ipsilateral legs. We may than propose that there may be separate mechanisms mediating landing reaction through stimulation in the single visual zone and in the double zone: Visual stimulus in the single visual field of one eye evokes reaction with the legs of both sides; visual stimulus in the superimposed visual field of one eye evokes reaction only with the legs ipsilateral to that eye (Fig. 3). The same values ±20° are the limit ones at which, in spontaneous fixation of elementary patterns by *Musca*, correspond the highest absolute values of the resultant torque signal which, in closed loop situation, is responsible for the stripe transport into the position of fixation (Reichardt, 1973).

Some confirmation of differences between effects of stimulation in the single and in the double vision field is obtained from further experiments on landing reaction:

a. Testing the isotropy of the visual field using a unidimensional expansion as the stimulus in front of the fly's head, it was found that, with normal binocular flies, the expansion in the vertical direction (*i. e.* stimulus entirely included in the double-zone of vision) has the greatest efficiency for evoking the landing reaction (Fig. 4 a) (Fernandez and Taddei, 1970). This test was repeated with one-eyed flies, and the result was that the greatest

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Figs 2^{+}, 2^{++}, 2^{+++}. Variation of the perceived angular velocity, ω, of the shifting image of a point P (moving with uniform rectilinear motion on any plane containing the fly's long axis) on the fly's eye (schematized as an hemisphere) as a function of the angle, α, formed by the anterior part of the fly's long axis and the straight line joining P to the center of the two eyes at any time t.

$$\omega = \frac{\pm v}{r} \cos^2 \alpha(t) - \frac{\pm w}{s} \sin^2 \alpha(t)$$
$$= \frac{\pm v}{r_0 \pm w\,t} \cos^2 \arctan \frac{s_0 \pm v\,t}{r_0 \pm w\,t}$$
$$- \frac{\pm w}{s_0 \pm v\,t} \sin^2 \arctan \frac{s_0 \pm v\,t}{r_0 \pm w\,t}\,.$$

r = Distance of P to the perpendicular of the fly's long axis on the eyes center at time t on the plane contaning P and the long axis. r_0 = The same distance at time t_0. s = Distance of P to the fly's long axis at time t. s_0 = The same distance at time t_0. v = Velocity along a direction normal to the fly's long axis. w = Velocity along a direction parallel to the fly's long axis. α is considered positive (from 0° to 180°) for the right eye and negative (from 0° to −180°) for the left eye. ω is considered positive for a movement of the image of P in the antero-posterior direction. The arrows representing the movements of P must be considered infinite in one or both directions. For every single diagram (except A), each of the infinite isocrones is represented by a point of the drawn curve, and all these points are aligned along the curve itself of the considered diagram. If, instead of a moving P, a sucession of points P move along the same line (as in our moving visual stimuli of Method B), the curves of all P's coincide with the curve drawn for one P, and the curve considered as the alignement of all the isocrones of a P represents also the superposition of all curves considered as the alignement of the isocrones of all P's. To confront the kinematic characteristics of the situations of different visual stimuli one must consider the variation of the isocrones for each situation, as they represent the variation in time of the perception at level of ommatidia. A represents the approach of 19 P's in front of the fly until the −90· +90° axis is reached. All P's are aligned along a line perpendicular to the line of motion, and 18 P's are placed symmetrically respect to the fly's lnog axis. The situation schematizes the natural landing stimulus. $w = 100$. $r_0 = 200$. The pointed curves are related to different moving P's with s = 0.5, 1, 2, 3.5, 5, 10, 20, 50, 100 (the s are not represented in scale in the drawing of the schematized fly) respectively from the top to the bottom. The curve of the P with $s = 0$ corresponds to $\omega = 0$. The broken line curves are the isocrones, each one representing the perceived ω's of all infinite points P of an infinite unidimensional object at a given time t; $t = 2$ (vertical line, 1.98, 1.96, 1.95, 1.9, 1.8, 1.5, 1 respectively from top to bottom; the shape of the t = const. curves is comparable with that of arcs of parabola, with vertical axis and chord extension of 90° on the α axis, which, in first rough approximation, coincide with the expansion into power series of $\sin^2 2\,\alpha$ curves. Note that the ommatidia that first perceive an ω of a given value are those at ±45°, *i. e.* the P that at a given t passes in front of the ommatidium at +45° or −45° is the P for which at that t the perceived ω is maximum; such a P, with increasing t, is a P always closer to the fly's long axis. Note also that the values of the perceived ω of a moving P with $\alpha = 0$ are not all $= 0$, because of the perception of the motion of such P due to the binocular vision that is not considered in present schematization of the two eyes as a sphere. B to T represent the movement of 1 or 2 P's along directions differently oriented with respect to the fly's head. Note that, due to the binocular vision, there are more negative ω's in G and more positive ω's in H than those showed by the diagram. Note also that, having tested each situation in its power to elicit landing reaction, as it can be seen in the final discussion, the results prove that (Taddei and Fernandez, 1972 a, b) situations schematized in B, *I*, one half of *I* with respect to the ω axis, M, O, R, S elicit landing reaction; for some of them particular conditions have to be imposed; situations C, E, L, N, P, Q, T do not elicit landing reaction; situations D, F, G, H are the limit situations, each one for a different reason, for which landing reaction not even with the imposition of particular conditions can be elicited; it is known that situations D, O, P, L, the mirror image of L with respect to the α axis, and — strongerly — L plus its mirror image with respect to the α and ω axes can elicit optomotor reaction; during classic elicitation of optomotor reaction with a rotating striped cilinder, ω = const. for all α with sign opposite for the two eyes; situation 0 plus its mirror image with respect to the ω axis (or P, plus idem) gives the zero value of the optomotor thrust reaction to bilateral progressive (or regressive) motion (Götz, 1968).

It is obvious that, when considering striped moving patterns and not only moving points, the value of the contrast frequency (ω/λ = ratio of perceived angular velocity to perceived wavelength of striped pattern), that, in the case of the optomotor response, is the response determining parameter, does not change with α; the simpler ω instead of ω/λ has been used here because nothing is charged with regard to the extreme values of the abscissa (= amount of stimulated ommatidia) and to the sign of the ordinate (positive or negative respectively for antero-posterior or postero-anterior movements).

efficiency is obtained by expansion in the horizontal direction, thus demonstrating that only binocular vision causes the increased efficiency of the vertical expansion seen in the zone of double vision, and that in monocular vision the double-vision zone has less efficiency to elicit landing reaction (Fig. 4 b). This situation, schematized in Fig. 5, shows that, if both eyes are used, the predominant information is carried from the zone of double vision of each eye, nevertheless two channels of information (see page 586) run from the zone of single vision to both ipsilateral and contralateral effectors (experiment of Fig. 4 a); but that, if only one eye is used, the predominant information is carried from the zone of single vision to both ipsilateral and contralateral effectors (experiments of Fig. 4 b). These results may be interpreted as a proof that the effect of the integration of the stimuli all over the visual field is not irrespective of the position of the stimuli in the visual field but depends on the position of the stimuli in the zone of single or of double vision (see also Eckert, 1970; Wehner, 1972). On the other hand, the zone of double vision is of particular importance for an Insect while binocular vision allows an animal to estimate the distance and depth of objects and is highly developed as in predatory Insects like *Mantins* as in rapidly moving ones like Diptera (Mazokhin-Porshnyakov, 1969); there is also evidence that *Musca* is able to distinguish three-dimensional objects from two-dimensional figures (Vogel, 1954, 1957).

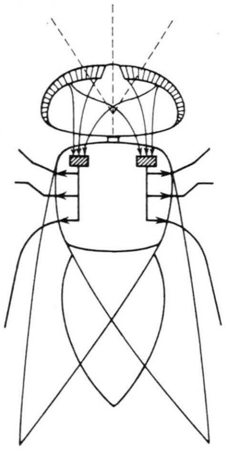


Fig. 3. Different mechanisms for single and for double vision zones.

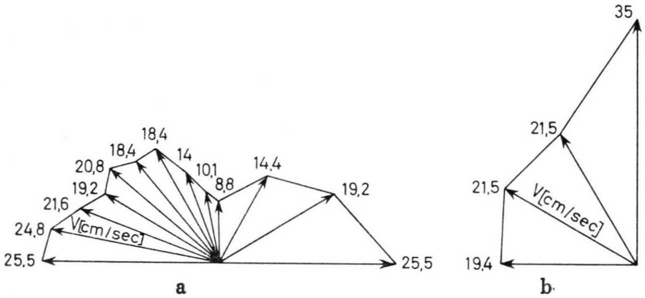
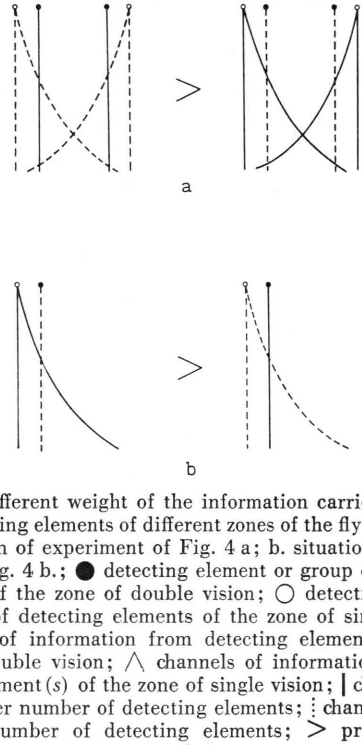


Fig. 4. Anisotropy of the vilual field, a. of a two-eyed fly, b. of a one-eyed fly.

The stimulus is a pattern "expanding" only in the direction of its length and formed by white and black moving stripes normal to the "expansion" direction; the fly is in front to the pattern center; the pattern can be presented in different positions on a vertical plane. V = velocity [cm/sec] of the "expansion" of the pattern necessary to produce landing reaction in the fly; length of the stimulating pattern, 30 cm; width of the pattern, 3 mm; spatial period of the white and black striped pattern, 8 cm; fly-stimulus distance, 9 cm in a., 5 cm in b.



a

b

Fig. 5. Different weight of the information carried from detecting elements of different zones of the fly eye.

a. Situation of experiment of Fig. 4 a; b. situation of experiment of Fig. 4 b.; ● detecting element or group of detecting elements of the zone of double vision; ○ detecting element or group of detecting elements of the zone of single vision; | channel of information from detecting element(*s*) of the zone of double vision; /\ channels of information from detecting element(*s*) of the zone of single vision; | channel used by a greater number of detecting elements; ⁞ channel used by a lower number of detecting elements; > predominancy symbol.

b. Testing the dependence of the reaction on the direction of stimulus presentation by means of a circular expanding pattern (Method B), it has been found that the stimulus presented in front of the fly (*i. e.* in the double zone of the vision) is most efficient and becomes practically inefficient if presented (always on a vertical plane) on the side of the fly parallel to the fly's long axis (Taddei and

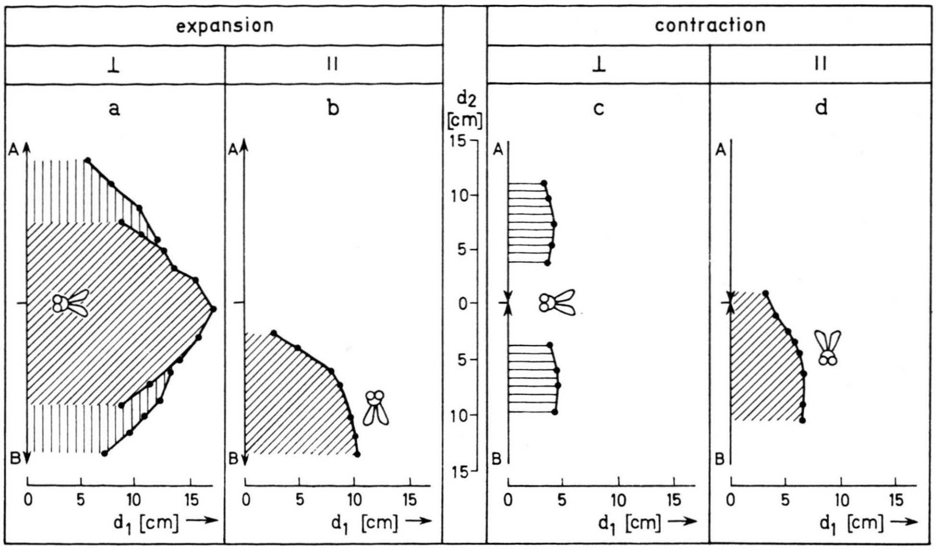


Fig. 6. Zones in which the fly reacts to a circular "expanding" or "contracting" pattern formed by white and black moving circular stripes, with the fly being perepndicular or parallel to the pattern: ▨ Zones of reaction along a horizontal diameter of the stimulatino pattern; ▤ and ▥ zones of reaction more evident if the fly faces respectively the lower or the upper half of the stimulating pattern (independently of the fact that the spirals forming the stripes — see Method B — are painted clockwise or counterclockwise).
AB = Horizontal section of the stimulating pattern plane; d_1 = distance [cm] from the pattern surface; d_2 = distance [cm] from the pattern centre; velocity of the moving pattern along a radius, ±61 cm/sec; spatial period of the white and black striped pattern along a radius, 8 cm. Note that in c., if one oye is blind, the zones of reaction reduce to only those on the side of the blind eye. The zones of more evident reaction if the fly faces the lower part of an "expanding" disk or the upper part of a "contracting" one could indicate a higher weight of the informations carried by the fronto-ventral part of the eye, which is normally the part more stimulated during descending flight in order to land.

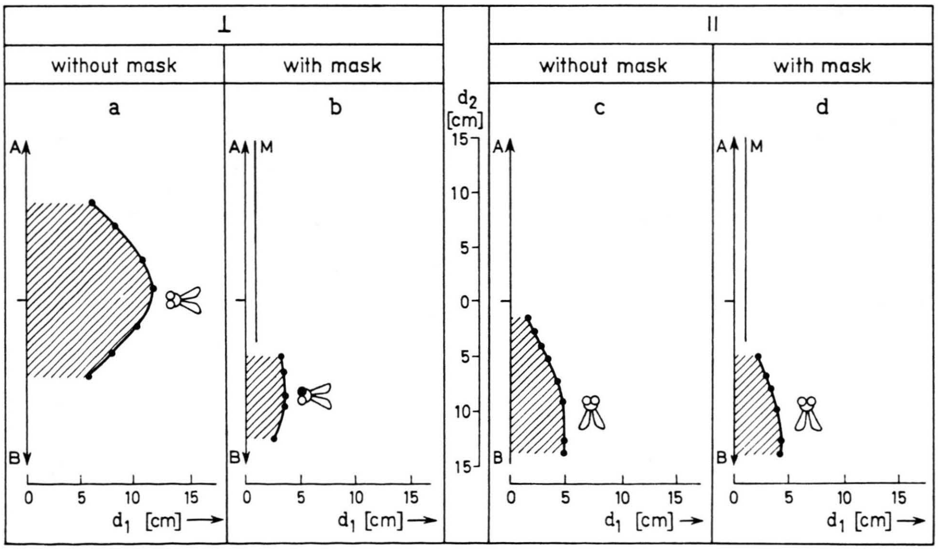


Fig. 7. Zones ▨ in which the fly reacts to a stimulus consisting in a pattern which "expands" only in the horizontal direction and is formed by white and black vertical moving stripes, with the fly being perpendicular or parallel to the pattern, both by covering or uncovering more than half the stimulus with a mask M. AB = Horizontal section of the stimulating pattern plane; d_1 = distance [cm] from the pattern surface; d_2 = distance [cm] from the pattern centre; velocity of the mowing pattern, 61 cm/sec; spatial period of the white and black striped pattern, 8 cm; vertical width of the stimulating pattern 2 cm. Note that in b., in the case in which the stimulating pattern be "contracting", the same zone of reaction is obtained if the fly has the left instead of the right eye blind; with a two-eyed fly (situation of Fig. 2^+ D), it is more problematic to obtain the reaction: The fly reacts only briefly, or must be rotated of few degrees towards the centre or the periphery of the disk (respectively if the pattern is "expanding" or "contracting").

Fernandez, 1967). This result agrees with the decrease of efficiency of a narrow optomotor stimulus as it deviates in horizontal directions from the frontal presentation to the fly (Eckert, 1970). This statement has been now found valid also if the axis of the stimulating plane is rotated on a plane different from the horizontal one. The experiments were repeated for the two extreme values of this test, the fly parallel and perpendicular to the stimulus plane, and in both cases under the following conditions: With one-eyed flies prepared in the second way and with two-eyed flies prepared in the first way; by covering or uncovering part of the stimulus with a mask until it was no longer an expansion but a lateral displacement (Fernandez and Taddei, 1970); by using a circular or a unidimensional (both vertical or horizontal) expansion as stimulus; with a pattern in expansion or in contraction; in all combinations of these conditions by testing the fly's landing reaction also in zones distant from the axis of the stimulating disk. The data, for a two-eyed fly tested with a circular stimulus, both in expansion and in contraction, are shown in Fig. 6, for a two-eyed fly tested with a unidimensional horizontal expanding stimulus, both by covering or uncovering more than half of the stimulus, are shown in Fig. 7. The results do not change qualitatively, when a one-eyed fly was tested or part of the stimulus was covered, unless otherwise stated in the legend of the two figures. The maximum reaction (maximum fly-stimulus distance) in Figs 6 a and 7 a and the minimum in Figs 6 b and 7 c were obtained at the centre of the stimulating disk and are consistent with previous data (Taddei and Fernandez, 1967). The results of experiments repeated with horizontal and vertical unidimensional expanding patterns are consistent with the data of Fig. 4 (in all cases there was greater efficiency of vertical unidimensional stimulus for two-eyed flies, and of horizontal for one-eyed flies).

The two types of reaction evoked by stimuli in the single vision zone or in the double zone are shown in the model described in Fig. 3, in which the lines does not represent axons but pathways. In each eye, a direct chanel of information runs from the zone of double vision to the ipsilateral effectors; on the other hand from the single vision field two direct channels run, one to the ipsilateral effectors and the other to the contralateral effectors. This arrangement may represent an economy of fibres from movement detectors of the double vision field, or may prevent double weighting of the information coming from this same zone. A typical case of information coming from this zone occurs when a flying fly sees wit both eyes a small object that lies in the direction of flight and that the fly is approching in order to land on it. This agrees with recent experimental work on the visual system of Insect in anatomy (Satija, 1958 on *Locusta*, quoted also in Bullock and Horridge, 1965), electrophysiology (Suga and Katsuki, 1962 on Orthoptera; Horridge *et al.*, 1965 on *Locusta;* Blest and Collett, 1965 on Lepidoptera; Collett and Blest, 1966 and Collett, 1970, 1971 on *Sphinx ligustri;* Bishop, Keehn and McCann, 1968 and McCann and Dill, 1969 on *Calliphora* and *Musca;* Kaiser and Bilhop, 1970 on the honeybee) and behaviour (Götz, 1968, 1969 on *Drosophila* and *Musca*); that work has demonstrated the existence of contralateral and ipssilateral fibres running from the optic lobes to the ventral chord as well as the existence of various kinds of interneurons that detect motion in preferred or non-preferred directions, all of these interneurons having monocular or binocular visual fields, and responding to ipsilateral or contralateral stimuli.

Monocular flies were also tested by the approach of a little vertical stick after the spatial relationships between receptors and effectors were exchanged by a 180° inversion of the position of the fly's head, as was done by Mittelstaedt, 1949 with *Eristalis,* rotating it around the animal's antero-posterior axis and fixing it in such position. Experiments showed that almost all of the flies whose heads had been inverted failed to fly and consequently to react. Of those few flies which did fly most did not react, and of those very few which did react almost all did so with all six legs regardless of the stimulus direction. The few remaining reacted to a stimulus in the superposed visual field only with the three legs with which the non-inverted head monocular flies react; of this last group a few flies continued to react only with those three legs if tested during a period of 24 hours. However most of the three legs reacting flies exhibited the following performance: During successive stimuli to landing the reaction showed a pattern in which a three legs response was followed after about 20 sec by a six legs response; after a half hour absence of stimulation the three legs then six legs response pattern was identically presented and this sequence was reproducible for a 24 hours period. Although the number of flies showing this pattern of response was extremely small, we have reported these findings because of the reproducibility and constancy of the phenomenon. We may then state that, in general, flies react to a stimulus in the superposed vision field with the three legs of the side of the seeing eye and that under the experimental condition of head inversion almost all of them correct their response by adding the response of the other three legs after a variable period, probably on the basis of proprioceptive information.

Relationships between Landing and Optomotor Reactions

To analyse these relationships, it would be valuable to know whether, and under which conditions, stimuli adequate to elicit optomotor reaction can be used to provoque landing reaction. During previous experiments we observed that on same occasions a lateral displacement of an object in the visual field of the fly is adequate to elicit the landing reaction. This phenomenon was observed during experiments reported in Figs 6 and 7 when the conditions were such that the fly was not able to see a complete expansion and still reacted; these conditions were attained in Figs 6 a, 7 a, 7 c when the fly was tested in a zone distant from the center of the stimulating pattern and close to the pattern surface being so unable to see more than one half of the pattern; in Figs 6 a and 6 b when the experiment was repeated with a mask covering more than one half of the disk; in Figs 6 a and 6 d; in a more precise sense, due to the unidimensionality of the stimulating surface, in Figs 7 b and 7 d.

It is to be noted that there are two conditions for a lateral displacement to be stimulating for landing: 1. It must have a higher intensity than an expansion stimulus (see the shorter fly-stimulus distance required in Figs 6 b, 6 c, 6 d with respect to 6 a, and – more properly due to the unidimensionality of the stimulus – in Fig. 7 b with a two-eyed fly, 7 c, 7 d with respect to 7 a, indicating that situation of Fig. 2^{+} B is a better stimulus for landing than that of half of Fig. 2^{++} I with respect to the ω axis), *i. e.* the threshold for landing evoked by a lateral displacement in the visual field is higher than the threshold for landing evoked by an expansion; 2. the position of the projection of the fly on the plane in which the stimulating pattern lies must fall well within the pattern (Figs 7 b and d). It was also observed that a fly presenting landing reaction to a stimulus, consisting of a circular expansion in all directions over a vertical plane, no longer reacted when the stimulus was changed to a lateral displacement at least in the horizontal direction by covering with a mask more than half of the stimulus with respect to its vertical diameter, if all other parameters did not change (Fernandez and Taddei, 1970); if now, repeating the experiment, the appropriate conditions for landing are imposed (by increasing the speed of expansion in the radial direction, or by decreasing the fly-stimulus distance, *i. e.* in both cases by increasing the perceived speed of expansion, or by shifting the fly over the stimulating area) after the expanding stimulus was changed in a lateral displacement stimulus along the horizontal direction, the fly reacts. In this experiment as in many situations of experiments of the first part of the present paper, the number of ommatidia stimulated was higher when the stimulus was an expansion, due to the different area of the stimulus, being all other parameters unchanged, and, as it is known (Goodman, 1960) that the efficiency of a landing stimulus is proportional to the number of ommatidia stimulated, this fact could give the reason of the necessity for a lateral displacement stimulus to have a higher intensity in order to evoke the landing reaction. But, repeating Figs 7 a and 7 d experiments having care to have a constant lenght (12 cm) of the unidimensional stimulus, the maximum fly-stimulus distance allowed for Fig. 7 d experiment (situation of Fig. 2^{++} one half of I with respect to the ω axis) is always below that allowed for Fig. 7 a experiment (situation of Fig. 2^{+} B). In addition it was noted that, moving at constant velocity two vertical sticks along a horizontal direction normal to the fly's long axis and at a definite distance d from the fly, one stick from this axis to the left and the other from the axis to the right in order to reproduce situation of Fig. 2^{+} B, the fly reacted till, increasing d, a maximum d was reached; if then only one stick was moved at the same velocity along a direction normal to the normal to the fly's long axis in the centre of the fly's head from front to back and for the same extension of the movement of the two above sticks (situation of Fig. 2^{++} one haf of I with respect to the ω axis), the maximum d allowed was much lower, indicating that the threshold for landing is higher when a lateral displacement instead of an expansion is used as a stimulus. This statement does not work if two lateral displacements over the two eyes are used instead of one; in fact, if the last reported experiment is repeated with two sticks moved on the sides of the fly (situation of Fig. 2^{++} I), the maximum *d* allowed is higher than that reached with one stick and of the same value than that reached with two sticks "expanding" in front of the fly. In addition, a subthreshold *d* of a vertical stick moving from front to back on the side of one eye became a *d* adequate for evoking landing reaction if on the side of the other eye is presented a series of black and white stripes moving from front to back at a subthreshold perceived velocity.

A third condition for a lateral displacement in the visual field of an eye to be stimulating for landing, that comes from Taddei and Fernandez, 1971, 1972 b, and from the experiments reported above, is that the perceived movement of the lateral displacement occurs from the front to the back of the fly (in agreement with Coggshall 1971, 1972 data on *Oncopeltus*). In Figs 6 b, 7 c, 7 d, fly parallel to the stimulus plane with an expanding pattern, the fly reacts only if facing the axis of the disk while in Fig. 6 d, fly parallel to the disk with a contracting pattern, the fly reacts only if facing the periphery of the disk, *i. e.* in all these cases the waves of black and white stripes arrived towards the fly from the side, in the direction from the front towards the side of the eye facing the stimulus plane; in experiments of Figs 6 b and 6 d repeated with monocular flies, the seeing eye was facing the stimulus plane. The content of this condition seems to be connected with the phenomenon of fixation of isolated markings on a homogeneous background by flying *Musca* (Reichardt and Wenking, 1969; Reichardt, 1973). In fact, both deal with difference in efficiency of forward (from the back to the front) and backward (from the front to the back) stimuli in evoking an optomotor reaction. The statement containing this third condition is corroborated also by the following experiments all performed with monocular flies: 1. Under unchanging environmental conditions a fly was rotated on its dorso-ventral axis and it presented landing reaction only if the rotation was clockwise (or counterclockwise) if the right eye (or respectively the left eye) was covered; 2. if experiment 1) was repeated after the position of the fly's head was inverted 180°, the rotation of the fly needed to be counterclockwise (or clockwise) if the right eye (or respectively the left eye) was covered; 3. if a little vertical stick is displaced horizontally in the visual field of the seeing eye always at the same distance from it, a landing reaction is elicited if the object is presented moving from the front towards the side of the seeing eye and not if in the opposite direction; 4. as a landing reaction of a binocular fly caused by a decrease of the total light flux is stopped by the presentation of a contracting pattern (Taddei and Fernandez, 1967, 1971, 1973), also a landing reaction of a monocular fly caused by the same stimulus is stopped by a lateral displacement of an object seen moving in front of the fly toward the side of the blind eye, but is not stopped if the object is moving in the opposite direction, *i. e.* as a lateral displacement satisfying the third condition has the same effect of an expanding stimulus, a lateral displacement satisfying the inverse of the third condition has the same effect of a contracting stimulus. The third condition is verified also if the stimulating moving wavefronts are presented under different angles around the fly's eyes on planes different from the horizontal one (in agreement with Coggshall 1971, 1972 data on *Oncopeltus*). The third condition clarifies that, in our laboratory conditions, the two components in opposite directions of a perceived horizontal unidimensional expansion are utilized each one from only one eye in order to evoke landing reaction, *i. e.* the two schematized Reichardt's movement detectors of Fig. 1 necessary for the perception of a unidimensional expansion must be in different eyes if all the expansion is expected to be stimulating for landing, although naturally nothing can be said against the functional existence of these two movement detectors in only one eye if utilized for other purposes or in other experimental conditions.

A fourth condition for a lateral displacement in the visual field, or in general for a moving stimulus, to be adequate to elicit landing reaction is that the useful perceived ω's (perceived in the antero-posterior direction of the eye) are perceived by the more anterior ommatidia, anyhow by ommatidia the axis of which forms an angle smaller than 90° with the fly's long axis. In fact a unidimensional contracting pattern presented to the latero-posterior part of the fly's eye (that produces the situation of Fig. 2^{+++} R) is still adequate to evoke landing reaction, although this occurs only occasionally, the reaction lasts only for a short time, the fly-stimulus distance must be much lesser than that still adequate if a unidimensional expanding pattern (with the same velocity of the white and black stripes) is presented to the latero-anterior part of the eye (situation of Fig. 2^{+++} M). This statement is valid also if the stimulus is perceived along eye's meridians (with respect to the fly's long axis) different from that lying in the horizontal plane. A contracting circular pattern presented on a vertical plane exactly in front of the back of the fly (situation of Fig. 2^{+} F), although provoking the perception of all ω's in the antero-posterior direction of the eye, does not evoke landing reaction, because part of the stimulus falls on the fly's blind zone and part on too posterior ommatidia.

Having ascertained that, under particular conditions, the fly shows a landing reaction to a lateral displacement that normally produces optomotor reaction, it would be interesting to know if that happens only because the fly is suspended at a fixed point with the head fixed to the thorax, *i. e.* it is not free to turn itself nor its head to produce an optomotor response. It is also to be investigated if, with the fly free to turn itself, there are at least some intensities of the stimulus that can evoke both landing and optomotor reactions. Then, when experiments of Figs 6 and 7 have been repeated with flies, head-thorax fixed, suspended by a 3.5 cm hair, *i. e.* free to turn themselves, the results were: a. In the cases in which the fly, perpendicular to the stimulating pattern, was tested in front of a zone of an expanding circular pattern different from the pattern's centre where it was expected to show a landing reaction, elicited by a lateral displacement (at least in one direction) in the visual field, it did, and subsequently it showed optomotor reaction, turning itself following the direction of the lateral displacement, ceasing at the same time to present the landing reaction; conversely, during classical experiments on optomotor reaction of flies, also landing reaction has been observed on some occasions (Reichardt's personal communication, 1970); b. if the fly, perpendicular to the stimulating pattern, was tested in front of the centre of a contracting circular pattern that simulates a receding object (Braitenberg and Taddei, 1966), *i. e.* in a zone in which it was expected not to show landing reaction, it displaced itself turning to one side without presentation of landing reaction and subsequently, after a brief presentation of landing reaction, it displaced itself turning to the other side, and so forth for many times following the direction of the motion of the white and black waves of the side opposite to that toward which it was turning, and oscillating from the situation of Fig. 2^{+++} O through 2^{+} C to the mirror image (respect to the ω axis) of 2^{+++} O and vice versa; if half of the above pattern (right or left side) was covered, the fly turned itself only once towards the covered side without presentation of landing reaction; c. if the fly, perpendicular to the stimulating pattern, was tested exactly in front of the centre of an expanding circular pattern that simulated and approaching object, it showed a landing reaction and immediately turned back and quickly flew away from the stimulating disk.

If then the fly, still fixed by the hair, is stimulated while standing on a base, with the stimulus of case a. it walks in the same direction as the motion of the wave front, while with the stimulus of case c. it takes off and goes quickly flying away from the stimulating disk. This last finding, that is quite similar to results reported in Goodman, 1960, clarifies that under laboratory conditions (an object approaching the fixed Insect rather than the Insect freely approaching a fixed object) landing reaction can also be provoked by an escape stimulus, *i. e.* by a high speed "expansion" perceived in the frontal direction and not expected by the Insect.

If then the fly is flying at velocity w towards an object on a background, in order to land on it, it perceives (in addition to the differences at each time among all the ω's of each moving discriminable point of the object and of the background that vary with continuity: See curves at $t=$ const. of Fig. 2^{+} A) a discontinuity in the differences between the ω of the last point of the periphery of the object and the ω of the first seen point of the background, cause the fact that the r_0's of object and of background differ and the fact that for some points of the background with some s's no ω is perceived because these points are hidden by the object; we may say also that such discontinuity increases in time cause the new points of the background hidden by the object. If then the object begins to move toward the fly at velocity w_{ob}, the fly receives an escape stimulus that consists in a not expected abrupt increase of the above discontinuity at the moment at which the object begins to move, and in a not expected increase in time of the above said expected increase in time of the discontinuity during all the motion of the object (Taddei and Fernandez, 1972 a, b).

Analogously, when the fly is freely approaching at velocity w a not rotating disk with painted spirals, it perceives ω's of the disk distributed as in Fig. 2^+ A and a discontinuity respect to the distribution of the ω's of the background as above stated; if, instead, the disk is "expanding" as it rotates, the superposition of the not expected perceived ω's as in Fig. 2^+ B could be considered an artificial escape stimulus.

If the fly, moving the wings as to produce a flight velocity w, is fixed ($w = 0$), the perceived ω's of all objects and background are $= 0$ on the contrary of the fly's expection, and an object approaching at a not expected $w_{\text{ob}} \neq \left\{\begin{smallmatrix}0\\ w\end{smallmatrix}\right.$ results in an escape stimulus not followed by an escape reaction; analogously, for a fly flying in the same fixed situation, the not expected perceived ω's of an expanding not approaching pattern could also be considered an artificial escape stimulus.

Considering now the results of experiments on the behaviour of the fly in consequence of the natural landing stimulus and of other artificial visual stimuli and the kinematic characteristics of all of them (which are represented by the isocrones of the respective curves of ω in function of α, assuming ω positive for a movement perceived in the antero-posterior direction: See Figs 2^+, 2^{++}, 2^{+++}), we can conclude saying that (Taddei and Fernandez, 1972 a, b): 1. The isocrones of the natural landing stimulus have the shape of $\sin^2 2\,\alpha$ over a fly's visual field of $\pi/2$ from the fly's long axis, with the ω's always positive; 2. the main condition for an artificial stimulus to be adequate to elicit landing reaction is that more than 50% of the ω's be positive (D, G, H of above figures are the low limit cases): See the "third condition" at p. 588; 3. the positive ω's must be seen in the anterior part of the eye (F is a low limit case): See "fourth condition" at p. 588; 4. then, the best condition for the landing reaction is attained when the positive ω's are equally distributed on the two eyes (*f. i.*, B, I); 5. if condition 2. is satisfied, it is acceptable that the $\sin^2 2\,\alpha$ curves modifies into $\cos^2 \alpha$ curves (B), or $\sin^2 \alpha$ curves (I), or intermediate cases; 6. it is acceptable also an asymmetric distribution of the ω's on one eye with respect to the distribution on the other eye in what it refers to the value and not to the sign of the ω's, but in this case more limiting conditions are imposed such as the necessity of increasing the stimulus intensity ("first condition": The threshold for one half of I with respect to the ω axis is higher than that for B; see maximum d_1 in Figs 7 a and c) and adequate spatial relationships between fly's eye and stimulus ("second condition"); 7. on the contrary, the more efficient stimulus for optomotor reaction must produce ω's of sign opposite for the two eyes; 8. it is acceptable an asymmetric distribution of the ω's on one eye with respect to the distribution on the other eye in what it refers also to the intensity of the ω's (*f. i.*, one half of I with respect to the ω axis, L) under the imposition of limiting conditions (Fermi and Reichardt, 1963, with one eye); 9. the fact that situations outlined in 6. and 8. can coincide explains the cases in which the same stimulus can produce both landing and optomotor reactions (*f. i.*, one half of I with respect to the ω axis); 10. the different main conditions outlined in 2. and 4. for landing and in 7. for turning optomotor reaction are clearly understandable by considering that: α. For the landing reaction, that is the consequence of a forward motion toward an obstacle, the resultant of the stimulation all over both eyes must be a vector in equilibrium with respect to the bilateral symmetry plane and of the same sense of the motion that naturally produces the reaction; β, for the optomotor reaction, that consist in a turning movement, the resultant of the stimulation must be asymmetric with respect to the bilateral symmetry plane in order to produce a momentum.

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