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An Application of the Cross-Correlation Coefficient to Pattern Recognition of Honey Bees

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Abstract

1. In training experiments with honey bees, the discrimination of 6-pointed stars of different form and contrast is measured. The following assumptions allow a quantitative description of these results.

2. The bee computes the two-dimensional cross correlation coefficient r_{xy} between the two shapes to be discriminated (the rewarded shape and the one seen at present). This presupposes, that the rewarded shape is stored in the memory point by point.

3. In addition to the cross correlation coefficient, the shapes are discriminated by means of their contour length and their contrast.

4. A noise is superimposed on the values stored in the memory. Because of this noise, the accuracy of detecting the outline of the stored shape depends on the value of the contrast. The lower the contrast, the less accurately is the outline detectable. The exactness of the stored value of the contrast itself is also diminished by the noise.

5. Although the results of these and of most previously published experiments can be described quantitatively by this model, some other results (Anderson, 1972; Mazochin-Porshnyakov, 1969) can certainly not be described in this way. In such cases, it seems more probable that bees use abstract parameters to discriminate the shapes because of the particular experimental method.

A. Introduction

The first experiments dealing with pattern recognition in honey bees were done by v. Frisch (1915), Hertz (1935b) and Wolf (1935). In recent years, Anderson (1972), Cruse (1972a, b), Mazochin-Porshnyakov (1969), Schnetter (1968, 1972), v. Weizsäcker (1970) and Wehner (1967, 1968b, 1969, 1971, 1972) have tried by quantitative methods, to find the criteria of pattern discrimination, which are the decisive ones for the bee. Several hypotheses have been discussed: Wolf (1935) proposed that the number of stimuli which a pattern generates on the compound eye as the bee flies over it is the decisive measure. Moreover, he postulated that the shape generating the greater number of stimuli – usually the shape with the greater contour length – would always be favoured by the bee independently of any training. In a similar way the contrast and the total area of a shape would influence pattern discrimination.

In contrast to this, Hertz (1933) found that bees could be trained in some cases to prefer the shapes with less contour length. Hertz assumed, therefore, that the bees apply at least two discrimination criteria: firstly the "figural intensity", which corresponds to the contour length of a shape, and secondly the "figural quality", which cannot be defined exactly, but which classifies together shapes as being of the same type (e.g. striped patterns, *n*-pointed stars, checkerboards, concentric annular rings). Schnetter (1968) later showed that a bee is well able to discriminate two shapes belonging to the same type (e.g. 4-pointed stars) independent of which of the two shapes has the greater contour length. He tested whether the difference of the contour length of two shapes (Schnetter, 1968) or the difference of the angles of the points (Schnetter, 1972) could be the decisive criterion for the bees. For shapes of the same type (4-pointed or 6-pointed stars) either difference could account for the discrimination, but neither could when the shapes were of different types.

Wehner (1969) could explain some of his results by assuming a point-by-point comparison of the shapes, as did, for example, Boynton *et al.* (1960) in describing psychophysical experiments. This means, that the presented shape would be compared with the rewarded shape which must, therefore, be stored in the memory point by point. This hypothesis however has not been formulated quantitatively. With respect to other experimental results Wehner (1971) postulated, that not only the point-by-point comparison, but other qualitatively described parameters (e.g. "orientation of a stripe") must be used by the bee when discriminating shapes.

Thus, none of these hypotheses provides a complete quantitative description of the existing experimental results. The purpose of the present paper, therefore, is to test a hypothesis similar to one which has been put forward by several authors dealing theoretically with pattern recognition (v. Seelen, 1970; Anderson, 1968). These authors suggested that the comparison of the two shapes may be done by using the two-dimensional cross-correlation function of the two shapes. Here I want to test the hypothesis that only one single value of the cross-correlation function is able to describe the experimental results. Firstly, I shall test this hypothesis with experimental results dealing with the discrimination of shapes of different contrast; later, I shall test it with the published results of Schnetter (1968) and Wehner (1967, 1968a,b, 1969, 1971), and with my own (Cruse, 1972a).

B. Experiments

1. Method

The experimental devise stood in a closed room which was about 50 m from the bee hive. The round, horizontally lying experimental plate was illuminated from above by six bulbs (15 W, DC). The illumination of the white experimental plane was 55 lux (reflection spectrum see Fig. 1). As shapes, circles and various six-pointes stars were used, all of them having the same area of 20 cm^2 (Fig. 2, see also Schnetter, 1968, Fig. 3). They were cut out of a sheet of aluminium, 0.5 mm thick, and coloured with black (b), dark grey (dg) or light grey (lg) epoxy varnish.

The luminance ratios of the white background and the shapes was 100:9.6 (black shapes), 100:47 (dark grey) and 100:71 (light grey). During the experiments eleven shapes lay on the plate in annular array. The distance from one shape to the next was 15 cm. One shape is rewarded: that is, on this shape the bee finds a little watch-glass with sugar water. On all other shapes the watch-glass is filled with water. After the bee has learnt to discriminate the rewarded (positive) shape from the unrewarded (negative) shapes, the number of choices of each shape was counted. Because during one visit the bee can choose the rewarded shape only once, whereas all other shapes can be chosen several times, one cannot really compare the number of choices of the rewarded, positive shape with the number of choices of the negative shapes. Therefore two positive shapes were presented at the same time, one of them unrewarded i.e. with only water in the watch-glass. Then, a measure called the *choice frequency* (ChF) – the number of choices of a negative shape as a percentage of the number of choices of the unrewarded positive shape – was used as a measure of discrimination of the two shapes. For further details see Cruse (1972a). This method allows many counts per unit time, but has the disadvantage that the lowest values of choice frequency are much higher than in experiments where only one pair of shapes had to be discriminated (Cruse, 1972a; Schnetter, 1968). This lowest value, where the choice frequency reaches a saturation level independent of increasing difference between the shapes, shall be called the value of *neutral choices* (N), following Jander (1968).

2. Series I. Positive and Negative Shapes with the Same Contrast

To look for the influence of the contrast on pattern discrimination, nine experiments with three different grey tones were performed. For each grey tone, in

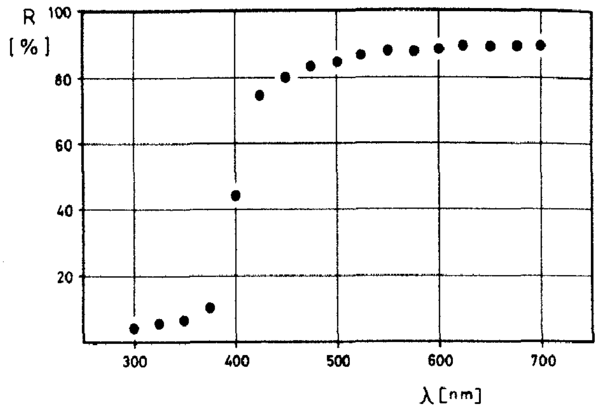

Fig. 1. Intensity R of light reflection from the experimental plate, measured against $MgO = 100\%$

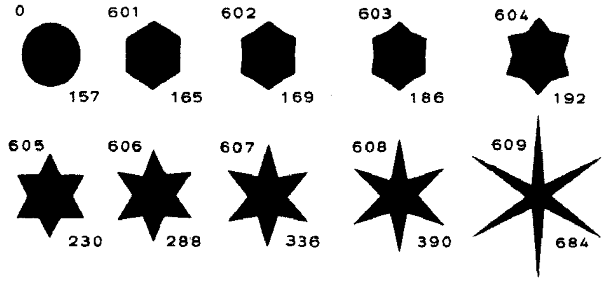

Fig. 2. Training shapes used in the experiments. All shapes have the same area of 20 cm^2. The number ab ove left gives the symbol of the shape used in the text, the number below right gives the contour length in mm

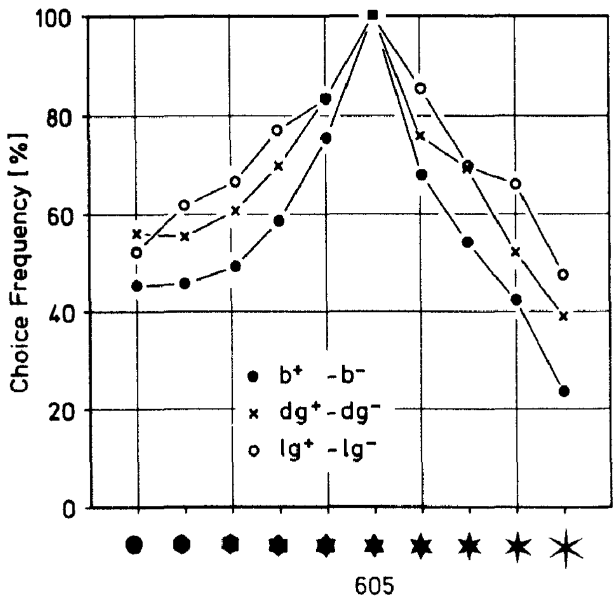

Fig. 3. The results of three experiments, using star no. 605 as the positive shape. The choice frequency of the unrewarded shapes has been measured. In each experiment the shapes had different grey tones: black (closed circles), dark grey (crosses) and light grey (open circles)

Table 1. Results of Series I. Positive and negative shapes have the same contrast. The choice frequency to the negative shape is measured in percent of the choices of the unrewarded positive shape. The standard deviation is shown in brackets

Shape		Choice frequency		
Pos.	Neg.	Black (in %)	Dark grey (in %)	Light grey (in %)
0	601	93 (± 9)	97 (± 15)	101 (± 5)
0	602	86 (± 17)	93 (± 6)	96 (± 9)
0	603	71 (± 9)	74 (± 11)	89 (± 11)
0	604	68 (± 7)	74 (± 13)	78 (± 10)
0	605	56 (± 10)	62 (± 11)	71 (± 8)
0	606	41 (± 5)	60 (± 9)	64 (± 9)
0	607	34 (± 7)	51 (± 7)	53 (± 7)
0	608	28 (± 10)	38 (± 12)	36 (± 9)
0	609	20 (± 4)	35 (± 16)	34 (± 13)
605	0	46 (± 6)	57 (± 5)	53 (± 15)
605	601	47 (± 8)	56 (± 6)	63 (± 23)
605	602	50 (± 7)	61 (± 13)	68 (± 18)
605	603	59 (± 20)	71 (± 16)	78 (± 24)
605	604	76 (± 8)	85 (± 15)	85 (± 15)
605	606	69 (± 17)	77 (± 16)	86 (± 15)
605	607	55 (± 11)	69 (± 7)	70 (± 11)
605	608	43 (± 6)	53 (± 14)	68 (± 7)
605	609	24 (± 10)	40 (± 11)	49 (± 14)
608	0	32 (± 7)	29 (± 8)	24 (± 7)
608	601	29 (± 9)	35 (± 7)	33 (± 15)
608	602	26 (± 10)	42 (± 10)	34 (± 8)
608	603	30 (± 14)	40 (± 12)	47 (± 8)
608	604	39 (± 12)	47 (± 12)	58 (± 15)
608	605	43 (± 12)	55 (± 7)	71 (± 13)
608	606	60 (± 6)	73 (± 9)	84 (± 12)
608	607	72 (± 10)	88 (± 11)	98 (± 8)
608	609	72 (± 10)	67 (± 9)	64 (± 10)

three different experiments, the circle, the star no. 605 and the star no. 608 were used as positive shapes. One example can be seen in Fig. 3. Here the star no. 605 has been rewarded. The ordinate represents the choice frequency. Higher values mean, that the shape is more easily confused with the positive shape than for lower values. The results are shown for black shapes (closed circles), dark grey shapes (crosses) and light grey shapes (open circles). The complete results are shown in Table 1. It can be seen, that black shapes are better discriminated from one another than dark grey ones, and these again better than light grey ones. Discrimination improves in the same way as when enlarging the difference of contour length.

3. Series II. Positive and Negative Shapes with Different Contrast

In order to see whether the contrast of the positive shape has a different influence on pattern discrimination than the contrast of the negative shape, I performed a second series of experiments with shapes of different contrast in the same experiment. As in Series I, the positive shape was presented twice – once rewarded, once unrewarded. On the experimental plate lay either two black shapes (the rewarded and the unrewarded positive shape), and nine unrewarded light grey shapes (the negative shapes), one of them with the same geometrical form as the positive shape, or, correspondingly, in an alternative experiment, two light grey and nine black shapes. In all these experiments one shape very unsimilar to the positive shape was removed in order to keep constant the number of shapes lying on the experimental plate.

These experiments were done only with black and light grey shapes. As in Series I the shapes no. 0, 605 and 608 have been used as positive shapes. When the positive shape was black, the number of choices of each light grey shape was determined (in percent of the choices of the unrewarded positive shape). When the positive shape was light grey, the number of choices of each black shape was determined.

When I did these experiments, I was interested only in the qualitative influence of the contrast. This was the reason why I measured the choices of the unrewarded positive shape only in the two experiments with the circles as positive shapes. In all other experiments I only measured the number of choices of the negative shapes, as one does in transfer experiments.

To compare the results of all experiments, the shape which had the same geometrical form as the positive shape but different contrast was used as a reference shape. In the first experiment (positive shape 0_b), the choice frequency of the shape 0_{lg} (light grey circle) was 53%, in the second experiment (positive shape 0_{lg}) the choice frequency of the shape 0_b was 67%. In this way the results of the other experiments were normalized: when the positive shape was 605_b or 608_b, the choice frequencies of 605_{lg} and 608_{lg} were set at 53%. When the positive shape was 605_{lg} or 608_{lg}, the choice frequency of 605_b and 608_b were set at 67%.

The results are summarized in Table 2. As can be seen, the light grey shapes can be better discriminated from a positive black shape than the black shapes from a positive light grey shape. This means that two shapes can be discriminated better if the positive shape has a higher contrast than the negative one, and worse if the positive shape has a lower contrast. This is also true if both shapes have the same geometrical form.

Qualitatively one can summarize these results in the following way: The difference of two shapes for bees increases with increasing contrast. The influence of the contrast of the positive shape is greater than the influence of the contrast of the negative shape.

C. Properties of the Cross-Correlation Coefficient

Before testing the hypothesis that the experimental results may be described by some value of the cross-correlation function, I shall first describe the most

Table 2. Results of Series II. Positive and negative shapes have different contrast. The choice frequency to the negative shape is measured in percent of the choices of the unrewarded positive shape. The standard deviation is shown in brackets

Shape Pos.	Shape Neg.	Choice frequency (in %)	Shape Pos.	Shape Neg.	Choice frequency (in %)
0_{b}	0_{lg}	53 (±10)	0_{lg}	0_{b}	67 (±11)
0_{b}	601_{lg}	46 (± 7)	0_{lg}	601_{b}	65 (±10)
0_{b}	602_{lg}	42 (± 4)	0_{lg}	602_{b}	63 (± 9)
0_{b}	603_{lg}	36 (± 4)	0_{lg}	603_{b}	58 (± 5)
0_{b}	604_{lg}	32 (± 5)	0_{lg}	604_{b}	52 (± 5)
0_{b}	605_{lg}	26 (± 8)	0_{lg}	605_{b}	44 (±11)
0_{b}	606_{lg}	24 (± 9)	0_{lg}	606_{b}	42 (± 7)
0_{b}	608_{lg}	18 (± 9)	0_{lg}	608_{b}	35 (±13)
0_{b}	609_{lg}	19 (±17)	0_{lg}	609_{b}	30 (± 9)
605_{b}	0_{lg}	23 (±10)	605_{lg}	0_{b}	38 (± 9)
605_{b}	602_{lg}	28 (±16)	605_{lg}	602_{b}	44 (±12)
605_{b}	603_{lg}	32 (±14)	605_{lg}	603_{b}	51 (± 5)
605_{b}	604_{lg}	39 (±14)	605_{lg}	604_{b}	59 (± 9)
605_{b}	605_{lg}	53	605_{lg}	605_{b}	67
605_{b}	606_{lg}	40 (± 7)	605_{lg}	606_{b}	61 (± 5)
605_{b}	607_{lg}	31 (±11)	605_{lg}	607_{b}	48 (± 9)
605_{b}	608_{lg}	25 (±13)	605_{lg}	608_{b}	45 (± 9)
605_{b}	609_{lg}	21 (± 9)	605_{lg}	609_{b}	39 (± 8)
608_{b}	0_{lg}	11 (± 5)	608_{lg}	0_{b}	25 (± 8)
608_{b}	602_{lg}	18 (± 3)	608_{lg}	602_{b}	30 (±12)
608_{b}	603_{lg}	21 (± 8)	608_{lg}	603_{b}	32 (±12)
608_{b}	604_{lg}	26 (± 7)	608_{lg}	604_{b}	36 (±11)
608_{b}	605_{lg}	32 (± 7)	608_{lg}	605_{b}	48 (± 8)
608_{b}	606_{lg}	36 (±13)	608_{lg}	606_{b}	53 (±15)
608_{b}	607_{lg}	42 (± 9)	608_{lg}	607_{b}	64 (±11)
608_{b}	608_{lg}	53	608_{lg}	608_{b}	67
608_{b}	609_{lg}	37 (± 9)	608_{lg}	609_{b}	53 (± 5)

important characteristics of the cross-correlation function. The formula for the cross-correlation function $F(r)$ of two given functions $f(x)$ and $g(x)$ is as follows: $F(r) = \int_{-\infty}^{\infty} f(x)\, g(x+r)\, dx$. The meaning of this formula is shown in Fig. 4 for two simple rectangular functions $f(x)$ and $g(x)$. One of the two functions, say $f(x)$ is fixed, and the other function $g(x)$ is shifted by the value r. Then $f(x)$ is multiplied with this new function $g(x+r)$ point by point and the integral of the product is taken. This gives the value of the cross-correlation function at point r. Figure 4 shows, how the cross-correlation function $F(r)$ of these two functions $f(x)$ and $g(x)$ arises. In an analogous way, a two-dimensional cross-correlation function $F(r, s) = \iint_{-\infty}^{\infty} f(x, y)\, g(x+r, y+s)\, dx\, dy$ for the two-dimensional functions $f(x, y)$ and $g(x, y)$ can be built up.

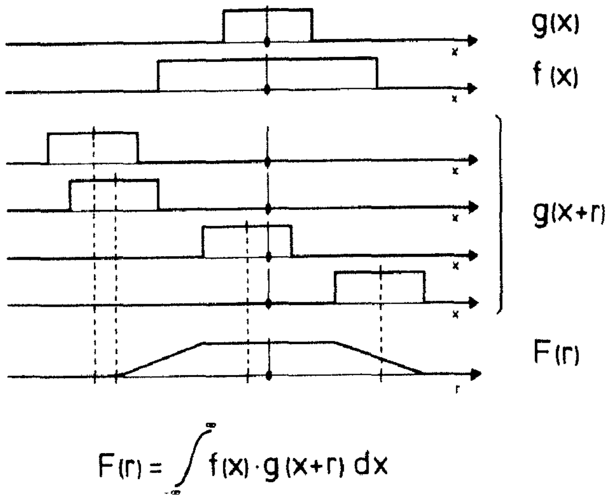

Fig. 4. Construction of the cross-correlation function $F(r)$ of two functions $f(x)$ and $g(x)$. For further explanation see text

Every optical pattern can be regarded as a two-dimensional function, where x and y are the coordinates of the plane of the receptor layer into which the pattern is projected, and where the values of the function $f(x, y)$ correspond to the values of intensity at the points (x, y). (Since, in the experiments discussed here, only dark shapes on a white background are used, intensity here means degree of darkness.) If therefore the central nervous system is to be able to "compute" the whole cross-correlation function of the shape seen at present and the rewarded shape, or only special values of this function, it is required that the rewarded shape be stored in the memory point by point.

Because the behaviour of the bees in these experiments can be described by a one-dimensional parameter (choice frequency from 0–100%), a whole function such as $F(r, s)$ cannot itself be an appropriate description of that behaviour. Therefore, to find a possible description, I looked for some special value of that cross-correlation function.

One possible parameter, the integral over the whole function $\iint_{-\infty}^{\infty} F(r, s)\, dr\, ds$, is ruled out because it depends only on the value of the total area of the positive and the negative shape. This means, that different shapes of equal area cannot be discriminated. Other general criteria for the form of the cross-correlation function are difficult to define, because the form of this function is very variable depending on the shapes to be compared. Therefore, a value of the cross-correlation function should be discussed, for which it is not necessary to compute the whole cross-correlation function beforehand.

This is the so-called cross-correlation coefficient, which corresponds to the normalized value of the cross-correlation function at point (0, 0):

$$r_{x,y} = \frac{\int\int_{-\infty}^{\infty} f(x,y)\, g(x,y)\, dx\, dy}{\sqrt{\int\int_{-\infty}^{\infty} f^2(x,y)\, dx\, dy \cdot \int\int_{-\infty}^{\infty} g^2(x,y)\, dx\, dy}},$$

if the origin of the coordinate axes x and y are set at the centre of gravity of the shapes. The cross-correlation coefficient r_{xy} can assume values between 0 and 1, considering functions with positive values only. The value of r_{xy} will be 1 when, and only when, the two shapes compared are completely identical, and it will be 0, when the two shapes have no common points i.e., when the condition $f(x_i, y_k) \neq 0$ and $g(x_i, y_k) \neq 0$, does not apply. This of course is an extreme case, which means that one of the two shapes doesn't exist at all. So the main characteristic of the cross-correlation coefficient with respect to pattern discrimination is that there should exist no invariant class referring to different shapes. Furthermore the cross-correlation coefficient is translation invariant, size invariant, but not rotation invariant. With those properties, the cross-correlation coefficient fulfills the most important conditions postulated by Sutherland (1968) for a system able to describe the pattern recognition of most studied animals.

The actual value of the cross-correlation coefficient of two given shapes can be more easily determined than the equation may suggest at first sight. Calling F^+ the total area of the positive and F^- of the negative shape, and A^+ and A^- the actual contrasts, the denominator $\sqrt{F^+ A^{+2} F^- A^{-2}}$ can be computed. If the two shapes are superimposed, so that the common area G reaches a maximum (Fig. 5), the value of the numerator is $G A^+ A^-$. Thus, the cross-correlation coefficient is as follows: $r_{xy} = \frac{G A^+ A^-}{\sqrt{F^+ F^- A^{+2} A^{-2}}} = \frac{G}{\sqrt{F^+ F^-}}$. As this formula shows, r_{xy} is independent of the contrast. Experimental results show however, that bees can discriminate between shapes of the same form but different contrast (Section B3). To describe these results, one may assume that, independently of computing the cross-correlation coefficient, the bee computes the difference of the contrast of the positive shape and the shape seen at present. This difference should then also be used for discrimination. To describe the results in another way, one could use a three-dimensional cross-correlation coefficient. To compute this, it must be assumed that the shapes

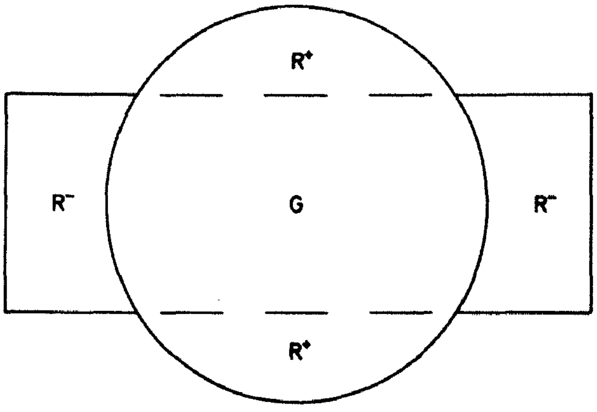

Fig. 5. The positive shape (circle) and the negative shape (rectangle) are laid on each other in such a way, that the common area G reaches a maximum. Then the non-overlapping areas of the positive shape, R^+, and the negative shape, R^-, can be determined

are projected in a three-dimensional space, with intensity being the third coordinate. In this three-dimensional space the shape may be regarded as a three-dimensional function in which the functional values of all points will be 1, with the coordinate of intensity less or equal to the actual intensity of the shape in the corresponding point of the two-dimensional function. The values of all other points in the three-dimensional space should be 0. Then the value of the three-dimensional cross-correlation coefficient is $r_{xyz} = \frac{G\,\mathrm{Min}(A^+, A^-)}{\sqrt{F^+ A^+ F^- A^-}} = \frac{G}{\sqrt{F^+ F^-}} \cdot \sqrt{\frac{A_1}{A_2}}$ with $A_1 \leqq A_2$. If $A_1 = A_2$, this coefficient corresponds to the two-dimensional cross-correlation coefficient r_{xy}.

Another value with very similar properties is the maximum of the normalized cross-correlation function. For this value you don't need the restrictions referring to the coordinate axes. But as the values of cross-correlation coefficient and this maximum are the same for most shapes, especially for all pairs of shapes discussed in this paper, we cannot discriminate between them. The values are only unequal for pairs of shapes for which the common area G is not maximum when the centres of gravity are superimposed. All the other properties are the same for the cross-correlation coefficient as well as for the maximum of the cross-correlation function. These both values are identical with respect to the results discussed in this paper.

Since the cross-correlation coefficient is translation invariant, but not rotation invariant, the shapes could only be superimposed by the bee by translatory movement. This is correct, when the shapes are demonstrated to the bee on a vertical screen. As Wehner (1972) showed, the position of the bee's head does not rotate relative to the vertical axis while looking at the shapes. But when the shapes are lying on a horizontal plate, no favoured axis relative to the shape exists, and so, in order to be able to detect the

Table 3. The weighting factors and standard deviations by which the experimental results can be described when using the three-dimensional cross-correlation coefficient r_{xyz}:

$$\mathrm{ChF} = (100 - N)\exp\left[-\left|C_1\left(\frac{1}{r_{xyz}^2} - 1\right) + C_2(\log K^+ - \log K^-)\right|\right] + N.$$

For details see text

Experiment no.	C_1	$\frac{A_1}{A_2}$ $(A_1 \geqq A_2)$	C_2	N	Standard deviation s (in %)	Mean of standard deviation of the single experiments $\bar{s}$ (in %)
I, 1 (b^+, b^-)	4.8	1.0	0.5	28	± 7.3	$\pm$ 9.7
I, 2 (dg^+, dg^-)	2.8	1.0	0.5	28	± 5.8	± 10.7
I, 3 (lg^+, lg^-)	2.2	1.0	0.5	28	± 8.0	± 11.8
II, 1 (b^+, lg^-)	4.8	1.3	0.5	28	± 6.8	$\pm$ 9.1
II, 2 (lg^+, b^-)	2.1	1.3	0.5	28	± 5.2	$\pm$ 9.1

positive shape, the bee would have to rotate while looking at the shapes. Therefore, as long as the experimental design doesn't give any preferred axis relative to the shapes, one has to translate and rotate the shapes until G reaches a maximum, when computing the common area G.

D. Application of the Cross-Correlation Coefficient to the Experimental Results

To describe the results of the experiments in terms of the equation for the cross-correlation coefficient r, an approximation function is required. This is unlikely to be linear. As a series of different computations showed, a good approximation can be obtained by the exponential function: ChF (choice frequency) $= 100\exp\left[-k\left(\frac{1}{r^2} - 1\right)\right]$, where k is an arbitrary constant. This equation however cannot yet be sufficient because it takes no account of the dependence on absolute contrast seen in Fig. 3 and Table 1. This dependence is not very surprising – it is also true for humans – but it cannot be explained by a cross-correlation coefficient r, as the above equations show. Without trying to find a hypothesis for it at present, one must try to find a description of this phenomenon by improving the approximation function. Since identical shapes always produce a coefficient of $r = 1$, this can only be done by using an additional weighting factor C_1 external to r: i.e.,

$$\mathrm{ChF} = 100\exp\left[-C_1\left(\frac{1}{r_{xyz}^2} - 1\right)\right],$$

where C_1 depends on the contrast.

The data fits this modified approximation function with a standard deviation of $\bar{s} = \pm 10.5\%$: this is not very well compared with the standard deviations of the experimental results. To make a better approximation, one can consider the hypothesis obtained by other experiments that the bees show a spontaneous preference for the shape with the greater contour length (Cruse, 1972a). Accordingly, the approximation function should be extended as follows:

$$\mathrm{ChF} = 100\exp\left[-\left|C_1\left(\frac{1}{r_{xyz}^2} - 1\right) + C_2(\log K^+ - \log K^-)\right|\right].$$

Here K^+ is the contour length of the positive, K^- of the negative shape, C_2 is a weighting factor. The standard deviation now reduces to $\bar{s} = \pm 8.5\%$.

Another property of the experimental results has not yet been taken into account by the approximation function; namely that the value of choice frequency does not reach the zero level (see Table 1, Fig. 3).

The lowest values are around 20–30%. Taking into consideration these so-called neutral choices N (Section B1), the approximation function becomes

$$\mathrm{ChF} = (100 - N)\exp\left[-\left|C_1\left(\frac{1}{r_{xyz}^2} - 1\right) + C_2(\log K^+ - \log K^-)\right|\right] + N.$$

With this approximation, the mean standard deviation is $\bar{s} = \pm 6.6\%$. The standard deviations and the weighting factors obtained by using this approximation function can be seen in Table 3. Comparing the standard deviations around the approximation function and the mean values of all standard deviations of the single choice frequencies (Table 1, 2), this approximation is found to be satisfying. Mean values of N and C_2 are used for this computation. The best values are a little scattered in the single series, but there is no systematic change. The values of $\frac{A_1}{A_2}$ are consistent with the hypothesis, because $\frac{A_1}{A_2}$ has the value 1.0 for the Series I, 1, 2, 3, in which $A_1 = A_2$. On the other hand $\frac{A_1}{A_2}$ has a value >1 for both Series II, 1 and II, 2.

Let us now look at the weighting factor C_1, the evident meaning of which is that a pair of different shapes can be discriminated more easily when the two shapes are black than when they are light grey. Comparing the different values of C_1, it is striking that within these experiments the value is correlated with the contrast of the positive shape. It could be supposed, that this factor C_1 has something to do with the storing of the rewarded shape in the memory. I shall refer to this question later (Section E).

As a qualification to the values of the weighting factors one should say something about how they were obtained. All these factors were obtained by looking for the minimum corresponding standard deviations, and then by taking the values of the weighting factor. In the case of Series II, 1 the minimum was very flat, giving several pairs of C_1 and $\frac{A_1}{A_2}$ which fitted the approximation equally well. Applying the same value for $\frac{A_1}{A_2}$ as obtained in the Series II, 2, a valid procedure according to the theory, I get exactly the same value for C_1 as in Series I, 1. So I chose this pair of weighting factors.

E. Meaning of Weighting Factor C_1

Although a sufficient description of the experimental results is obtained with the model using the three-dimensional cross-correlation coefficient r_{xyz}, it has a decisive disadvantage: it requires a three-dimensional storage space to store the positive shape. This seems to be very unlikely because very uneconomical. Since the experimental results can be as well described by application of the two-dimensional cross-correlation coefficient r_{xy}, using some additional assumptions, only the two-dimensional coefficient r_{xy} will be used in the following. This means that for storing the shape only a two-dimensional layer is used in the memory. Before discussing these necessary assumptions, let me first speculate on the physiological meaning of the weighting factor C_1. The effect that can be described by changing the weighting factor C_1, is that the same pair of shapes will be the better discriminated, the higher the contrast. As mentioned above, the value of C_1 is correlated with the contrast of the positive shape. The essential difference in the treatment of the positive and the negative shape is that the positive shape must be stored in the memory, while the negative one need not be, as the experimental procedure of Wehner (1967) shows, and, if there are enough negative shapes, surely is not. Therefore, one can assume that the weighting factor C_1 has something to do with the storing of the shape in the memory. If one takes into account that some kind of noise is superimposed on the stored signals in the memory, it must be that this noise influences the accuracy of determination of the margin of the shape. The possible accuracy of this determination depends on the signal-to-noise ratio; that is, with a constant noise amplitude, it depends on the value of contrast. The higher the contrast, the better the outline is detectable.

To explain why shapes with lower contrast are confused with one another to a higher degree than shapes with higher contrast, one can assume the following. When comparing the shapes, there is a tendency to make both shapes as similar as possible. That means that the shapes will at first be superimposed until the common area G reaches a maximum (Fig. 5). Then, if there is an inexactly definable outline, the common area G is enlarged in the range of the uncertainty of the outline. This leads to a higher cross-correlation-coefficient, and so a greater confusion. As explained above, this effect increases with decreasing contrast.

In order to find out if this consideration is consistent with the experimental results, it is necessary to do a computation in which the two shapes are compared point by point. This was done in the following way. First one has to carry out a spherical transformation with the shapes in order to take into account the distortion of the shapes when projected to the convex eye of the bee (Hertz, 1935a; Wehner, 1969).

This is done by projecting the shapes onto a sphere of 5 cm radius, which corresponds to a distance of 5 cm between shape and bee. Then the area of the shape is divided into small elements of 1 mm^2, which are arranged orthogonally. When seen from a distance of 5 cm, two neighbouring elements are seen as 1.1° apart. As Kirschfeld (1973) could show, the angle between the axes of two ommatidia is 3.2° in the x-direction (horizontal) and 2.3° in the y/z-direction (vertical). This means that each unit of area seen by one ommatidium consists of three elements of area in this computation. Therefore the screen used here is finer than that caused by the ommatidial array. The screen doesn't become coarser until the distance between shape and bee becomes lower than 2–2.5 cm. At these small distances, on the other hand, the distortion of the shape can no longer be described by a spherical transformation, as the measurements of Kirschfeld (1973) show.

Table 4. The weighting factors and standard deviations by which the experimental results can be described when using the two-dimensional cross-correlation coefficient r_{xy}:

$$\mathrm{ChF} = (100 - N)\exp\left[-\left|C_1\left(\frac{1}{r_{xy}^2} - 1\right) + C_2(\log K^+ - \log K^-) + \Delta f(A)\right|\right] + N.$$

For details see text

Experiment no.	C_1	p	$\Delta f(A)$	C_2	N	Standard deviation s (in %)	Mean of standard deviation of the single experiments $\bar{s}$ (in %)
I, 1 (b^+, b^-)	4.8	0.0	0.0	0.5	28	±8.1	± 9.7
I, 2 (dg^+, dg^-)	4.8	0.4	0.0	0.5	28	±7.8	±10.7
I, 3 (lg^+, lg^-)	4.8	0.7	0.0	0.5	28	±8.9	±11.8
II, 1 (b^+, lg^-)	4.8	0.0	0.65	0.5	28	±7.8	± 9.1
II, 2 (lg^+, b^-)	4.8	0.6	1.4	0.5	28	±4.9	± 9.1

To get the values for the common area G and the non-overlapping area R^+ and R^- (Fig. 5), the values of corresponding points of both shapes must be compared. If both points have a value of intensity greater than zero, they belong to the non-overlapping area R^+ or R^-, except in the following case: corresponding to the consideration discussed above, a point not belonging to the common area G but neighbouring such a point, and belonging to the non-overlapping area R^- of the negative shape, must be added to the common area G with a certain probability. That means, that the value of this point has to be multiplied by a factor $p \leqq 1$, and then added to G. The smaller this value, the more accurately the outline of the shape is defined in the memory.

This computation produces a satisfactory description of the experimental results of Series I with a factor $p=0$ for black shapes, $p=0.5$ for dark grey shapes and $p=0.7$ for light grey ones. The other weighting factors and the standard deviations are to be seen in Table 4. In these computations, the only points which are regarded as "neighboured" to a point of the common area G are those four which lie in the orthogonal grating directly beneath this point.

In order to avoid a possible confusion, one should emphasize, that the screen used here represents the unknown screen of the hypothetical storage elements and has nothing to do with the screen caused by the ommatidial pattern. As an estimate, however, one can say that this would probably not be more subtile than the screen of the ommatidial pattern. Accordingly the noise discussed here is assumed to be produced in the memory itself and has nothing to do with a visual noise produced by the transfer-properties of the ommatidia or by the background of the presented shape.

To describe the results of the Series II by means of the two-dimensional cross-correlation coefficient r_{xy}, one must firstly discuss some additional assumptions, as mentioned above. As discussed in Section D, one could imagine, that the contrast of a shape is measured and stored separately as an independent parameter of this shape, and that the dissimilarity between the values of contrast of the two shapes also influences the discrimination of the shapes. This means, that the approximation function has to be enlarged by an additional term $\Delta f(A)$, which represents this influence. As computations show, the real difference cannot fit the results of Series II. Therefore, assumptions are made which partially correspond to the assumptions dealing with the storing of the geometrical form of the shape:

1. The term $\Delta f(A)$ is proportional to the difference of the logarithms of the contrast values A^+ and A^-.

2. Onto the stored signal in the memory representing the value of the contrast of the positive shape A^+, a noise is superimposed which influences the accuracy of the determination of this value.

3. When comparing the two values of contrast, there is a tendency to make both values as similar as possible.

In order to make possible a simple description, let us assume that the value A^+ stored in the memory can only fall between the limits $(A^+ + d)$ and $(A^+ - d)$. d is a function of the amplitude of the superimposed noise, which is regarded as constant. With this assumption one obtains

$$\Delta f(A) = |k \cdot \mathrm{Min}(\log(A^+ + s) - \log(A^-))|$$

with $-d \leqq s \leqq +d$.

Here k is any weighting factor, and s is chosen as a value between $-d$ and $+d$ for which the value of $\Delta f(A)$ is a minimum (see assumption 3). As the

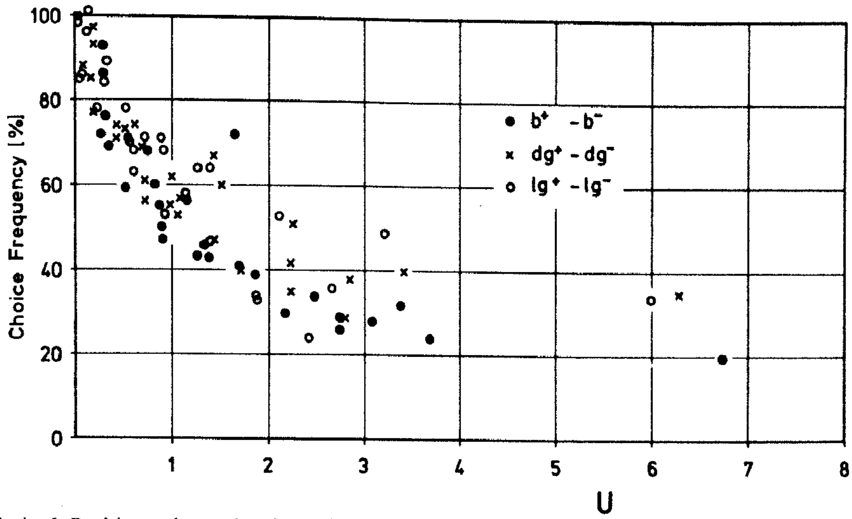

Fig. 6. Results of Series I. Positive and negative shapes have the same contrast. The choice frequency of the negative shapes (ChF) is plotted against the value of $U=\left|C_1\left(\frac{1}{r_{xy}^2}-1\right)+C_2(\log K^+-\log K^-)+\Delta f(A)\right|$, computed for each pair of shapes. Closed circles: black shapes, crosses: dark grey shapes, open circles: light grey shapes

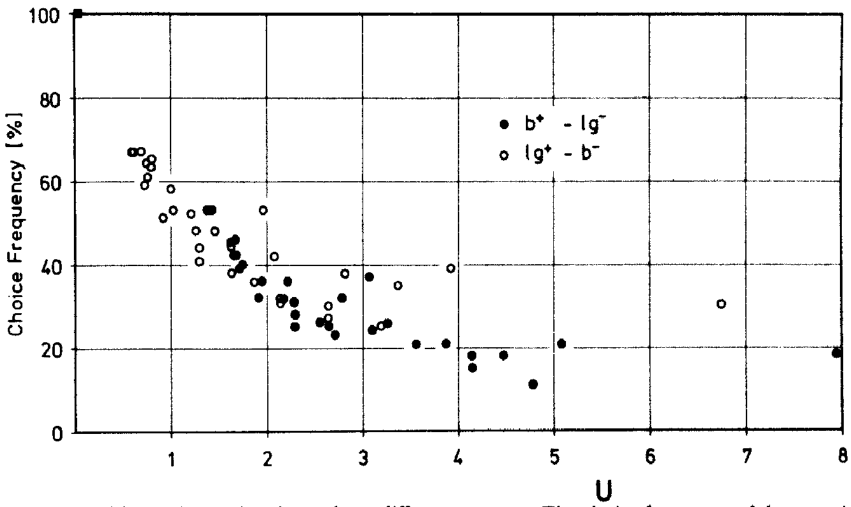

Fig. 7. Results of Series II. Positive and negative shapes have different contrast. The choice frequency of the negative shapes (ChF) is plotted against the value of $U=\left|C_1\left(\frac{1}{r_{xy}^2}-1\right)+C_2(\log K^+-\log K^-)+\Delta f(A)\right|$, computed for each pair of shapes. Closed circles: positive shapes black, negative shapes light grey. Open circles: positive shapes light grey, negative shapes black

weighting factors and standard deviations which are obtained by the approximation function

$$\mathrm{ChF}=(100-N)\exp\left[-\left|C_1\left(\frac{1}{r_{xy}^2}-1\right)+C_2(\log K^+-\log K^-)+\Delta f(A)\right|\right]+N$$

in Table 4 show, this description is also satisfying.

Since for the four unknown values of $\Delta f(A)$, the factors k, d, A_b and A_{lg}, only two equations are available, these values cannot be computed. But in order to show that the term $\Delta f(A)$ can assume the values shown in Table 4, one example should be demonstrated: $A_b=1000$, $A_{lg}=240$, $d=145$, $k=0.64$.

Finally, the experimental results of Series I and Series II can be seen in Fig. 6 and Fig. 7 respectively. On the abscissa are the values of $U=\left|4.8\left(\frac{1}{r_{xy}^2}-1\right)+0.5(\log K^+-\log K^-)+\Delta f(A)\right|$ computed for each pair of shapes: on the ordinate, the choice frequency is applied in the same way as in Fig. 3.

F. A Comparison with Former Experiments

Although the present results can be described by the approximation function discussed above, it is not possible to make predictions from them. Because, above all, the shapes applied here are rather similar to one another (Fig. 2) and can be arranged in a continuous series, nearly every form-parameter, such as contour length, for example, can give a good description of these experiments by itself. On the other hand, I earlier developed an empirical approximation function with which I could describe a great number of experimental results with very different shapes (Cruse, 1972a, b). This empirical function has for $A^+ = A^-$ the form:

$$\mathrm{ChF} = 100 \exp\left[-\left|C_1' \frac{R^+ + R^-}{G} F^+ + C_2' \log \frac{K^+}{K^-}\right|\right].$$

R^+ and R^- are the non-overlapping areas of the positive and the negative shape (Fig. 5). As the equations are similar, one would expect that these experiments can also be described by an application of the cross-correlation coefficient.

Ignoring the value of neutral choices N, the difference between the equations lies in the two terms: (1) $\frac{R^+ + R^-}{G} F^+$ and (2) $\left(\frac{1}{r_{xy}^2} - 1\right) = \left(\frac{F^+ F^-}{G^2} - 1\right) = \left(\frac{R^+ + R^-}{G} + \frac{R^+ R^-}{G^2}\right)$. So the difference lies in the factor F^+ existing in (1), not in (2), and in the term $\frac{R^+ R^-}{G^2}$, existing in (2), not in (1). F^+ and F^- stand for the total area of the positive and the negative shape.

Let us look first at some experiments (Cruse, 1972a) in which I tested the discrimination of shapes of different forms and different size. These experiments can be described by the approximation function discussed here with a mean standard deviation of $\bar{s} = \pm 12.7\%$, which is not significantly different from $\bar{s} = \pm 12.2\%$ given by the empirical formula. The different factors were $\bar{C}_1 = 0.24$, $\bar{C}_2 = 0.09$, $N = 30$. The experimental results of Schnetter (1968) for the discrimination of 4-pointed and 6-pointed stars can also be described by this approximation formula with a standard deviation of $s = \pm 8.6\%$ when the weighting factors $C_1 = 0.3$, $C_2 = 6.0$ and $N = 0$ are used. A second experiment of Schnetter (1968, Fig. 5) is consistent only with the description by the cross-correlation coefficient, not with the empirical formula. Here Schnetter tested the discrimination of two shapes of equal form, but different size. The discrimination was found to be independent of size over a very wide range. According to the empirical formula, the discrimination should improve with increasing size. Wehner (1967, Fig. 2, 3; 1968, Fig. 6, 7, 12, 16; 1969, Fig. 3) did experiments which could not be described by the empirical formula very well ($s = \pm 14.7\%$). These results can be described by the approximation function with a mean standard deviation of $\bar{s} = \pm 11.7\%$ using the factors $N = 5$ and $C_2 = 0$. $C_1 = 1.5$ was the weighting factor for all series except two: in the first of these, C_1 was 0.02 and in terms of the results mentioned above (Section D), the shapes of this series were very thin stripes ($\alpha \leqq 5°$, the width is here described by the angle, under which it is seen from a distance of $\geqq 5$ cm): When considering the contrast-transfer properties of a compound eye, as discussed by Götz (1965) for Drosophila, such small shapes should seem to the bee to have a lower contrast than in reality, corresponding to a smaller value of C_1. In the second series (Wehner, 1968, Fig. 12) C_1 was 0.3. Here the width of the positive stripe was $\alpha \leqq 11°$, whereas the width of the negative stripes varied from $\alpha \leqq 1°$ to $\alpha \leqq 103°$. With respect to the contrast-transfer function, the contrast of a stripe should be the lower, the smaller the stripe is. This would mean that the term $\Delta f(A)$ should be different for each pair of shapes. Additionally, the area of the stripes should increase, with increasing width, whereby smaller stripes are influenced in a relatively larger measure. As the directional-intensity function of a single ommatidium, as measured by Eheim and Wehner (1972), shows, the widening of the shapes is expected to be 7°. If one takes this into account in the computation, you get a description with the particular values of $\Delta f(A)$ shown in Table 5. Qualitatively, these values correspond to the form of the contrast-transfer function (Götz, 1965).

Table 5. The values of $\Delta f(A)$ necessary to describe the experimental series of Wehner (1968, Fig. 12). The angles refer to a distance of 5 cm, corresponding to the experimental device. The length of all stripes was 130°, the width of the positive stripe 11°

Width of neg. stripe	1°	2°	3°	5°	33°	53°	84°	103°
$\Delta f(A)$	2.6	1.5	0.6	0	0	0	0	0

Wehner (1971) did experiments, the results of which he interpreted by assuming that the bees applied the qualitative parameter "orientation of a stripe". Since these results have been obtained by transfer experiments (that is, in the test the positive shape cannot be seen by the bee) a quantitative evaluation is only possible in a restricted way. Whereas these results could be described by means of the empirical formula with a standard deviation of $s = \pm 12.5\%$, applying the cross-correlation coefficient the standard deviation becomes $s = \pm 6.8\%$.

G. Discussion

As shown in the sections above, a great number of published experiments can be described by this approximation function. Since the various assumptions which have been necessary to build up this function are described in different sections, all these assumptions should be summarized here:

1. The positive shape is stored point by point in the memory.

2. The two-dimensional cross-correlation coefficient r_{xy} (or the maximum of the cross-correlation function, see Section C) of the shape seen at present and the positive shape stored in the memory is computed. The measure for the probability of the bee's visiting the shape seen at present is a function of this value r_{xy}.

3. This function also depends (a) on the difference between the contour length of both shapes as a sort of spontaneous preference for the shape with greater contour length, and (b) on the absolute value of the difference of the contrast of both shapes. These differences are computed as the differences of the logarithms of the contour lengths or the contrast values respectively.

4. There is a continous noise superimposed on the stored signals which represent the positive shape. Because of this noise, the outline of the shape stored in the memory point by point is the less accurately detectable, the lower the contrast of the shape. When comparing two shapes by cross-correlation, there is a tendency to make both shapes as similar as possible. This means, for geometrically different shapes, that within this range of inexactly definable outline, the common area G is enlarged.

5. In an analogous way, a noise is superimposed on the stored value of the contrast of the positive shape. Therefore, this value cannot be determined exactly. When comparing the contrast of the positive shape with the contrast of the shape seen at present, again the tendency exists to make the difference as small as possible.

If one looks at shapes with the same contrast, only assumptions no. 1, 2 and 3 a are necessary. When contrast is changed from experiment to experiment assumption no. 4 is necessary in addition. If, furthermore, the contrast of the positive and the negative shape is different, assumptions no. 3b and 5 have also to be applied.

The exponential function, used here as an approximation function, may be not the best approximation possible. Above all, it is unlikely that a good approximation function starts with a slope very different from zero. It seems more probable that a subthreshold deviation from the positive shape should give a coefficient $r_{xy} < 1$, but not yet a measurable discrimination. Such a function, starting with a flat slope, could be demonstrated experimentally for the colour discrimination of the honey bee by v. Helversen (1972). Indeed, in my computation I find some corresponding systematic deviations from my approximation function, especially for the experiments of Wehner. As however the function of v. Helversen cannot be described in a simple analytical manner, I have not attempted to improve the approximation by using this function.

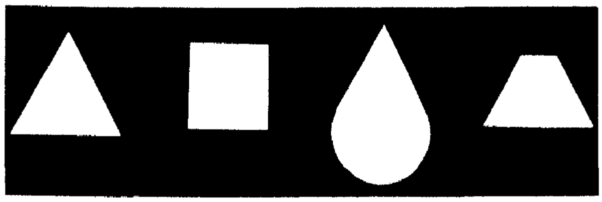

Fig. 8. Some of the shapes used in the experiments of Anderson (1972)

The different weighting factors which are used in describing the results of the different authors can probably be accounted for the different experimental conditions (contrast, light intensity, number of shapes presented at the same time) or to different training methods. The influence of the kind of the training method was first made use of by Schnetter (1968) in order to get better discriminations. Similarly, Anderson (1972) obtained a significant discrimination following special pretraining of pairs of shapes, which could not be discriminated before.

Nevertheless, there are experimental results which cannot be described by means of the model discussed here. The just-mentioned results of Anderson (1972), in fact, are only obtained in transfer experiments. Although, therefore, a qualitative computation is only appliable in a restricted way, it is clear that at least some of these results cannot be described by the model discussed here. Anderson trained bees on an upright triangle as positive shape and a square as negative shape, both on a vertical screen. In the test, various other shapes were diplayed in pairs: for example, similar shapes of different size, a triangle turned about 180°, a trapezoid, and a triangle which is enlarged by a segment of a circle (Fig. 8). While the bees treated the upright triangles of different size, and the triangle enlarged by the segment of a circle as similar to the positive shape, the triangles of different orientation, the squares and the trapezoid were treated as more similar to the negative shape. If the animal used the cross-correlation coefficient, the trapezoid should have been much more similar to the triangle than the triangle enlarged by a segment of a circle. I would interpret these results, therefore, to mean that in these experiments the bees applied the pair of abstract parameters "shape with pointed top – shape with flat top", though this cannot be proved from the results. Under "abstract parameter" here, such a quantity should be understood which cannot be represented by a numerical value.

Mazochin-Porshnyakov (1969) also tried to explain his results by postulating the application of such abstract parameters as "inside – outside", "coloured – of one colour" and "large – small".

Although the application of such abstract parameters by the bee could again not be proved, it seems to be very probable. This ability could be understood as being applied on one particular level of the CNS, the processes implied in the model described here being realized, if at all, at other levels of central nervous processing. If the application of such abstract parameters by the bee could be proved, it could be inclused in the model discussed here by the addition of further assumptions, making use, perhaps of abstract algorithm, as usually proposed only for higher vertebrates.

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