3. A Qualitative Model for Pattern Discrimination in the Honey Bee

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Abstract. Experimental results on the pattern discrimination of the honey bee can be described by a difference function, defined for every pair of shapes. This function consists of two terms. The first term is an application of a two-dimensional cross-correlation, the second one is a comparison of the contour length of the shapes and is a qualitative measure for the number of alternating stimuli on the ommatidial elements produced by movement of the shapes.

When an image of a figure is formed by the optic apparatus of an eye on the receptor layer, this two-dimensional image will be translated by the receptors into a three-dimensional intensity-locus function. Of these three coordinates, one plane is given by the arrangement of the receptors, the third coordinate by the amplitude of the excitation of the different receptors, evoked by the intensity of the different points of the image. This intensity-locus function ("I-L function") of a shape is either immediately processed, e.g. stored, or the information is reduced in great measure by generalisation of a few specific parameters of this I-L function. Accordingly, in pattern recognition, either the perceived I-L function is compared with a stored I-L function or the measured parameters with the values of stored parameters.

One hypothesis often found in literature on the nature of this processing assumes that two shapes are compared by computing a two-dimensional cross-correlation, with the coefficient of this correlation giving the difference between the two shapes. The value of this coefficient, irrespective of the norming factors, is equal to the value of the largest common volume of both I-L functions. In the discrimination of shapes of the same contrast, with I-L functions of the same amplitude, the correlation coefficient corresponds to the value of the largest common area G (fig.1). The exclusive application of a cross-correlation coefficient would mean, however, that parts of shapes which do not overlap this common area G have no influence on the capacity of discrimination. Thus, for example, all shapes which totally cover a comparative shape would not be distinguished from this shape, because the common area being considered always corresponds to the one which the comparative shape would show when covered by itself. That this is not true, however, concerning the pattern discrimination of the honey bee is shown by the results of many experiments (CRUSE, 1972, SCHNETTER, preceding contribution, WEHNER, 1969). The hypothesis should therefore be extended by considering, besides the correlation coefficient, other qualities of the correlation function of the two I-L functions. As a first approximation, we shall attempt to include in the description of the difference between two shapes, the non-overlapping areas R^+ and R^- of the positive and the negative shapes (fig.1). One could use $U = f(R^+, R^-, G)$ as a function describing this difference. In addition to this, WOLF (1935) and other authors could show that, at least in spontaneous-choice experiments, the number of stimuli which a shape generates on the compound eye when the bee flies over it is the decisive measure. Although it is not known how these stimuli are measured, the length of contour of a shape seems to be a qualitative measure. Therefore a second term of the form $f(K^+, K^-)$ should be added to the difference function (K^+ and K^- are the lengths of contours of the positive and negative shape). Because the spontaneous tendency (WOLF, 1935) as well as the I-L function depend on the value of the contrast A the latter should appear in both terms: $U = C_1 f_1 (R^+, R^-, G, A^+, A^-) + C_2 f_2 (K^+, K^-, A^+, A^-)$, where C_1 and C_2 are weighting factors.

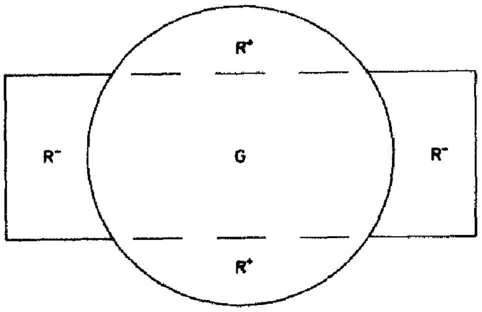

Fig.1. The rewarded (positive) shape (circle) and the unrewarded (negative) shape (rectangle) are laid on each other in such a way, that the common area G reaches a maximum. Then the non-overlapping areas of the positive shape R^+, and the negative shape, R^-, can be determined

In order to be able to formulate this hypothesis more exactly, and at the same time to prove it, several forms of difference functions have been examined using data taken from the literature and our own experiments, initially with no respect to the contrast. A good fit was found between the difference function

$U = \left| C_1 \frac{R^+ + R^-}{G} (G + R^+) + C_2 (\log K^+ - \log K^-) \right|$ and the experimental data. This is shown first with results of SCHNETTER (1968) for discrimination of rectangles of different inclination and area. WEHNER (1968, 1969) (fig.3.) can be described by this difference function. Since the shapes tested in the experiments of WEHNER were shown to the bees on a perpendicular wall, the bees do not discriminate them rotation-invariantly, as they do shapes shown on a horizontal plane. This has to be taken into account in determination of the areas R^+, R^- and G. In the same way results of own experiments with different shapes, e.g. stars, checkerboards and concentric annular rings (CRUSE, 1972), can be described by this difference function (fig.4.). I shall refer to some deviations as well as the meaning of the weighting factors later. Because this function is asymmetrical corresponding with the experimental results, one cannot define a metric in the pattern discrimination as HELVERSON (this volume) does with colour discrimination.

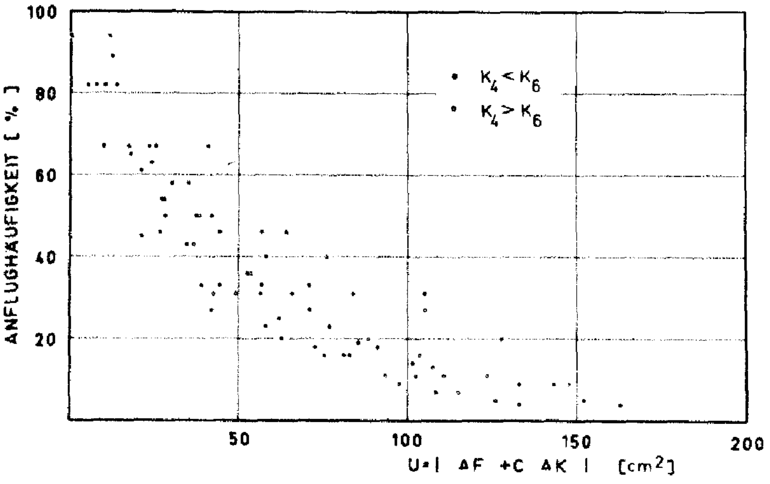

Fig.2. Results of SCHNETTER (1968). The frequency of choices (Anflughäufigkeit) on the negative shape is plotted against the value of the difference function U computed for every pair of shapes

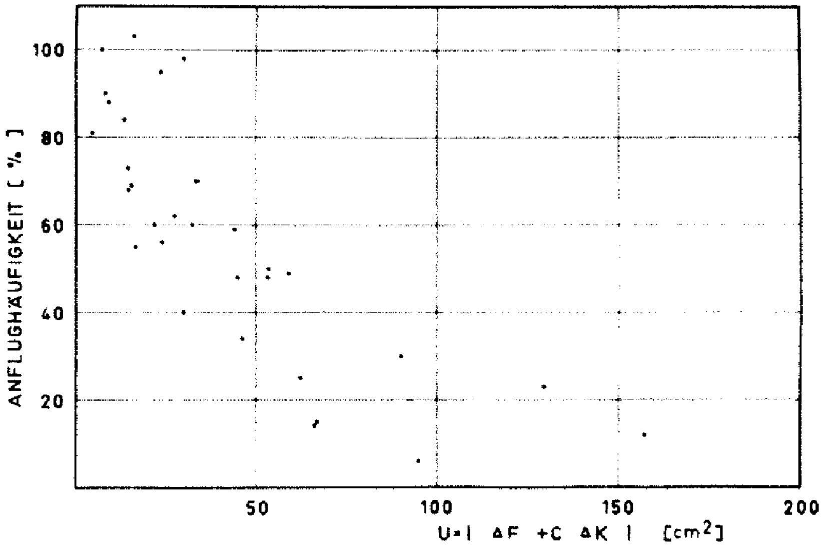

Fig.3. Results of WEHNER (1968, 1969). Coordinates see fig. 2

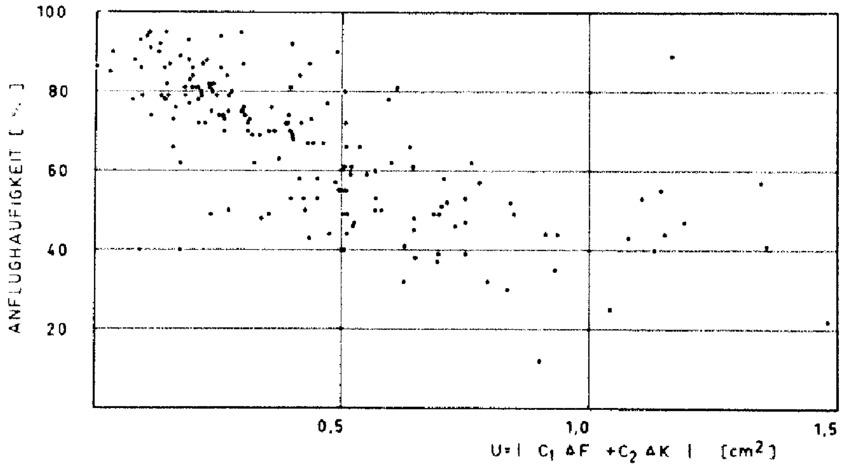

Fig. 4. Results of CRUSE (1972). Coordinates see fig. 2

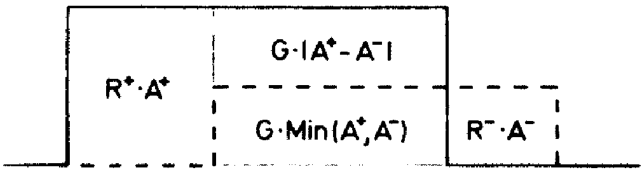

Fig. 5. Schematic cross-section through the superimposed intensity-locus functions of the positiveshape (full lines) and the negative shape (dashed lines)

If one is to apply the difference function on the discrimination of shapes of different contrast, one has to take into account, as stated above, the three-dimensional nature of the I-L functions. As shown by a schematic cross-section through two superimposed I-L functions of different contrast A^+ and A^- (fig. 5), the value of the common space is $G \cdot \mathrm{Min}(A^+, A^-)$, where A^+ and A^- are values of the contrast of the positive and the negative shape. After standardisation, this value corresponds with the correlation coefficient $G \cdot A^+ \cdot A^-$. So the difference function could be extended for shapes of different contrast in the following way:

$$U = C_1 \frac{R^+A^+ + R^-A^- + G\,A^+ - A^-}{G\,\mathrm{Min}\,(A^+, A^-)} \qquad A^+\,(G + R^+) + C_2(A^+\log K^+ - A^-\log K^-)$$

In fact experimental results could be described with this difference function, both when the shapes had the same contrast, which was changed in different presentations (fig.6), and when the shapes had different contrast themselves (fig. 7) (CRUSE, 1968).

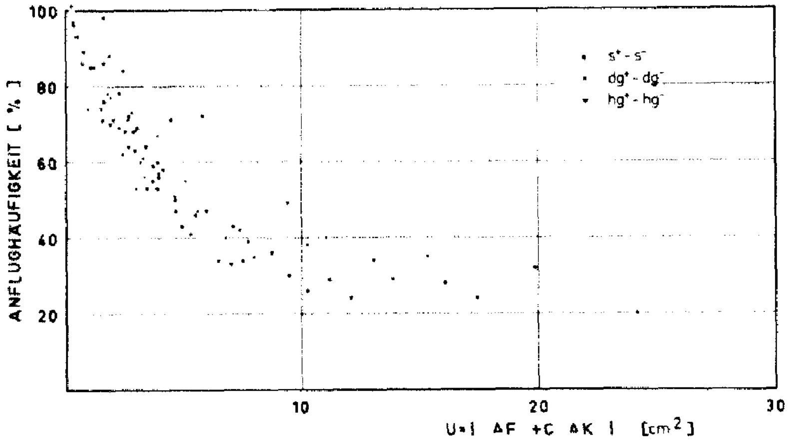

Fig. 6. Results of CRUSE (1968). Positive and negative shapes have the same contrast. Coordinate see fig. 2. Circles: black shapes; crosses : dark grey shapes; triangles: light grey shapes

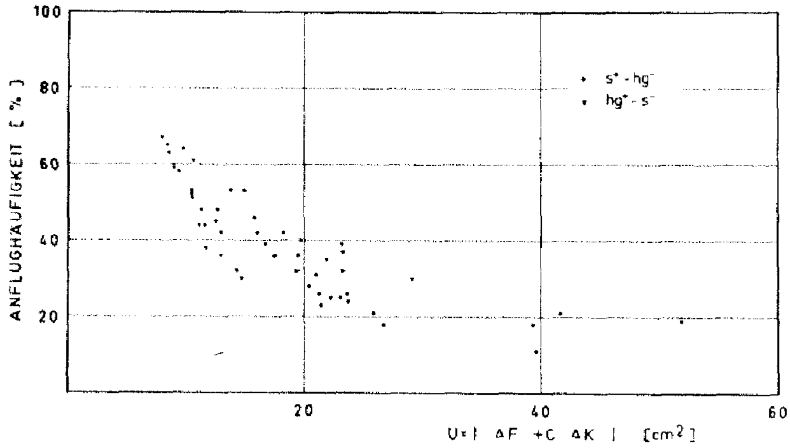

Fig. 7. Results of CRUSE (1968). Positive and negative shapes have different contrast. Coordinates see fig. 2. Circles: positive shape light grey, negative shapes black; triangles: positive shape black, negative shapes light grey

A comparison of figures 2 and 7 with figure 4 shows that the standard deviation in figure 4 is much higher. Since the method in all experiments was practically the same - several different shapes presented at the same time on a horizontal plane - the only difference between the two series of experiments was that in figs. 6 and 7 only sixpointed stars, and in fig. 4 very different kinds of shapes were used. So one could assume, that the kind of shape influences the choice of form parameters. In fact, assuming that the bees are actually applying the discussed difference function, it can be shown that the weighting factors C_1 and C_2 are chosen differently in different experiments (CRUSE, 1972). Probably, however, with respect to the results of MAZOCHIN-PORSHNYAKOV (1969), besides the difference function the bees apply other parameters according to the problem to be solved. How difficult the proof of the use of such problem-orientated parameters is, can be shown by the results of WEHNER (1971). He measured the discrimination of pairs of stripes of different inclination and different (within pairs, however, equal) length. A pair of very short stripes of different inclination can hardly be discriminated much better. WEHNER concluded, therefore that during the experiment something has changed in the bees' interpreting apparatus. These results, however, can also be qualitatively described by the difference function. Table 1 shows the comparison between the computed and the measured discriminations (for simplicity, I put $C_2 = 0$). On the one hand, the quantitative deviations with the short stripes could be explained by a lower intensity of choices. On the other hand, results of SCHNETTER (preceding contribution) can only be described after changing the difference function:

$f_1 (R^+, R^-, G)$ to $f_1' (R^+, R^-, G) = \frac{R^+ + R^-}{G}$

With this somewhat different function the results of WEHNER (1971) can be described quantitatively (table 1).

Table 1. The discrimination of stripes of equal width (50°), different length (shown in angular grades) and different inclination (+ 45° and - 45°, shown by the sign) from a positive stripe of the length 130° and the inclination + 45° (WEHNER, 1971). A comparison of measured and computed discriminations.

	discrimination (%)		
neg. shape	WEHNER (1971)	$\frac{R^+ + R^-}{G}$	$F^+ \; \frac{R^+ + R^-}{G}$
110 +	100	100	100
110 -	4	6	5
90 +	100	100	100
90 -	8	10	9
70 +	100	100	100
70 -	51,5	34	47

From these results one can formulate the hypothesis that one part of the pattern discrimination of the honey bee could be reduced to a two-dimensional cross-correlation of the two shapes to be compared. Hereby not only the coefficient, but also other qualities of the correlation function will be used by the bees. Another part of the pattern discrimination could be a comparison of the number of alternating stimuli in the ommatidial elements produced by the movement of the shapes relative to the flying bee.

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