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Dorsoventral Asymmetry in the Visual Field of the Bee, *Apis mellifica**

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Summary. 1. Bees can be trained to a special orientation α_{tr} of a black-and-white disk (one half black, the other half white; angular diameter 130°), offered on a vertical screen. Different test inclinations α_t of the contrast line between the black and white area of the disk are discriminated from α_{tr} (direction sensitivity curve, Figs. 3 and 4).

2. Insertions of contrasting sectors into the black and white area of the training pattern diminish the reaction frequency to that pattern (W- and B-functions, Figs. 6 and 7). Therefore the direction sensitivity curve can be approximately calculated by means of the B- and W-functions, because a rotation of the black-and-white disk is accompanied by the insertion of a white sector in the previously black area and vice versa (Fig. 5).

3. The effect of inserting contrasting areas in the black-and-white disk is the stronger, the more these insertions are located in the medial lower part of the visual field (Fig. 9, Tables 3 and 4).

4. The results provide strong evidence for the conclusion that the different positions of the visual field are topographically represented in the central nervous system of the bee, and that the middle lower part of the frontal visual field is most decisive for pattern recognition. They do not agree with the classical theory of form perception in insects, which is based on an integration of the stimuli effects all over the visual field, irrespective of their position within the visual field.

Introduction

As deduced from the classical experiments on pattern recognition in bees (Hertz, 1933, 1935; Zerrahn, 1933; Wolf, 1934, 1935; Wolf and Zerrahn-Wolf, 1935; Sakagami, 1956; Schnetter, 1968) insects should discriminate between different geometrical figures only or predominantly by means of the total amount of black and white contours, i.e. by the frequency of intensity changes produced by the pattern at the flying insect's eye. Concerning with optomotor responses Hassenstein (1958) and Götz (1964) have found for the beetle *Chlorophanus viridis* and the fly *Drosophila melanogaster* that the information about the pattern movement is integrated over the whole eye, irrespective of the special region within the visual field, to which the moving stimuli are projected. For pattern recognition, however, some recent experiments performed by training bees (Wehner and Lindauer, 1966; Wehner,

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1967a, b) or recording spontaneous orientation runs of a few other insects (*Schistocerca gregaria*: Wallace, 1958; *Apis mellifica*: Jacobs-Jessen, 1959; *Formica rufa*: Jander and Voss, 1963; Voss, 1967; *Nemobius sylvestris*: Campan and Medioni, 1963; *Drosophila subobscura* and *D. obscura*: Koch, 1967; *Papilio demoleus*: Vaidya, 1969; *Musca domestica*: Reichardt and Wenking, 1969; *Cataglyphis bicolor*: Wehner, 1969; *Carausius morosus*: Jander, 1970) have proved a more complex system of form perception. These experimental data fail to be explained by a mere summation of neuronal responses evoked by illumination changes all over the visual field. One of the most striking results consists in the finding that the direction and—more generally—the position of the stimuli within the visual field is an essential parameter for pattern recognition. This statement is supported by electrophysiological recordings from *Limulus polyphemus* (Snodderly and Barlow, 1970), from the crayfish (Yamaguchi and Wiersma, 1965; Wiersma and Yamaguchi, 1965, 1966, 1967; Woodcock and Goldsmith, 1970) and from some insect species (Horridge, Scholes, Shaw, and Tunstall, 1965; Collet and Blest, 1966; Bishop and Keehn, 1966, 1967; Bishop, Keehn, and McCann, 1968; Swihart, 1968; Horn and Rowell, 1968; McCann and Dill, 1969; Zenkin and Pigarev, 1969; Bishop, 1970; Kaiser and Bishop, 1970; Palka, 1969; McCann and Foster, 1971; Collett, 1970, 1971; Mimura, 1970, 1971), where directionally sensitive units could be found. In studying visual orientation performances in bees we succeeded in obtaining direct evidence for the conclusion that the visual field of the bee must be topologically represented in the central nervous system and that different parts of the visual field are not to the same extent involved in pattern recognition.

Methods

Apparatus. By means of an apparatus previously described (Wehner, 1968) the bees (*Apis mellifica mellifica*) were trained to a special arrangement of black and white areas presented on a vertical screen. Although all other more previous experiments dealing with pattern recognition in bees have been performed with horizontally arranged figures (Schnetter, 1968; Mazokhin-Porshnjakov, 1968, 1969a, b; Weizsäcker, 1970) the vertical screen is most suitable for studying form perception; for using this experimental arrangement the direction and relative position of the patterns within the visual field can be exactly defined. In the experiments described in that presentation we used circular screens with the two halves respectively black and white (pattern contrast $I_w—I_b/2\bar{I}=0.95$). As the bees had to fly to the center of the screens, which were presented within a Plexiglass box at a certain distance from the bee's eye, the angle size of the pattern screen as well as its position in the visual field of the bee could be calculated. In all experiments dealt with here the diameter of the screen was 130°.

Training and Test Procedure. In this apparatus the individually marked bees were first trained to a special inclination of the boundary between the black and white area and then confronted with both the training inclination α_{tr} and a test

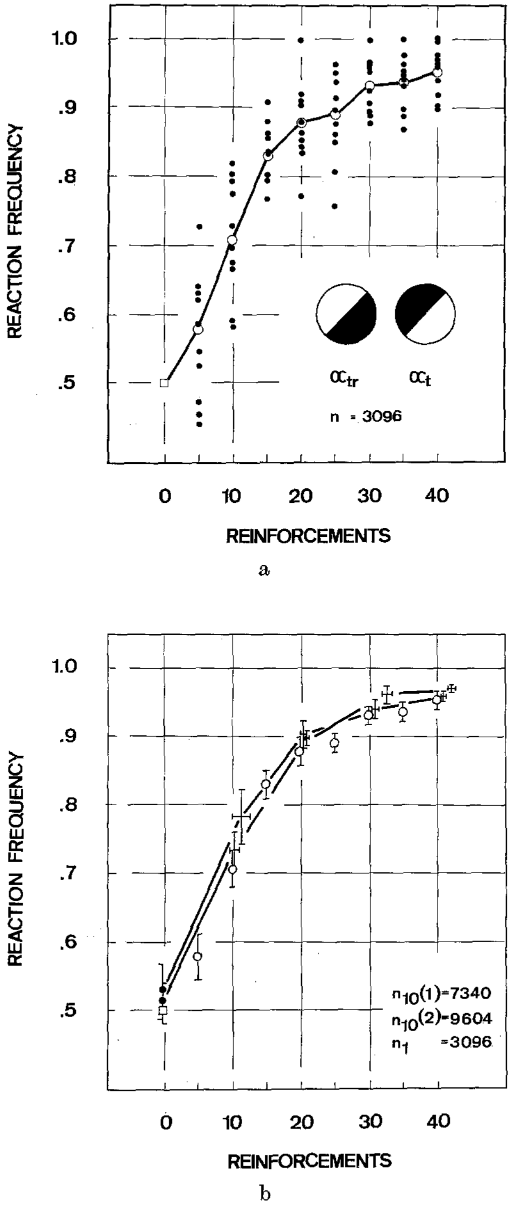


Fig. 1. Learning curves, obtained for 10 individually trained bees (*a*) and groups of 10 simultaneously trained and tested bees (*b*). In *b* the mean values of *a* are graphed for comparison. α_{tr} training pattern; α_t test pattern; reaction frequency $[n(\alpha_{tr})/n(\alpha_{tr}+\alpha_t)]$. In *b* the standard deviations are presented for the reaction frequencies as well as the numbers of reinforcements

inclination α_t varying by $0° \leq \Delta\alpha \leq 180°$ from α_{tr}. These tests for studying the accuracy of visual goniometry were not performed until the previously determined learning curves of the bees had reached a reaction frequency of at least 0.95 for α_{tr}, when $\Delta\alpha = 180°$ was tested (Fig. 1). Curves representing the acquisition and retention of learning are described previously (Wehner, 1967, 1968). In the now following tests, when the constant training and the varying test inclinations were simultaneously presented, the reaction frequency of the bees to α_t was recorded and graphed in relation to the maximal reaction frequency of 50%, which is only valid for $\Delta\alpha = 0°$. As the reaction frequency (*RF*) for α_t is calculated according to the equation $RF = 2n(\alpha_t)/\mathrm{n}(\alpha_{tr} + \alpha_t)$, *RF* varies within the range of $0 \leq RF \leq 1$. The lower the reaction frequency is, the better is the test pattern α_t discriminated from the training pattern α_{tr} (angle-discrimination-function, *A*-function).

The critical tests always consisted in 4 test minutes instantaneously following each other. In these test minutes the position of the test and the training pattern alternatively varied between position 1 and 3 (left and right). During training only one pattern, the training pattern, was presented in the central position of the apparatus (position 2).

During the 4 test minutes no extinction of learning could be proved. On the contrary, minimal reaction frequencies to α_{tr} were always obtained in the first test minute (Fig. 2, Table 1).

In most of the experiments dealt with here groups of 10 ± 2 individually marked bees were used. The same results, however, were obtained by control series performed with single bees. For comparison see the learning curves presented in Fig. 1b.

Statistical Analysis. In all graphs of that presentation the reaction frequencies *RF* are given as mean values of the 4-minutes-tests. As these standardized tests are considered to be experimental units, strongly performed in the same way

Table 1. Reaction frequencies of the 4-minutes-tests (1), of minute 1 and minute 4 (2) as well as of minutes 1 + 2 and minutes 3 + 4 (3). Each value is the mean value of 5 individually tested bees. On the whole, there are no statistically significant differences between the first part and the second part of the test procedure (see *p*-values, calculated by means of 2 × 2 tables). $\alpha_{tr} = 45°$, $\alpha_t = 225°$, $\Sigma N = 3096$

		Reinforcements							
		5	10	15	20	25	30	35	40
(1)	$n(\alpha_{tr})/N$	0.58	0.71	0.83	0.88	0.89	0.93	0.94	0.95
	N	413	480	449	349	422	344	313	326
(2)	$n_1(\alpha_{tr})/n_1$	0.52	0.69	0.78	0.87	0.82	0.91	0.87	0.94
	n_1	126	176	139	113	124	101	87	83
	$n_4(\alpha_{tr})/n_4$	0.68	0.71	0.83	0.83	0.94	0.95	0.95	0.98
	n_4	85	90	112	64	78	77	59	66
	p	*<0.05*	0.70	0.31	0.48	*<0.05*	0.33	0.13	0.17
(3)	$n_{1,2}(\alpha_{tr})/n_{1,2}$	0.57	0.68	0.80	0.88	0.88	0.91	0.93	0.95
	$n_{1,2}$	240	294	220	181	239	184	157	163
	$n_{3,4}(\alpha_{tr})/n_{3,4}$	0.61	0.77	0.86	0.87	0.92	0.93	0.94	0.94
	$n_{3,4}$	173	186	229	168	183	160	156	163
	p	0.42	*<0.05*	0.09	0.95	0.24	0.57	0.84	0.97

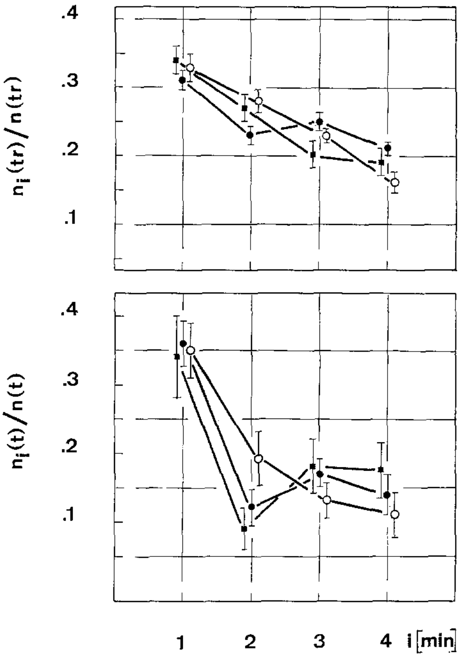


Fig. 2. Distribution of the flights to the training pattern (*tr*; *above*) and to the test pattern (*t*; *below*) during the 4 minutes of one test. The data are presented as proportions of the numbers of flights in the minute $i\,[n_i(tr)$ resp. $n_i(t)]$ to the total numbers of flights $n(tr)$ resp. $n(t)$ during all 4 test minutes. Example of 3 test situations. Each point represents the mean value ± standard deviation of 10 individually tested bees

during all series of experiments, mean values, standard deviations (s) and mean errors of the mean values (s_m) can be calculated from the reaction frequencies of the 4-minutes-tests. Therefore s_m is determined according to

$$s_m = \pm \sqrt{\frac{\Sigma(x_m - x_i)^2}{n(n-1)}}$$

where x_i means the standardized reaction frequency $0 \leq RF \leq 1$ of a 4-minutes-test unit (n=number of test units). For statistical analysis these units are considered as single measurements and the reaction frequencies as the results of these measurements. When one calculates s_m according to

$$s_m = \pm \frac{\sqrt{p \cdot q}}{n}$$

where p means the reaction frequency to $\alpha_{tr}[n(\alpha_{tr})/N]$, q the reaction frequency to $\alpha_t[n(\alpha_t)/N]$ and N the total number of decisions $[N = n(\alpha_{tr} + \alpha_t)]$, much smaller values are obtained for s_m.

From these reaction frequencies stimulatory values of the pattern configurations can be calculated by means of special transformations, f.e. by referring to a probit transformation (Jander, 1968) or an angle transformation $x = \arcsin \sqrt{RF}$ (Wehner, 1968). Here the former one is used. A mingled choice transformation preceeding the probit transformation has only little effect on the reaction frequencies, because the percentage p_n of mingled choices never exceeds $p_n = 0.02$. The natural zero point of the scale of stimulatory values was determined as the probit value $PR_0 = 2.67$ of a white disk presented in front of the white pattern screen of the apparatus (remission spectrum see Fig. 3, p. 327, in Wehner, 1968). In order to receive absolute stimulatory values, PR_0 is subtracted from all probit values, and the differences are standardized according to the maximal difference representing the stimulatory value of the training pattern. A numerical example of the whole procedure is given in Table 2.

Homogeneity between the experiments of one series and differences between two series are tested by using a $2 \times n$ resp. 2×2 table (χ^2-test).

Definitions and Abbreviations. α_{tr}: inclination of the boundary between the black and the white half of the pattern disk during training. The inclination of the contrast line is defined as the direction of that radius of the disk, which is part of the contrast line and leaves the black area to the right, when one looks from the center to the periphery. $\alpha = 0°$ means the horizontal direction with the lower part of the visual field being black. Otherwise, for $\alpha = 180°$ the black area extends to the upper part of the visual field. For the spatial positions of 0°, 90° etc. see Fig. 5.

α_t: inclination of the contrast line confronted with α_{tr} in the critical tests.

$\Delta\alpha$: in the angle discrimination tests (*A-function*), when the black-and-white disk is rotated out of the training position α_{tr}, $\Delta\alpha$ means the difference between the training inclination and the test inclination: $\Delta\alpha = |\alpha_{tr} - \alpha_t|$. (+) counterclockwise rotation, (−) clockwise rotation. When black and white sectors are inserted into the contrasting areas of the disk (*B- and W-functions*), $\Delta\alpha$ represents the angle width of the inserted sector.

Table 2. Calculation of the stimulatory value (ST) of a test pattern from the reaction frequency (RF) to that pattern, f.e. shown for the inserting of black sectors into the white area of the training pattern (●-curve in Fig. 7). $\Delta\alpha$ angle size of the black sector inserted into the white area of the training disk; c.ch. comparative choices, calculated from the reaction frequencies after elimination of the indifferent choices p_n; $\%(\Delta\alpha)_{\text{c.ch.}} = [\%(\Delta\alpha) - 0.5\, p_n]/[100 - p_n]$; $p_n = 2\%$; $PR_0 = 2.67$, probit value of a white disk (no pattern). For further explanations see table of abbreviations (p. 261)

$\Delta\alpha$	n	$\%(\Delta\alpha)$	$RF(\Delta\alpha)$	$\%(\Delta\alpha)_{\text{c.ch.}}$	$PR(\Delta\alpha)$	$PR(\Delta\alpha) - PR_0$	$ST(\Delta\alpha)$
0°	—	50.0	1.00	50.0	5.00	2.33	1.00
20°	627	45.5	0.91	45.4	4.88	2.21	0.95
40°	610	28.2	0.56	27.8	4.41	1.74	0.75
60°	974	22.9	0.46	22.4	4.24	1.57	0.67
80°	744	24.5	0.49	24.0	4.29	1.62	0.70
100°	512	26.8	0.54	26.4	4.37	1.70	0.73
120°	461	28.0	0.56	27.6	4.41	1.74	0.75
140°	786	19.4	0.39	18.8	4.11	1.44	0.62
160°	1111	16.3	0.33	15.6	4.00	1.33	0.57
180°	585	6.9	0.14	6.0	3.45	0.78	0.33

RF: reaction frequency to a special test pattern, when it is confronted with the training pattern; f.e. the reaction frequency to α_t is calculated as $RF(\alpha_t)=2n(\alpha_t)/n(\alpha_{tr}+\alpha_t)$.

PR: probit value.

ST: stimulatory value of a pattern configuration calculated by means of the reaction frequency (*RF*) to the test pattern, an indifferent choice transformation and a probit transformation. After detection of the zero point by determining the reaction frequency to a white disk, the absolute probit values are standardized according to the maximum stimulatory value $ST=1$, which is due to the training pattern.

A-function: angle-discrimination-function (direction sensitivity function), quantitatively describing the decrease of the stimulatory value of the pattern disk, when it is rotated by increasing values of $\Delta\alpha$ out of the training inclination α_{tr}.

B- and *W*-functions: black-function resp. white-function, representing the stimulatory values of those test patterns, which are produced by insertions of differently arranged and differently sized black resp. white sectors into the contrasting areas of the training pattern.

In all these functions (*A*, *B* and *W*) the calibration of the abscissa refers to $\Delta\alpha$ of the test pattern, while the ordinate represents the reaction frequencies (*RF*) to the test patterns resp. the stimulatory values (*ST*) of the test patterns.

Results

I. The Topological Representation of the Visual Field

The A-Function. In the first series of experiments, the results of which are presented in Fig. 3, the boundary between the black and white area of the training pattern was inclined by 45° to the horizontal in such a way that the black half was offered to the lower right and the white one to the upper left of the screen. Using that inclination of the constant training pattern the results obtained are surprising at first view: the reaction frequencies for the varying test patterns α_t representing the accuracy of visual goniometry depend on the direction of rotation. The inclinations α_t are better discriminated from α_{tr} when α_t moves counterclockwise from α_{tr} $(+\Delta\alpha)$ than when it moves in the opposite direction $(-\Delta\alpha)$. The differences between the curves obtained for the two situations are statistically significant with $p<0.001$ (2×2-table, χ^2-test) for 6 out of 8 points.

In a more suitable way the accuracy of goniometry is presented in the direction-sensitivity-diagram of Fig. 4a and compared with the direction sensitivity obtained by testing single black stripes on the circular white screens (Fig. 4b; Wehner, 1968). As half-width of the direction-sensitivity-curve a value of $(\Delta\alpha)_{0.5}=82°$ is measured for the black-and-white disks, but only $(\Delta\alpha)_{0.5}=37°$ for the stripes, indicating a more accurate detection of angle positions by means of black stripes.

The W- and B-Functions. If one wants to detect the stimulus properties being involved in the mechanism of angle discrimination one

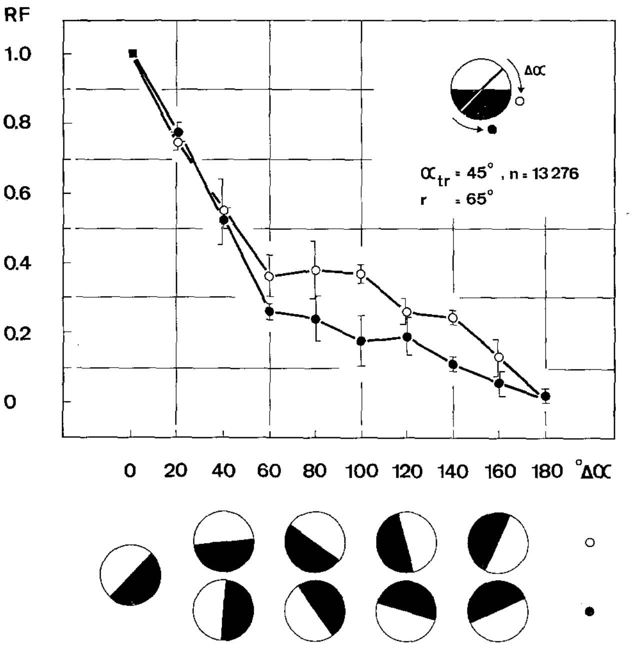


Fig. 3. Direction sensitivity function (*Δ*-function). The reaction frequencies *RF* of the test patterns (*abscissa*), simultaneously presented with the training pattern (α_{tr}), are graphed in relation to $RF = 1.0$ for $\Delta\alpha = 0°$ (α_{tr}). Clockwise (○) and counterclockwise (●) rotation

must first deal with the stimulus alterations during rotation of the pattern disk. According to Fig. 5, the training pattern α_{tr} is converted into a test pattern α_t by special areas becoming black, which were previously white (negative contrast change; upper part of the disk in Fig. 5), and vice versa (positive contrast change; lower part of the disk in Fig. 5). Since we are able to record the effects of both transformations by separately inserting white sectors (*W*-function) and black sectors (*B*-function) in the contrasting semi-circles of the training pattern, both effects due for a particular α_t-pattern can be tested alone. As previous studies performed with black stripes on a white screen have already shown (summary in Wehner, 1967a, 1969), the position of black and white areas within the visual field is most decisive for the discrimination between different inclined patterns, when these patterns are offered on a vertical screen and are identical with respect to all other stimulus properties.

The reaction frequencies to the patterns with the insertions of black and white sectors into the contrasting areas of the training patterns

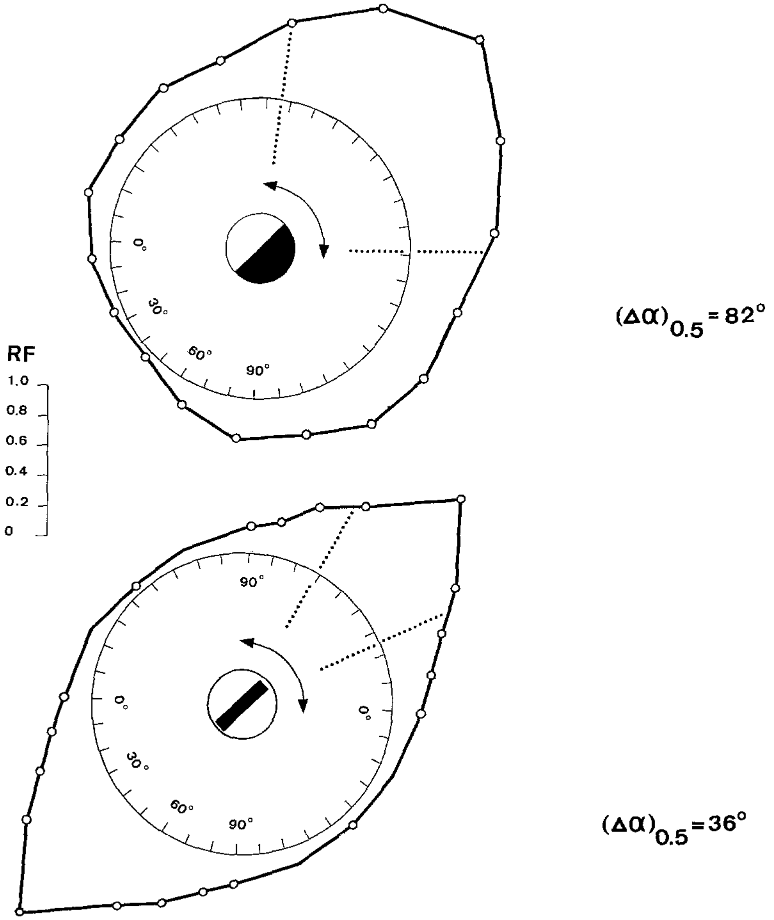


Fig. 4. Direction sensitivity curves for a black-and-white disk (diameter 130°) and a black stripe (127° × 50°). $(\Delta\alpha)_{0.5}$ half width

are presented in Fig. 6 (W-function) and Fig. 7 (B-function). As in the A-function (Fig. 3) the discrimination of the transformed patterns from the training pattern depends on the position within the visual field, where the insertions of black and white sectors are made. When a white sector is inserted into the lower part of the black area (counterclockwise rotation, •-curve in Fig. 6), the reaction frequency to the test pattern is more strongly diminished than in the upper part of the black area (clockwise rotation, o-curve in Fig. 6). The same is true for the insertions of black sectors into the white area (B-function; compare • and o in Fig. 7).

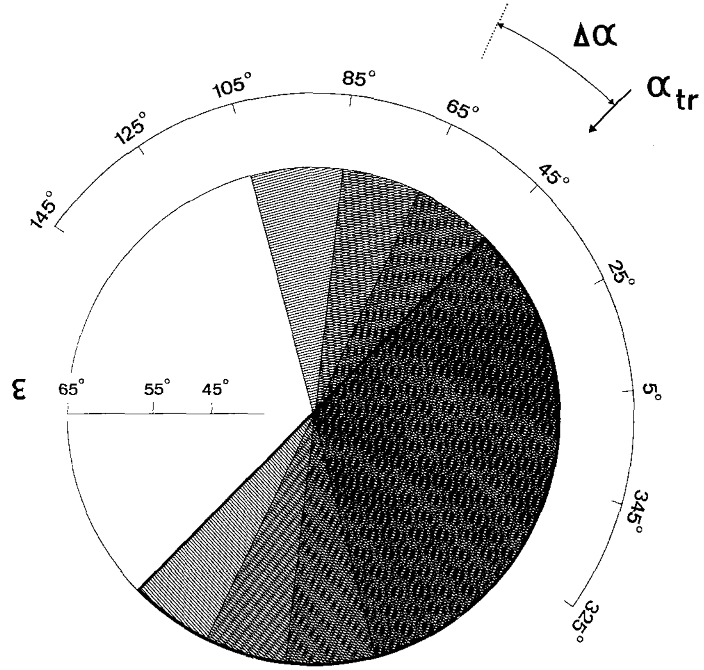


Fig. 5. Stimulus changes involved in rotating a black-and-white disk out of its training position α_{tr}. For each value of $\Delta\alpha$ positive and negative reversions of contrast occur within opposite parts of the visual field. α inclination of the contrast line; ε visual angle

On the whole, there are smaller reaction frequencies to the test patterns within the *W*-function than within the *B*-function. That effect, however, does not only depend on the insertions of black resp. white sectors, as one might suggest at first view, but on the fact that in the *W*-function the contrast changes occur in the middle lower part of the frontal visual field, whereas that region does not change contrast in the *B*-function. As it will be shown in more detail (p. 267), this part of the visual field is most decisive for pattern recognition. In control tests bees were trained to a black-and-white disk, the contrast line of which extended in the same direction $\alpha_{tr}=45°$, but which was rotated by 180° according to the training pattern used in the experiments of Figs. 3, 6, and 7 (see right part of Fig. 9). Now the *B*-function showed smaller reaction frequencies (i.e. stimulatory values in relation to the stimulatory value of the training pattern) than the *W*-function.

Reconstruction of the A-Function by Means of the W- and B-Functions: A-Function.* We now can try to approximate the *A*-function by

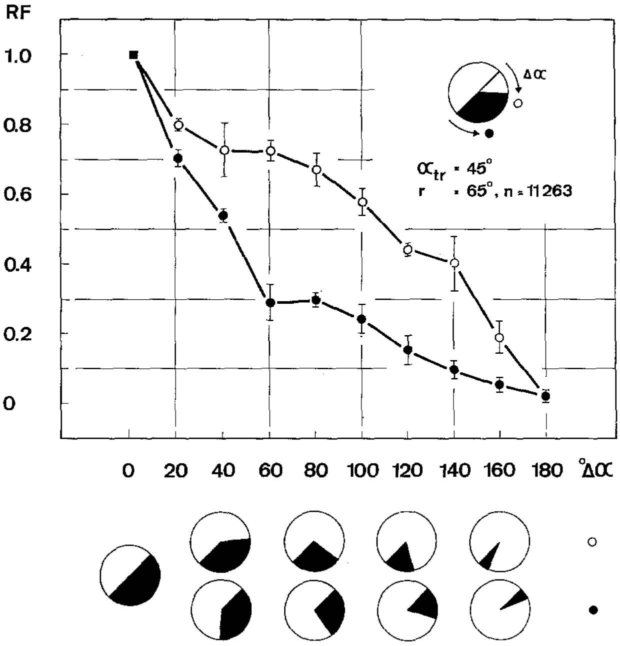


Fig. 6. The effect of inserting white areas in the black half of the training disk (*W*-function). *RF* reaction frequency to the test patterns (*abscissa*) simultaneously presented with the training pattern (α_{tr}). Clockwise (○) and counterclockwise (●) rotation

means of the *B*- and *W*-functions, because the α_t-pattern corresponding to a particular value of $(\Delta\alpha)_i$ in the *A*-function may be regarded as a superposition of the $(\Delta\alpha)_i$-patterns of the *W*-function and the *B*-function. As all stimulatory values are given in relative units $0 \leq ST \leq 1$, the mathematical procedure describing superposition is multiplying the corresponding stimulatory values

$$\mathrm{ST}\,[(\Delta\alpha)_i]_{*A} = \mathrm{ST}\,[(\Delta\alpha)_i]_B \cdot \mathrm{ST}\,[(\Delta\alpha)_i]_W.$$

By this a theoretical angle-discrimination-curve (A*-function) can be calculated, which fits very well the experimental data (A-function). The results are given in Figs. 8a and b for clockwise and counterclockwise rotation of the training disk.

The shape of the *A**-function very exactly coincides with that of the *A*-function: when the α_{tr} pattern is rotated out of the training position by $\Delta\alpha = 20°$ and 40°, the stimulatory value of the disk strongly decreases. For rotations within the range $60° \leq \Delta\alpha \leq 120°$, however, nearly the same stimulatory values are obtained, whereas $\Delta\alpha = 140°$

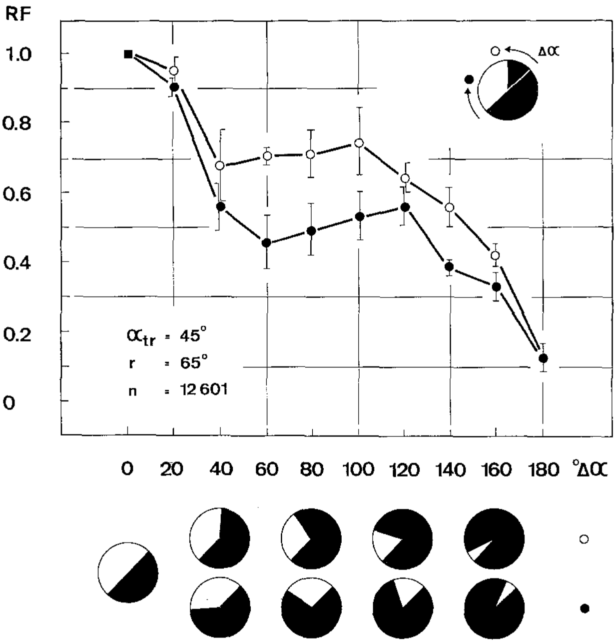


Fig. 7. The effect of inserting black areas in the white half of the training disk (*B*-function). Clockwise (●) and counterclockwise (○) rotation. For further explanations see Fig. 6

(counterclockwise rotation, Fig. 8b) as well as $\Delta\alpha=160°$ and 180° again cause a strong decrease of the stimulatory value. Therefore contrast changes near the contrast line of the training pattern are more effective in reducing the stimulatory value of the pattern disk than contrast changes within the black and white areas. The *A*- and *A**-functions for $+(\Delta\alpha)$ (Fig. 8b) nearly coincide with the corresponding *W*-function (■-data), meaning that the contrast changes in the middle lower part of the frontal visual field are so effective that their influence alone is able to describe the *A*-function. The loss of stimulatory efficiency caused by the corresponding contrast changes in the upper part of the visual field (▲-data) has no or only little effect on the *A*-function. This significance of particular regions within the visual field will be demonstrated in the next chapter.

II. The Structure of the Visual Field

The inclination of differently inclined contrast lines, produced by using black-and-white disks, remarkably depends on the direction of rotation ($\Delta\alpha$ positive or negative, Figs. 3, 8a and b), unless the contrast

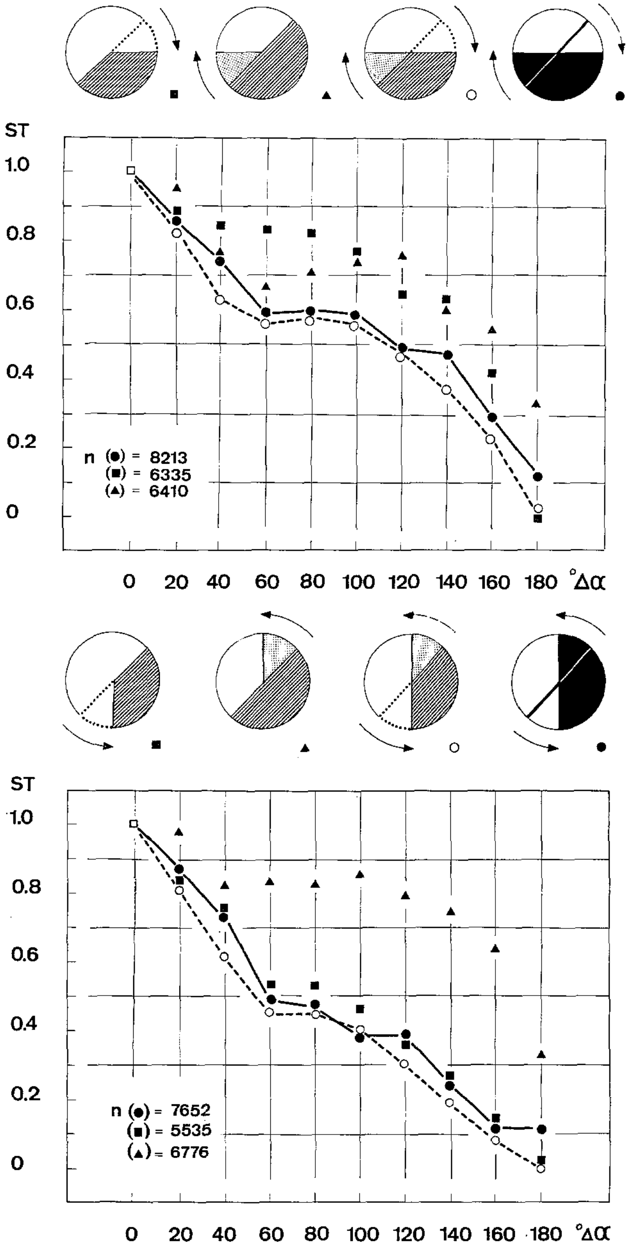


Fig. 8. Calculation of the A^*-function (○) by means of the W-function (■) and the B-function (▲). ● A-function, experimentally determined as the W- and B-functions. For mathematical procedure see p. 266. ST stimulatory values, calculated from the reaction frequencies to the $\Delta\alpha$-patterns by means of a mingled choice transformation and a probit transformation (see Table 2). *a* (*above*) clockwise, *b* (*below*) counterclockwise rotation of the training disk ($\alpha_{tr}=45°$)

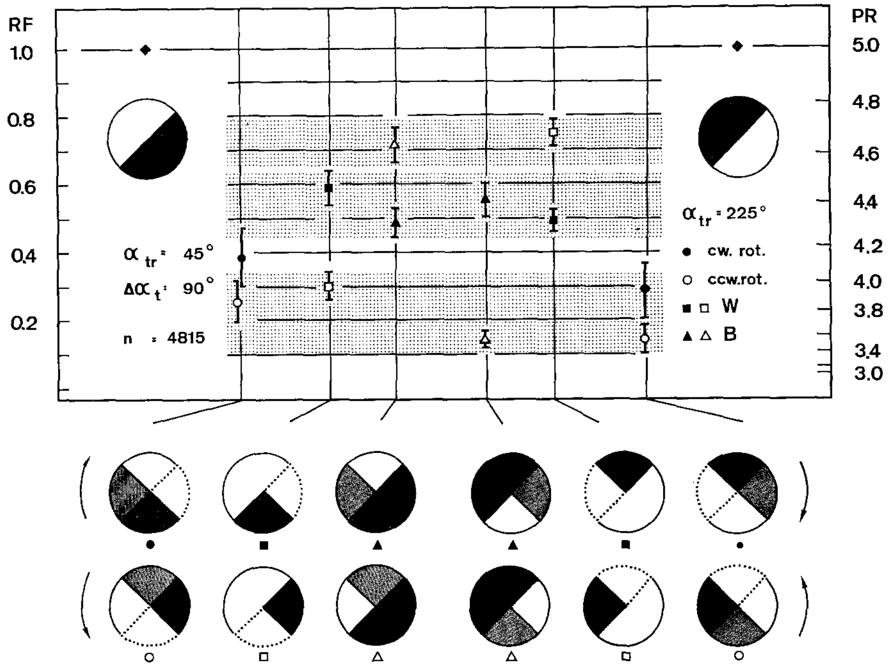


Fig. 9. The effect of inserting black (▲, △) or white (■, □) sectors ($\Delta\alpha=90°$) in the contrasting areas of the training disks ($\alpha_{tr}=45°$, 225°). Both insertions are simultaneously made in patterns ● and ○. *Filled signatures* clockwise rotation; *open signatures* counterclockwise rotation; *RF* reaction frequencies to the test patterns (*abscissa*), when simultaneously presented with the training pattern; $RF(\alpha_{tr})=1.0$; *PR* probit scale; $PR(\alpha_{tr})=5.0$. The reaction frequencies to the contrast changes in the upper, middle and lower part of the visual field are indicated by the 3 grey horizontal stripes

line is oriented vertically ($\alpha_{tr}=90°$ or 270°, meaning that the black area is on the right or on the left side of the vertical contrast line). The same is true for increasing insertions of contrasting areas in the black and white halves of the pattern disk. From these findings we may conclude that there exists a dorsoventral asymmetry in the visual field of the bee.

In order to get more detailed informations about that dorsoventral asymmetry, a black or white sector (*B*-values or *W*-values; $\Delta\alpha=90°$) is shifted from the lower part ($\alpha=270°$) to the lateral parts ($\alpha=0°$ and 180°) as well as to the upper part ($\alpha=90°$) of the visual field. Using $\alpha_{tr}=45°$ and $\alpha_{tr}=225°$ as training patterns, all combinations between these 4 positions $\alpha=0°$, 90°, 180° and 270° and the insertions of black and white sectors could be tested (Fig. 9, Table 3). The contrast changes

Table 3. χ^2-values of the differences between the reaction frequencies, obtained by inserting black resp. white sectors in different parts of the visual field. The insertions of 90° wide black (B) and white (W) sectors are made in the right (0°), upper (90°), left (180°) and lower (270°) quarter of the visual field. The training patterns (*left*) and the test patterns (*right*) are graphed below the signs of the particular series. For comparison see Fig. 9

	W 90°	W 180°	W 0°	W 270°	B 90°	B 180°	B 0°	B 270°
W 90°	314	▓ 15.34	░ 5.62	▓ 49.81	0.22	▓ 15.24	▒ 7.15	▓ 81.57
W 180°		447	2.15	▓ 12.23	▓ 14.53	0.01	0.97	▓ 37.54
W 0°		N =	359	▓ 22.75	░ 4.49	2.34	0.16	▓ 51.07
W 270°				422	▓ 51.14	▓ 10.89	▓ 17.71	▒ 10.63
B 90°					473	▓ 14.35	░ 6.00	▓ 82.28
B 180°						395	1.13	▓ 35.45
B 0°							312	▓ 44.60
B 270°								299

▓ $p < 0.001$
▒ $p < 0.01$
░ $p < 0.05$

within the training pattern are the more effective, the more they are located in the lower part of the visual field. These results are confirmed by training bees to patterns with $\alpha_{tr} = 0°$ and 180°, i.e. to patterns the black halves of which extend to the lower resp. upper part of the visual field (Table 4). According to Table 3 there are statistically significant differences ($p < 0.001$ and < 0.01, 2×2 table) between the effects of contrast changes in the upper, lower and lateral parts of the visual field, except of 3 cases ($p < 0.05$) referring to a comparison of the upper and lateral visual field regions: *B* 90°—*W* 0°, *W* 90°—*W* 0° and *B* 90°—*B* 0°. No differences are found between the right and left lateral fields and between black and white insertions within the same field positions (with exception of the lower visual field: *W* 270°—*B* 270°; $p < 0.01$).

A more precise function representing the sensitivity of different field positions to contrast changes within the visual field is given in Fig. 10. In these experiments a black sector ($\Delta\alpha = 30°$) is successively inserted in the white training disk at varying field positions, which differ from one another by 30°. The results clearly prove that it is not the total lower hemisphere of the visual field responding most effectively to contrast changes, but only the median part of the lower frontal field. Even the reaction frequencies to the black sectors in the positions $\alpha = 0°$ and $\alpha = 30°$ are significantly different with $p < 0.001$ (2×2 table,

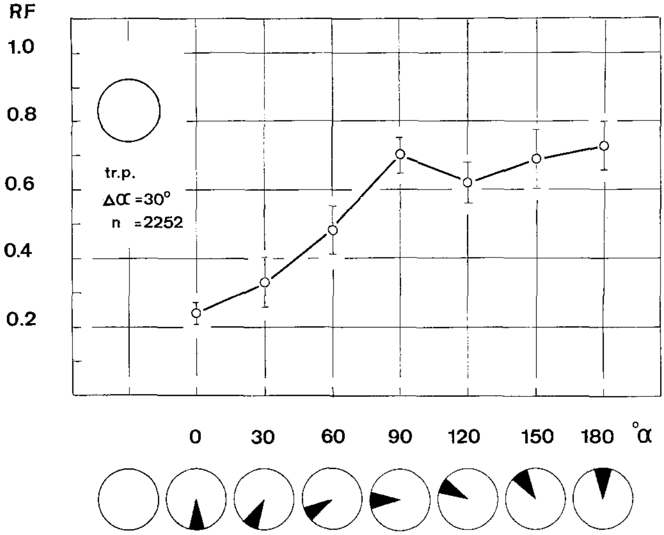


Fig. 10. The effect of inserting a black sector ($\Delta\alpha = 30°$) in varying regions α of a white training disk (*tr. p.*). *RF* reaction frequency to the test patterns (*abscissa*) in comparison to that of the training pattern ($RF = 1.0$)

$n = 626$). On the other hand, there is no difference between the reaction frequencies to $\alpha = 90°$ and $\alpha = 180°$ ($p = 0.48$; $n = 698$). From both these findings we may conclude that only a relative small sector of the lower part in the frontal visual field is most important for pattern recognition.

Discussion

It can be read off Fig. 3, how precise the bee's visual system is able to discriminate different inclinations of contrast lines. The half-width of the direction sensitivity curve (angle-discrimination-function, *A*-function) was found to be $(\Delta\alpha)_{0.5} = 37°$ for single stripes and $(\Delta\alpha)_{0.5} = 82°$ for black-and-white disks. Furthermore, there is no statistically significant difference between the direction sensitivity curve of single stripes and equidistant stripe patterns (Wehner and Lindauer, 1966; Wehner, 1967b).

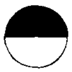
Using electrophysiological recordings from the medulla and lobula regions of the fly's visual pathway, Bishop *et al.* (1968) and McCann and Dill (1969) have investigated directional selective units, which respond to particular inclinations of equidistant stripe patterns. When the pattern diameter is 20° and the spatial wavelength of the pattern 8°, a half-width of the direction sensitivity curve of 75° resp. 90° for the motion patterns resp. form patterns can be read off Fig. 13 in McCann and Dill (1969). Even larger values were found (Bishop *et al.*, 1968, Fig. 10; McCann and Foster, 1971, Fig. 15). None of the units electrophysiologically studied has proved until now such a precise detection of directions, as it is found in the orientation studies described here. Units of a more integrative type (Mimura, 1971) may be responsive for these pattern discrimination effects.

In order to explain direction sensitivity neurophysiologically, one often refers to the well known mechanism of lateral inhibition (Barlow and Levick, 1965, and Michael, 1968, in vertebrates; Collett and Blest, 1966, in arthropods). Recently, however, Mimura (1971) has found in the fleshfly, *Boettcherisca peregrina*, that the number of inhibitory neurons or off-units is very few and that they are only located centrally and not in the medulla region. From these findings he concludes that inhibitory neurons may play some role in the integrative action, but that they probably do not participate very much in the analysis of the direction of motion. In the medulla-lobula region he has found a special unit arrangement for the detection of directional stimuli: units responding to adjacents parts of the visual field are neuroanatomically grouped in one line. These results remarkably resemble the findings of Hubel and Wiesel (1959, 1962) dealing with the mechanism of direction sensitivity in the cat's striate cortex. They are also in agreement with the data of Bishop *et al.* (1968), who found that units in the medulla region, which are not sensitive to the direction of motion, have small receptive fields, and that units in the lobula-lobula plate region show directional sensitivity in a very wide visual field, even including the contralateral side. Nearly the same properties were found in the four types of directionally selective motion detecting units in the bee (Kaiser and Bishop, 1970). These units, located in the region between lobula and protocerebrum, most strongly respond to upward, downward, outward and inward movement, respectively (for *Musca* see McCann and Foster, 1971). Their acceptance angle extends over the whole visual field of the eye.

We now want to present a mechanism of directional sensitivity based on the behavioral data on pattern recognition. As it can be derived from the angle-discrimination-curve of Fig. 3, the test pattern is the better discriminated from the training pattern, the more the actual distribution of black and white areas within the visual field differs from that during training. By definition, the training pattern consisting in a black-and-white disk (Fig. 5) with its contrast line oriented in the directions $\alpha_{tr}=0°$ (Table 4), 45° (Figs. 1a, b, 3, 4, 6, 7, 9; Table 3) 180° (Table 4) and 225° (Fig. 9, Table 3), has the stimulatory value $ST=1$. This stimulatory value is decreased, when (1) the pattern disk is rotated by $\Delta\alpha$ out of the training position (A-function) and (2) black and white sectors of increasing size $\Delta\alpha$ are inserted into the contrasting areas of the training pattern (B- and W-functions). Therefore the contrast changes simultaneously involved in the rotation of the disk can be produced and tested separately. By a simple mathematical procedure (p. 266) a theoretical angle-discrimination-curve (A^*-function) can be calculated from the B- and W-functions. As shown in Figs. 8a, b, that A^*-function suits very well the experimental data of the A-function.

Testing the angle discrimination of *black stripes* on a white screen (Wehner, 1969a), the results can be explained by the same mechanism. If one calculates, however, the A^*-function according to the equation given on p. 266, the stimulatory values differ by a mean value of +15% from the experimental data, i.e. the A^*-function indicates higher stimulatory values than the A-function. Therefore a slightly modified mathematical procedure was used in that presentation (Wehner, 1969a, p. 589). That modification is now known not to be necessary: for the W-function was not determined by means of the residual black areas, remaining in the training position of the stripe when it is rotated out of α_{tr}, but by varying rectangular stripe-shaped black areas (Fig. 3 in Wehner, 1969). These black stripes coincided with the residual black areas of the rotated training stripe only in size, but not in configuration and visual field position.

Table 4. The insertions of contrasting sectors ($\Delta\alpha = 80°$ pattern B) into the black resp. white area of the training pattern A. Insertions into the lower hemisphere (test No. 1 and 3) have a significantly stronger effect than insertions into the upper part of the visual field (test No. 2 and 4). n = total number of choices performed by the trained bees, which had previously received at least 60 rewards on pattern A, p = p-value of the difference between the reaction frequencies of test No. 1 and 2 resp. 3 and 4 (2 × 2 table). The mean reaction frequencies and their mean errors are indicated

Test No.	Pattern		Reaction frequency for B $[n(B)/N]$	n	p
	A	B			
1			0.08 ± 0.02	533	<0.001
2			0.40 ± 0.00	534	
3			0.16 ± 0.02	567	<0.001
4			0.33 ± 0.03	481	

From all these experiments two main conclusions may be drawn: (1) By training bees to a particular arrangement of black and white areas in the visual field, one finds a central representation of the positions of these contrasting areas, meaning that the distribution of the black and white areas is projected to a reference grid which preserves them spatially. This finding was only possible by introducing the vertical screen into the study of pattern recognition in bees. Using a horizontal screen, in the flying bee no definite adjustment of the visual coordinates to the pattern can be obtained. From our work on vertically arranged distributions of black and white areas, however, one may conclude that either the eyes of the flying bee are always kept constant in the same position by proprioceptive control of head and thorax (Lindauer and Nedel, 1959) or that there will be "space-constant fibres" in the optic ganglia of the bee detecting a certain direction of visual stimuli irrespective of the position of the eyes. Those space-constant fibres have been found in the eyestalk of the crayfish (Wiersma and Yamaguchi, 1966). Evidence for a central representation of different parts of the visual field can be taken from electrophysiological work on crustaceans and flies (Bishop *et al.*, 1968; McCann and Dill, 1969; McCann and Foster, 1971; Mimura, 1970, 1971). From the behavioral point of view Horridge (1966a, b) has found in *Carcinus maenas* as well as in *Locusta migratoria* an "optokinetic memory" describing that crabs and locusts give directional eyestalk respectively head responses to a striped drum, which has been moved during a dark period, but remains stationary during the test. As in our experiments with bees the positions of white and black areas must be correspondingly represented in a central nervous grid.

(2) Our special finding that different parts of the visual field are of unequal importance for pattern recognition leads to a concept of form perception in insects not consistent with the classical theory, which has been based on an integration of the stimulus effects all over the visual field. Our experiments on pattern recognition in the fly *Drosophila melanogaster* (Wehner, in prep.) have also shown that arrangements of black and white areas are only "attractive" in special parts of the visual field. In the crab *Uca* movement stimuli are most effectively responded when they are situated within a stripe extending from 5° below to 20° above horizon (Kunze, 1963). In the crayfish *Cambarus* all the space constant fibers mentioned above have their visual fields in the upper hemisphere (Wiersma, personal communication). Finally referring to our results with bees the finding that the median lower part of the visual field is most decisive for pattern recognition agrees with the fact that in flying bees these regions of the eye are normally directed towards horizon landmarks.

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