

SOME EXPERIMENTS ON FORM PERCEPTION IN  
THE NYMPHS OF THE DESERT LOCUST,  
*SCHISTOCERCA GREGARIA* FORSKÅL.

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INTRODUCTION

During an investigation into the importance of the visual sense in the behaviour of the desert locust it was found that individuals were attracted towards conspicuous objects in their environment and, if given a choice, showed a preference for certain shapes of object. The present paper is an account of the experiments performed to study this response in more detail.

Although these experiments are by no means exhaustive, their results indicate a few of the figural properties which are important to this insect. Spontaneous attraction towards objects in the visual environment and discrimination between the shapes of these objects has been shown in the case of several insects. It has been studied in bees (Hertz, 1929-37; Wolf & Zerrahn-Wolf, 1934, etc.; see References), in butterflies (Ilse, 1932), in caterpillars (Hundertmark, 1937*a*), and in grasshoppers (Williams, 1954). In this paper a general comparison is made between this previous work and the present results, and suggestions are advanced as to the possible basis of form discrimination in the desert locust.

METHOD AND MATERIAL

The principle of the experiments was to present an insect with two types of object in the visual field and to study its relative attraction to them.

The apparatus consisted of a circular arena 2 ft. in diameter with a wall 10 in. high. The wall was of white card and the floor was covered with white paper which was renewed from time to time. The objects were pieces of black card fastened on to the wall of the arena. Eight objects were used in each test, four of one shape and four of another. These shapes were arranged at equal intervals round the wall, the different shapes alternating with each other. In this way it was hoped to ensure that an insect placed in the centre of the arena had an equal chance of seeing both types of object. Light was supplied from a 100 W. opaque bulb hung 2 ft. above the centre of the arena and surrounded by a white shade. The experiments were performed in a darkened constant temperature room maintained at 28° C.

The animals used were nymphs of the phase *gregaria* of the desert locust *Schistocerca gregaria* Forskål. In most cases fifth-instar nymphs were used, but

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when unavailable they were replaced by fourths. These details are given in the table of results. There appeared to be no difference in behaviour between the two instars as can be seen from the experiments in which both were used (Exps. 2 and 9).

The animals were fed 1 hr. before testing.

#### OBSERVATIONS

An insect was placed gently in the centre of the arena and observed. It was found that it usually remained stationary for a short period (about a quarter of a minute). It then swayed the front part of the body slowly from side to side several times before starting to walk. This swaying motion is called 'peering' (Kennedy, 1945). After peering the insect set off and continued to walk until it reached the wall of the arena. During this journey it might pause from time to time, peer and then continue in the same direction as before or change to a new direction. In most cases an insect would go to one of the black objects present.

A run was terminated when the insect first touched the arena wall and this point was noted, taking the centre of the insect's head as the reference. A hit was scored if this point was on the black object or within 0.25 in. of the edge. This latter criterion was seldom needed because the orientation to the object edge was extremely accurate. Misses occurred when an insect touched the arena wall at a white part. (In a few experiments special criteria had to be used because of the nature of the objects; details of these are given in the appropriate parts of the text.) Several runs were made with the same animal (see Table 1). After every three runs or so the arena was rotated with respect to the floor. The paper floor was replaced when it had become marked (e.g. by excreta or regurgitated gut content). These precautions were to ensure that the choice was not biased by a tendency on the part of the insect to walk in any particular direction with respect to stable features of the environment, e.g. the bulb, or to follow any sort of scent track. Neither of these changes produced any disturbance of behaviour.

When an insect was placed in the arena care was taken not to point it directly at one object.

#### RESULTS

The results are presented in Table 1 and summarized pictorially in Fig. 1. On the null hypothesis that there is no attraction to the objects as compared to the white background the insects should pay equal visits to all parts of the wall. Thus the proportion of hits to misses should be in the same ratio as the respective lengths of circumference occupied by the figures and the white spaces. In fact it can be calculated that the actual ratio of hits to misses obtained differs highly significantly from this expectation. In all cases the number of misses is less than half the total number of hits. In comparing the relative attractiveness of each of a pair of figures therefore the misses are ignored and the distribution of hits is compared with a chance 50:50 distribution by  $\chi^2$ . The values of  $P$  as calculated by this method are given in the table.

Table 1. *The results obtained in spontaneous choice experiments to study form discrimination in the nymphs of the desert locust**Schistocerca gregaria*

(The table includes a verbal description of the figures used and these are also shown in Fig. 1)

Exp.	Figures		Results		$P$ $\chi^2$	Animals	
			Hits	Misses		Instar	No.
1	Rectangles of equal breadth; different height, area and perimeter	Rectangle 10 in. $\times$ 2 in. Rectangle 5 in. $\times$ 2 in.	34 6	0	$<0.01$	5	40 each, 5 times
2a	Rectangles of equal height; different breadth, area and perimeter	Rectangle 10 in. $\times$ 2 in. Rectangle 10 in. $\times$ 4 in.	66 22	12	$<0.01$	5	10 each, 10 times
2b	Rectangles of equal height; different breadth, area and perimeter	Rectangle 10 in. $\times$ 2 in. Rectangle 10 in. $\times$ 4 in.	28 9	13	$<0.01$	4	10 each, 5 times
3a	Same as 2 but with broad rectangle subdivided by extra vertical white stripe	Rectangle 10 in. $\times$ 2 in. Rectangle 10 in. $\times$ 4 in. with vertical white stripe 0.25 in. broad	30 41	29	0.1-0.2	4	20 each, 5 times
3b	Control for 3a, same as 2	Rectangle 10 in. $\times$ 2 in. Rectangle 10 in. $\times$ 4 in.	26 16	8	0.1-0.2	4	10 each, 5 times
4	Rectangles of equal height; different area, breadth and perimeter	Rectangle 5 in. $\times$ 2 in. Rectangle 5 in. $\times$ 0.25 in.	50 29	21	0.01-0.02	4	20 each, 5 times
5	Rectangles of equal area; different height and perimeter	Rectangle 6 in. $\times$ 1 in. Rectangle 3 in. $\times$ 2 in.	72 9	19	$<0.01$	5	10 each 10 times
6	Rectangles of equal area and equal perimeter; different height	Rectangle 2 in. $\times$ 1 in. vertical Rectangle 2 in. $\times$ 1 in. horizontal	43 17	30	$<0.01$	4	10 each, 10 times
7	Equal panels of black and white	Black 10 in. $\times$ 9 in. White 10 in. $\times$ 9 in. Edges	4 4 22	0	$<0.01$	5	30 each, once
8	Straight sided figures; one vertical, one at 45°	Rectangle 6 in. $\times$ 1 in. vertical Stripe 1 in. broad oblique	40 17	3	$<0.01$	5	12 each, 5 times
9a	Figures with long axes vertical, equal height; one straight, one wavy	Rectangle 8 in. $\times$ 1 in. Wavy stripe 8 in. tall, 1 in. broad	75 20	5	$<0.01$	5	20 each, 5 times
9b	Same as 9a	Rectangle Wavy stripe	46 18	11	$<0.01$	4	15 each, 5 times
10	Figures with long axes vertical, equal height; one straight, one serrated and of different area	Rectangle 8 in. $\times$ 1 in. Vertical figure 8 in. tall 1 in. max. breadth, 16 serrations/side	114 65	21	$<0.01$	5	40 each, 5 times
11	Figures with long axes vertical, equal height, equal area; one straight, one serrated	Rectangle 8 in. $\times$ 2 in. Vertical figure 8 in. tall, 2.5 in. max. breadth, 8 serrations/side	30 15	10	0.02-0.05	5	11 each, 5 times
12	Tall serrated figure, short rectangle	Rectangle 4 in. $\times$ 2 in. Serrated figure as in Exp. 11	13 44	18	$<0.01$	5	20 each, 5 times
13	Figures of equal diameter; different complexity of contour	16-pointed star 3 in. diameter Circle 3 in. diameter	59 27	14	$<0.01$	5	20 each, 5 times
14	Figures of equal diameter; different complexity of contour	8-pointed star 3 in. diameter Circle 3 in. diameter	30 12	18	$<0.01$	5	10 each, 5 times

*Statement of results*

The results show firstly that in all cases (except Exp. 7) the insects orientated quite definitely to the black objects present.

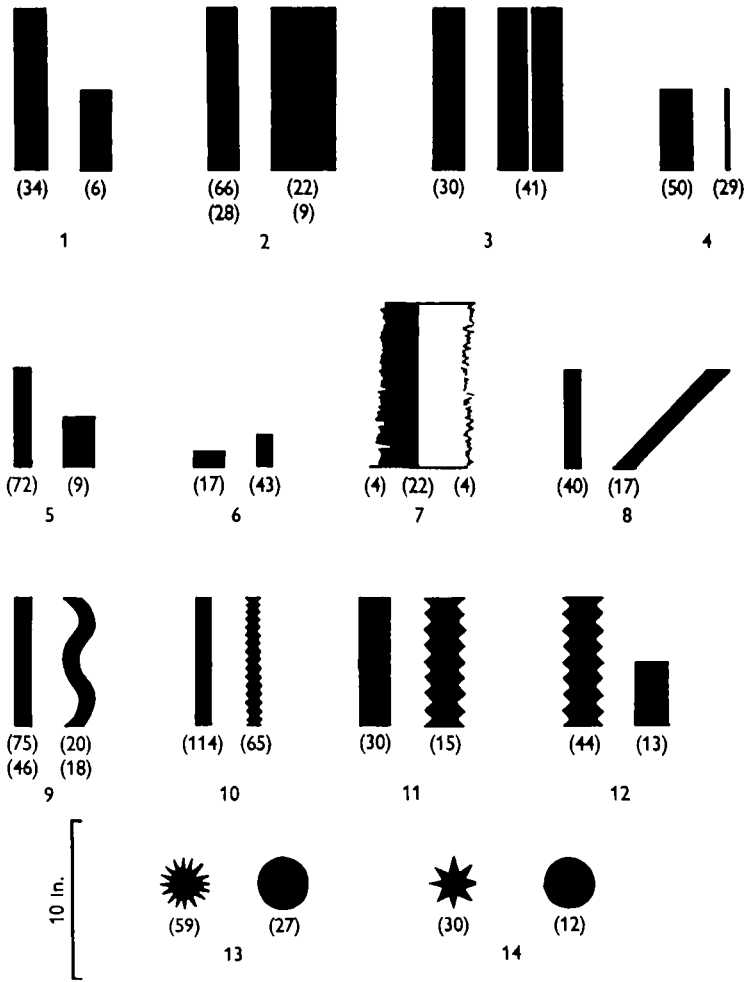


Fig. 1. Diagram summarizing the results of spontaneous choice experiments to study form discrimination in nymphs of the desert locust *Schistocerca gregaria*. The shapes are all to the same scale, which is shown. The single number below each pair of shapes is the number of the experiment. The number in brackets below each shape indicates the number of visits to that shape. Where there are two sets of bracketed numbers these are referred to as *a* and *b* in Table 1.

*First experiment*

In this experiment (rectangles of breadth 2 in.; one 10 in. tall, the other 5 in. tall) the insects showed a preference for the taller figure. It was not clear, however, exactly which properties of the tall figure made it more attractive. Apart from the

obvious feature of height the taller figure had also a greater area and perimeter than the shorter one. Exps. 2-7 were intended to evaluate the importance of these properties. These will now be discussed.

### *Area*

The effect of area was tested in two ways:

- (1) By comparing figures of equal height and different area (Exps. 2-4).
- (2) By comparing figures of equal area and different height (Exp. 5).

The result of Exp. 2 (rectangles 10 in. tall; one 2 in. broad, one 4 in. broad) showed that in this situation it was not the figure of greater area which was chosen.

In Exp. 4 (rectangles 5 in. tall; one 2 in. broad, one 0.25 in. broad) the figure of greater area was chosen. This may, however, have been due to the fact that the smaller figure was extremely narrow.

Exps. 2 and 4 thus suggested that the effect of area was variable. Furthermore, it was found that the bias in favour of the narrower stripe in Exp. 2 could be significantly reversed by subdividing the broad figure with a vertical narrow white stripe (Exp. 3). Thus it appeared that not only was the effect of area variable but also that it could be outweighed by the number of vertical black/white edges.

In contrast to the variable effect of area, Exp. 5 showed that the effect of height was very marked. The figures were of equal area (rectangle 6 in. tall, 1 in. broad and rectangle 3 in. tall, 2 in. broad) and the taller was preferred.

### *Perimeter*

Exps. 2-5 suggested that the effect of perimeter was also variable. Thus the chosen figure in Exp. 2 had a smaller perimeter than the alternative figure. In Exps. 4 and 5 the chosen figure had a greater perimeter than the other. It is significant that in these last two cases the greater perimeter is due to a greater length of vertical edge.

In Exp. 6 not only were the figures of equal area but also of equal perimeter (rectangles 2 in.  $\times$  1 in.; one with long side vertical, the other with long side horizontal). The taller figure was chosen. The larger number of misses (30) was probably due to the small size of the objects. This small size was rendered necessary since the largest side could not be much greater than 2 in. otherwise the breadth of the horizontal figure would complicate matters. (This arose from Exp. 2, where it was found that a very broad object was not attractive, irrespective of height.)

### *Tall black/white edge*

The experiments so far had demonstrated the variability of the effect of area and perimeter and emphasized the importance of tallness as an attractive feature. It was possible to be more specific and to say that it was the length of the vertical black/white edge which was important. In all the experiments the insects were seen to orientate to the vertical black/white edges when approaching the figures. Also, the addition of extra black/white edges (Exp. 3) increased the attractiveness of a

figure. (In this experiment the insects also orientated to the vertical black edges in the centre of the figure.) Finally, if the whole of the circumference of the arena were divided into equal panels of black and white (Exp. 7) the insects orientated to the vertical black/white boundaries.

### *Verticality*

The importance of the verticality of the black/white edge was tested in Exp. 8. Both figures had straight edges but in one case the long edge was at  $90^\circ$  to the horizontal while in the other it was at  $45^\circ$ . Both figures were of the same vertical height (6 in.). An insect reaching the arena wall at any point within the horizontal projection of the oblique was counted as orientating to that figure.

The insects showed a significant preference for the vertical figure.

### *Straightness of edge*

Exps. 9–11 were designed to evaluate the importance of the verticality of a figure as a whole as compared with the verticality of its edge. It is obvious that in one sense it is impossible to have an edge which is vertical if it is not straight. However, it is possible to have a figure which, as a whole, is vertical, i.e. with the long axis in the vertical plane, although the edges of the figure are not straight and therefore not vertical. In Exps. 9–11 all the figures were vertical in this sense and a comparison was made between a vertical figure with a straight edge and one with a wavy or serrated edge. The results showed that in these situations a straight edge was more attractive than a wavy or serrated edge.

In these experiments it should be noted also that the chosen figure was that with the smaller perimeter in each case.

It was clear also that area was of little importance in these cases. In Exp. 9 the negative figure was the larger in area, in Exp. 10 it was the smaller and in Exp. 11 the areas of the figures were equal.

### *Equating attractiveness of properties*

The importance of the straight vertical edge had been clearly demonstrated in the preceding experiments. Exp. 12 showed, however, that the effect of this property could be outweighed by a preponderance of a different property in the alternative choice figure. In this situation the taller figure was preferred, although it had a serrated edge whereas the short figure had a straight edge.

### *Complexity of contour*

Hertz found that, for bees, the amount of the contour was an important figural property. Exps. 13 and 14 tested the importance of this property for locust nymphs in situations where none of the figures possessed a straight vertical edge. Under these conditions the figure with the more broken-up contour was preferred.

## DISCUSSION

Since the results reported here are similar in many respects to those obtained by previous workers for other insects it is unnecessary to compare them individually in detail and only the main results will be so considered. These are: (1) attraction to figure edges; (2) preference for vertical edges as against oblique, wavy or serrated edges; (3) importance of complexity of contour.

Attraction to figure edges is well known. Kalmus (1937) described it in the nymphs of *Dixippus morosus* and called the response 'photo-horotaxis' (see also Hundertmark, 1937*b*). Certain lepidopteran larvae (Hundertmark, 1937*a*) and sawfly larvae (personal observation) also show the response, as do certain grasshoppers (Williams, 1954).

Preference for a vertical edge as opposed to an oblique edge is shown by *Lymantria* caterpillars (Hundertmark, 1937*b*). Williams found that, although his grasshoppers did not show any preference for a vertical stripe as against a vertical zig-zag of stripes, nevertheless they did show a preference for vertical stripes as against horizontal stripes. The present results also show that the vertical edges of the figures are more important than the horizontal edges.

Hertz (1929*b*, 1931, 1933) and Zerrahn (1934) showed that, for bees, the more complex the contour the more attractive the figure. Ilse (1932) showed the same for certain butterflies.

It is fairly well established that in any theory of form discrimination in insects the operative stimuli to be considered are the changes in the intensity of light falling on the ommatidium when an image moves on the retina (Hertz, 1929*a, b*, 1931, 1933, 1934*a, b*, 1935, 1937; Wolf, 1935; Autrum, 1948, 1952). Henceforth, for shortness, such changes will be referred to as 'stimulus changes'.

Before proceeding with the discussion the following point must be made with regard to the units involved. Underlying most previous work on insect vision has been the mosaic theory of image formation by the apposition eye (Müller, 1829, in Wigglesworth, 1953). This theory supposes that each ommatidium receives light from only a very limited region of the visual field. Thus 'each ommatidium receives the impression of a luminous area corresponding to its projection on the visual field' (Wigglesworth, 1953). Previous workers have interpreted their findings in terms of the visual field of the ommatidium as strictly equivalent to the projection of the ommatidial angle (e.g. Baumgärtner, 1928; Wolf, 1935; Gavel, 1940; Hassenstein, 1951). It has been shown, however, by Burt & Catton (1954) that in *Locusta migratoria migratorioides*, and in the hive bee that the visual fields of the ommatidia overlap to a considerable extent, and these authors suggest that this is probably true of most compound eyes. It is desired to point out here that the argument which follows is not affected in principle by this factor of overlap since, whatever the functional units, be they single ommatidia or groups of ommatidia, their distribution will be determined by the distribution of the ommatidia in the eye.

Many of the results of the present experiments are immediately explicable on the basis that the insects are attracted to the figure whose contour produces the

greatest number of such changes per unit time as it moves past the eye. Clearly the vertical contours will be the important ones since they are perpendicular to the direction of the insect's motion when walking on a horizontal surface\* and will thus produce the greatest number of stimulus changes per unit time for any movement of the insect. Figures with longer vertical contours will be more attractive than those with shorter ones (Exps. 1, 5 and 6). If the lengths of the vertical edges are equal an increase in the number of vertical contours will increase the attractiveness of a figure (Exp. 3. Compare experiment and control). Complexity of a figure contour will also increase the number of stimulus changes per unit time and thus increase the attractiveness of the figure (Exps. 13 and 14).

A difficulty arises in the case of Exps. 8-11. It is probably justifiable to consider that, to a first approximation, the number of ommatidia stimulated by the movement of a contour is proportional to the area 'swept out' by the contour. Thus if a figure moves a certain distance  $X$  in a straight line the area swept out by its leading contour is  $LX$ , where  $L$  is the length of this contour. This will be the area swept out by a vertical contour of length  $L$  moving a distance  $X$  horizontally. Considering an oblique contour moving the same distance horizontally, it can be shown that if the oblique contour is of such a length as to reach the same vertical height as the vertical contour then it will sweep out the same area as does the latter; i.e. it will stimulate the same number of ommatidia. Hence, it would appear that the vertical and oblique figures in Exp. 8 should stimulate the same number of ommatidia for the same movement over the eye. Thus, purely on this basis they should be equally attractive. The same argument applies in the case of the wavy and serrated edge (Exps. 9-11). Yet in each case the vertical edge is chosen. These experiments therefore suggest that, apart from the number of receptors stimulated, special significance attaches to the spatial distribution of the receptor cells which are stimulated at any particular instant. To be more specific, an important feature of the stimulus may be the proximity of the groups of ommatidia which are stimulated. It is possible that, apart from three unique orientations, the passage of the image of an oblique edge over the retina may result in more spatial and temporal dispersion of the ommatidia which are stimulated than is the case for a vertical contour. (The unique directions are a consequence of the hexagonal nature of the ommatidium and are the directions in which a straight line will pass through the centres of adjacent ommatidia—see Gavel (1940) and Hassenstein (1951). The pattern of the ommatidial projections will also have this feature.)

The results of Exp. 2 remain to be considered, for it is clear that they are not explicable on the bases already postulated. The long contours of both figures are vertical and of equal length so that they will stimulate the same number of ommatidia in the same spatial pattern. The previous postulates are conceived in terms of ommatidia undergoing simultaneously changes of the same 'sign', i.e. all either responding to an increase in light intensity (going 'on') or to a decrease in light

\* This motion of contours over the eye will be produced also by the peering movement already described. A detailed account of this movement and its significance will be published elsewhere. It is relevant to state here that there is evidence to show that it is a scanning movement.



intensity (going 'off'). With respect to Exp. 2 it can be suggested either that the spatial distribution of ommatidia which are stimulated simultaneously whatever their 'sign' is important or that the shortness of the time interval between the 'on' and 'off' state of any one ommatidium is important. These features are not mutually exclusive, and both depend on the distance between the moving contours, i.e. on the breadth of the figures.

Hertz (1929*b*) advanced the opinion that a spontaneous choice of certain figures, such as she had found to occur in bees, would also be found in other arthropods with different living requirements, and that these would reflect the properties of a simple nervous system. It is interesting, therefore, to consider the present results in the light of the theories of form discrimination which have been put forward in the case of the bee (Hertz, 1929*a*, 1931, 1933, 1934*a, b*, 1935, 1937; Wolf, 1934; Zerrahn, 1934; Wolf & Zerrahn-Wolf, 1934, 1936).

The view of Wolf & Zerrahn-Wolf can be stated very briefly. They believed that the bees were attracted to the figure which caused the greatest number of stimulus changes per unit time as the bee flew over it and that only this total number was important. They found that, in the figures studied, there was a linear relationship between the percentage choice of a particular figure and its contour length. They concluded therefore that 'recognition and distinction of patterns by bees is based upon the transitory stimulation produced by a pattern and that the pattern as such is of no importance' (Wolf & Zerrahn-Wolf, 1936).

Hertz (1931, 1935) denied that this was a complete explanation. She herself distinguished two main classes of figural property which determined a figure's attractiveness and on which figures were differentiated. These were figural intensity and figural quality. Figural intensity was, in effect, number of stimulus changes per unit time. Figural quality depended on the spatial rate of change of angle of a contour line, the greater this rate of change the more attractive the figure. Figures such as small circles with strongly curved contours or those with serrated contours possessed this quality (Hertz, 1933).

As has been discussed above, a theory based on number alone does not seem to be the complete explanation of form discrimination in the desert locust, and it has been suggested that the spatial and temporal separation of the ommatidia which are firing is also important. The importance of this spatial and temporal distribution was pointed out by Hertz (1935), and it therefore seems that the present findings are more in general agreement with her theory than with that of Wolf & Zerrahn-Wolf. The present results do, however, appear to differ in detail from what would be expected on Hertz's theory, for on this latter basis wavy and serrated figures should possess greater figural quality than the vertical ones and should be preferred to them.

The present findings suggest that different criteria are used for form discrimination in different situations depending on the nature of the figures involved. It seems that whenever the figures produce greatly differing numbers of stimulus changes per unit time the discrimination is made on this basis. (Hence in Exp. 12 the attractiveness of the taller stripe is greater than that of the shorter vertical stripe.)

It should be noted also that where there is such a large difference between the figures the preference in each case is strongly marked (see Exps. 1, 5). When figures produce approximately equal numbers of stimulus changes per unit time it seems that the discrimination may be made on the basis of the spatial and temporal proximity of the ommatidia involved. The results of such experiments suggest that this discrimination is perhaps less readily made.

#### SUMMARY

1. Nymphs of the desert locust are spontaneously attracted to simple forms in the visual environment, and show a preference for certain figures.
2. Experiments are described which analyse certain of the important properties which make a figure attractive to this insect. The insects show a preference for long straight vertical edges as opposed to short straight vertical edges. Straight vertical edges are preferred to straight oblique edges and vertical figures with straight edges are preferred to vertical figures with wavy or serrated edges. In the absence of straight vertical edges a preference is shown for the figure with the more complex contour (for figures of comparable size).
3. It is postulated that in this insect form discrimination is based on the number of stimulus changes per unit time produced by moving contours and on the spatial and temporal distribution of such changes.
4. The results are compared with those of previous workers and in particular with those of Hertz and of Wolf and Zerrahn-Wolf on the bee.

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