

Visual discrimination of discontinuous figures in the rabbit

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(Received 8 March 1989)

(Revised version received 11 May 1989)

(Accepted 11 May 1989)

Key words: Visual discrimination; Discontinuity of figure; Rabbit

Rabbits were trained to discriminate between vertical and horizontal striations. After the 90% correct level had been reached transfer to vertical and horizontal rows of dots was studied. It was found that performance depended on the distance between adjacent dots. With angular dot separations (measured from the centers) larger than 4.9° , performance was below the 75% correct level. This result is discussed in relation to the size of the receptive fields of orientation-selective neurons in the binocular visual cortex.

INTRODUCTION

An early experiment by Lashley showed that rats, which were trained to discriminate between vertical and horizontal striations, were able to generalize to either a single continuous bar or a discontinuous one^{7,8}.

In the rabbit the situation seems to be different. Rabbits trained to discriminate between bars of different orientation did not transfer to rows of dots¹⁴. The animals learned to discriminate these rows of dots only after considerable retraining. From these and other experiments it was postulated that the rabbit has two mechanisms of orientation discrimination: one where the straight edges of the bars are the cues by which the animals discriminate the patterns; and the other one which extrapolates bands across the retina in which a high density of contrast, irrespective of shape, is present. It was further postulated that orientation-selective units were exclusively involved in the first mechanism.

This theory was challenged by Hughes³. He described orientation-selective units in the visual cortex of the rat which treated rows of dots as equivalent to bars. It seems obvious that this mechanism requires that the distance between adjacent dots does not exceed the diameter of the receptive fields. However, the conditions under which the rabbit behavioral experiments were done¹⁴ differed considerably from those in Hughes' experiments. During visual discrimination the distance between the targets and the eyes varied sometimes between 0 and 10 cm^{12,14}. Due to the relatively large variations of the distance between targets and the eyes, it is hard to estimate what the distance between the dots on the retina was during visual discrimination testing.

In the experiments to be described, visual discrimination of striated patterns and rows of dots of different orientation was studied under circumstances which are suitable for studying quantitative relations between results obtained with behavioural and electrophysiological methods.

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A discrimination apparatus was used which had a distance of 25 cm between the targets and transparent viewing doors that the animal had to open to reach the food^{9,13}. Under these circumstances the retinal projection is clearly focussed. It has been shown that in this training apparatus the image is projected on the temporal part of the retina^{1,4,6,16}. In addition, two recent publications are available in which the receptive fields in the temporal retina are described in great detail^{5,10}.

MATERIALS AND METHODS

Animals

The animals were 12 adult Dutch-belted rabbits. All animals started training at the age of approximately 5 months. During training all animals were kept at 80% adult body-weight. A daily ration of food pellets was given following each training session.

Apparatus

A pattern discrimination training box for rabbits was used^{9,13}. The automatic control system and basic pretraining procedure have been described elsewhere^{11,12}. The apparatus essentially consisted of a test chamber with one wall having two top-hinged panels on which visual displays could be back-projected.

To make a correct choice the animal was required to press the panel illuminated by the correct display. This response was automatically rewarded by the delivery of a 100-mg pellet of food, after which the displays were turned off and the trial was ended. Responses made to the panel with the incorrect display produced no reward but terminated the trial, as a non-correction training procedure was used. A 6-s intertrial interval was used throughout all training.

The patterns were back-projected on a 10-cm diameter translucent circular window in each panel. The position of the correct and incorrect display was randomized by a computer-controlled sequence of haphazard alternations with the main constraint that no position could recur more than 3 times consecutively.

At first the animals were trained to discriminate vertical vs horizontal striations. The width of the

black and white stripes was 1.25 cm. Fifty trials were given per day. In all cases the vertical striations were rewarded.

After the 90% correct level had been reached on two consecutive days, the vertical and horizontal striations were placed at a distance of 10 cm behind the viewing gates of the training apparatus. If the 90% correct level was reached again on two consecutive days, the targets were placed at 12.5 cm distance. This procedure was repeated in steps of 2.5 cm until the targets were at 25 cm¹⁵. At that distance the solid angle under which the targets were seen was 22.62°; the width of the stripes was 2.86°.

Following this procedure training was continued, but now the vertical and horizontal striations were randomly alternated with rows of dots (see Fig. 1), in order to determine the ability to discriminate orientation differences using discontinuous linear displays. The diameter of the dots was 1.25 cm (2.86° at 25 cm) in all cases.

From refraction and scleral image studies^{1,4} with chequerboard patterns 25 cm in front of the eye, it is known that optimal focussing takes place in the temporal area of the retina. To ascertain that the dots were well focussed on the retina, we studied the sharpness of the transscleral image in enucleated albino rabbit eyes¹. Within 15 min after enucleation under urethane anaesthesia the various patterns (diameter 10 cm), shown in Fig. 1, were placed 25 cm in front of the eye. The eye was rotated in such a way that the image fell on the temporal retina⁶. The scleral image was then photographed through the posterior surface of the globe of the eye. Examples of such images of both continuous and discontinuous linear displays are shown in Fig. 2.

RESULTS

At first the rabbits were trained to discriminate vertical vs horizontal striations at a distance of 25 cm. After the 90% correct level had been reached on two consecutive days, training was continued during 5 days (A in Fig. 1), with 50 trials of patterns of vertical and horizontal striations randomly alternated with 50 trials of vertical and horizontal rows of tangent dots. In

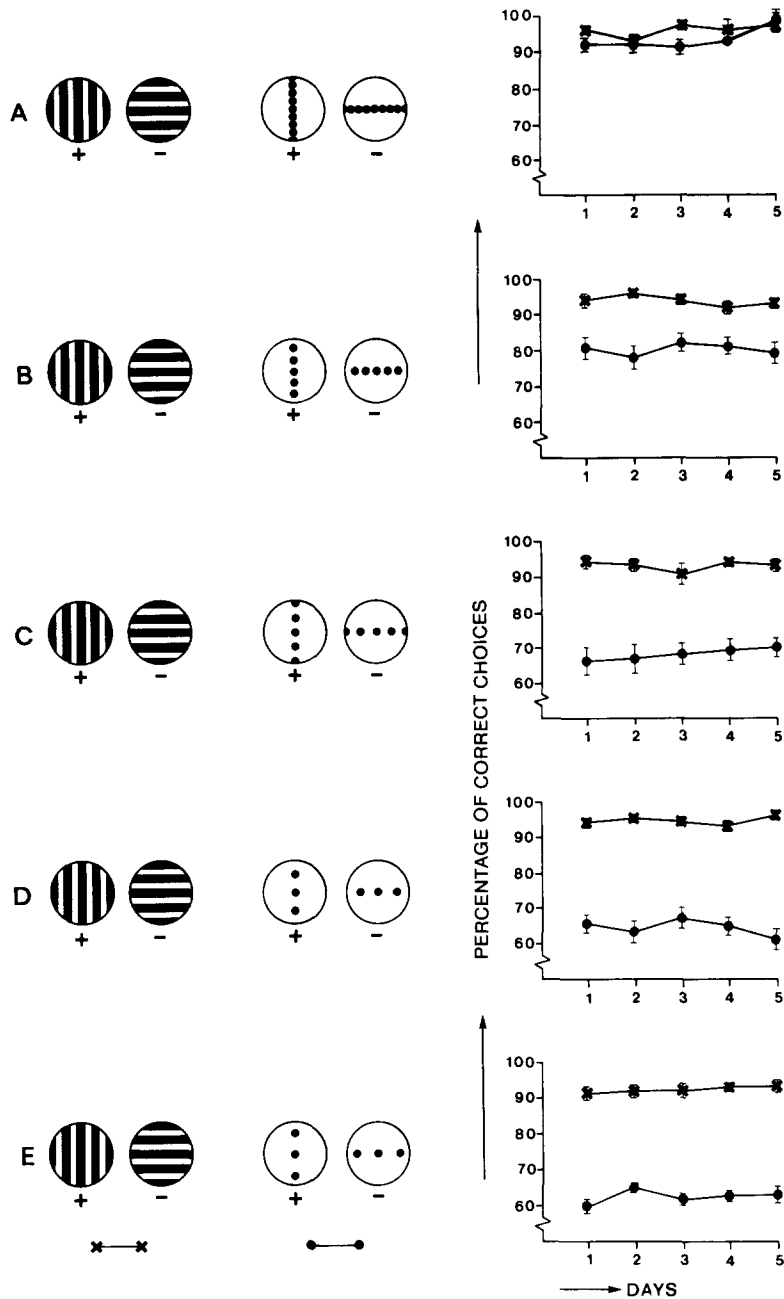


Fig. 1. Twelve rabbits were trained to discriminate between vertical and horizontal striated patterns at a distance of 25 cm. One hundred trials were given per day. After the 90% correct criterion had been reached the procedure was altered. On 5 consecutive days 50 pairs of striated patterns and 50 pairs of rows of tangent dots were presented in random sequence (A). The diameter of the patterns was 10 cm, stripe width and diameter of the dots was 1.25 cm. This means that at 25 cm distance the solid angle under which the patterns were seen was 22.62° , the stripe width and the diameter of the dots was 2.86° . The same procedure was followed with rows of dots which were separated from each other. In B, angular distance between the centers of adjacent dots was seen under an angular distance of 4.29° . In C, D and E these angular distances were 5.72° , 7.15° and 8.58° resp. The average scores and standard errors for striations (crosses) and rows of dots (dots), on 5 consecutive days, are plotted.

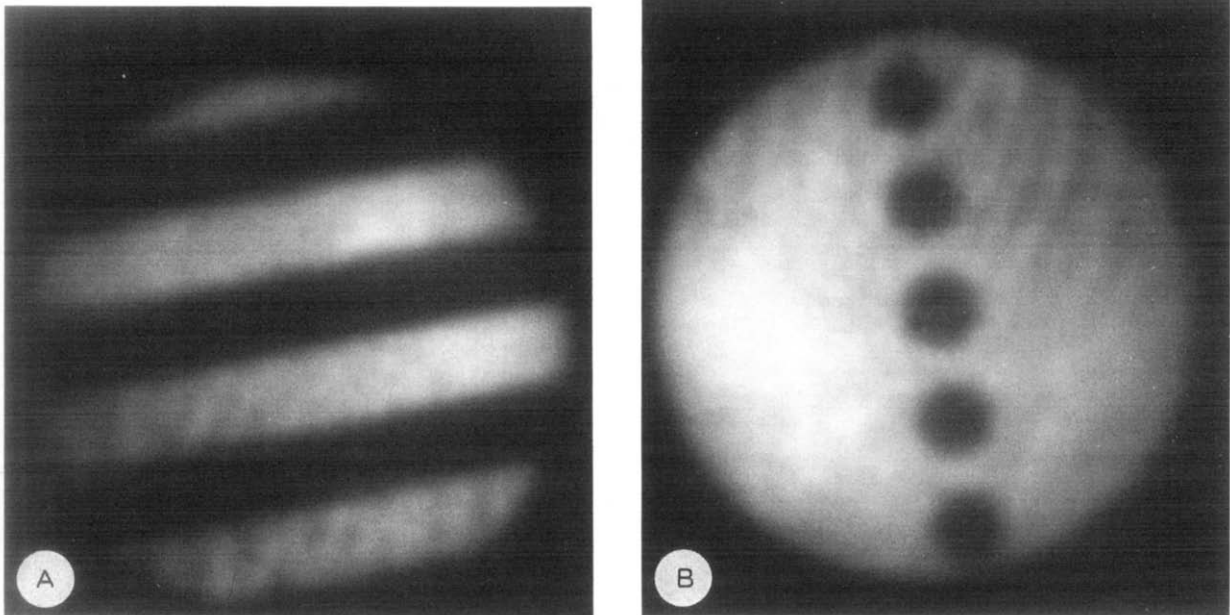


Fig. 2. Scleral images of striations and dots (as shown in B) in enucleated albino eyes. The patterns were placed at 25 cm in front of the eye. The enucleated eye was rotated in such a way that the pattern was projected on the temporal retina. Diameter of the patterns was 10 cm, that of the scleral image 2.9 mm.

Fig. 1A the average scores and standard errors on 5 successive days are plotted. In Fig. 1B–D the distances between dots were increased, in such a way that the interdot distance increased linearly for each series by a half dot diameter. Only in series B were the average scores above the 75% correct level; for the remaining series the results were below this criterion level.

In Fig. 2 examples of transscleral images of a grating and a row of dots as used in Fig. 1B are given. The size of the transscleral image was 2.9 mm. These photographs show that the dots are well focussed on the retina. This decisively rules out the possibility that the relatively high scores in Fig. 1B were due to the fact that rows of dots blur into a bar on the retina.

DISCUSSION

Hughes argued that the trigger features of cortical orientation-selective units could well explain the rabbit's ability to discriminate rows of dots of different orientation. He argued that simple cells in the visual cortex could respond differentially to both bars and rows of dots which were projected

parallel or perpendicular to the boundary between the excitatory and inhibitory area, provided that two adjacent dots were, at least partially, simultaneously projected within the receptive field.

Visual discrimination is known to be mediated by the temporal retina⁶. In two publications the size has been studied of the cortical receptive fields in the binocular area corresponding to the temporal retina^{5,10}. In the study by Hughes and Vaney⁵ the diameter of directional and orientation-selective fields was found to be $2.8 \pm 1.9^\circ$. This is in agreement with the median value for simple cells given by Swadlow¹⁰.

In Fig. 3 the percentages of correct choices are plotted against the distances between the centers of two consecutive dots seen from the distance of the viewing windows (25 cm). For each animal the average percentage of correct choices out of 250 trials with each set of dots was determined. The average results and standard errors of all 12 animals are plotted. Using the distance between the centers of the dots was not arbitrary. The rationale was that comparison of the distance between the centers and the diameters of the receptive fields gives an indication of the possi-

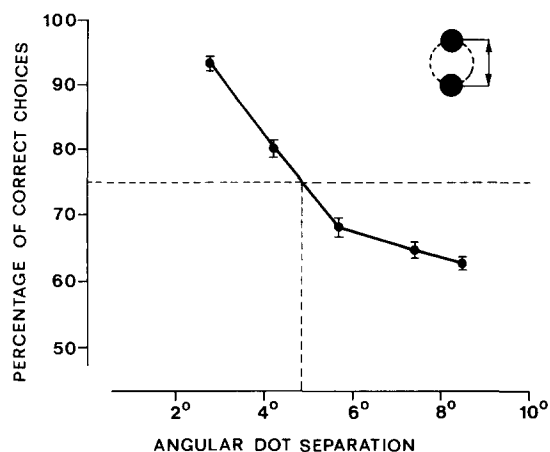


Fig. 3. Average percentage of correct choices and standard errors plotted against the distances between the centers of two consecutive dots seen from the distance of the viewing windows (25 cm).

bility of simultaneous projection of substantial parts of two consecutive dots within one receptive field. As Fig. 3 shows, the score is below the 75% correct level when the dot distance is 5.7° . By interpolation this means that when the angular dot separation exceeds 4.9° , the behavioral scores fall below the 75% correct level. From Hughes and Vaney's observations this would mean that the scores drop below 75% correct when 13% of the orientation-sensitive units have a diameter equal to or larger than the distance between the centers of two adjacent dots. With 6% of the orientation-sensitive cells (5.71°) equal to or larger than the angular dot separation, the score dropped to the $68.3\% \pm \text{S.E.M. } 1.5\%$ correct level. Thus the behavioral results obtained in the present experiment are in agreement with Hughes' hypothesis that discrimination of rows of dots is due to the activation of orientation-sensitive cells. Whether this also applies to our earlier experiment^{2,14} will be the subject of a further study.

ACKNOWLEDGEMENTS

The authors are greatly indebted to Mrs E. Benckhuijsen-Bongers for her help in the prepara-

tion of this manuscript and to Mr B.L.F. Weijer and Mr H.W. Dronk for technical assistance.

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