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THE MECHANISM OF VISION: I. A METHOD FOR RAPID ANALYSIS OF PATTERN-VISION IN THE RAT*1

From the Institute for Juvenile Research, Chicago

K. S. LASHLEY

Our knowledge of the character of vision in mammals below the primates is fragmentary and uncertain. Experimental studies have been limited to the carnivora and rodentia and the results which they have given, especially in the studies of pattern-vision, are at variance both with the popular notion of vision in these animals and with what we should expect from the high degree of differentiation of the optic systems.

The existing studies give little evidence that the rodents are sensitive to visual patterns. Yerkes (8) and Waugh (7) were unable to establish a differential reaction in mice to visual patterns. Lashley (3) succeeded in training rats to distinguish between horizontal and vertical lines, but failed to get discrimination of other patterns. Fields (1, 2) obtained discrimination of an upright and an inverted triangle in the rat, but the significance of this as evidence of pattern vision has been questioned by Munn (5), who found that Fields' apparatus presented differences in size of the stimulus objects and who could not demonstrate discrimination when this element was controlled. During the past ten years I have trained six groups of rats for pattern vision with various modifications of the discrimination box, continuing training for 500 or more trials, but always with negative results.

All of this work has been done with some form of the discrimination box and Fields has raised the question whether the failure to gain evidence of pattern-vision may not have been due to a defect in the method rather than to visual defects of the animals. During the past summer I hit upon a method for testing vision in the rat which confirms Fields' criticisms and reveals a capacity of the rat to discriminate visual patterns which is little inferior to that of pri-

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mates. The results of the method call for a revision of our ideas of vision in lower mammals and offer possibilities for the study of many problems in the physiology of vision.

The essential feature of the method is that it requires the animal to jump against the stimulus patterns from a distance, instead of to run past them, as in the discrimination box. A form of apparatus which has proved satisfactory is shown in Figure 1. It consists

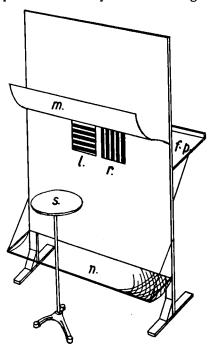


FIGURE 1
Apparatus Used for Testing Discrimination of Visual Patterns
For explanation see text

of a screen of three-ply pine, 3 by 5 feet, having two square holes 5.5 by 5.5 inches (l and r) cut at a convenient height. The openings are at the same level and spaced 2 inches apart. Attached to the back of the screen, $\frac{1}{4}$ inch below the lower edges of the openings, is a platform, 12 inches wide (f.p.), which serves as a landing platform when the rat jumps through one of the openings. A circular

stand (s) is placed with the nearest edge 25 cm.² in front of the middle of the screen and the animals are trained to jump from the stand through the holes to the platform (f.p.) where food is placed. A projecting sheet of metal (m) serves to deflect the rat through the openings in case he jumps too high and a net (n) catches him in case of a fall. The screen is painted black.

The openings are closed with squares of heavy cardboard upon which the patterns to be discriminated are drawn or pasted. The cards are 6 inches square and stiff enough to resist the impact of a heavy animal. They are held in place against the back of the screen by inserting the lower edge in a shallow groove in the food-platform and fixing the top either by a rigid turn-button or by a light spring. In training, one card, bearing the negative stimulus, is fixed rigidly; the other is held by the spring so that when the rat jumps against it the card falls back and allows him to reach the platform.

I have usually trained the animals by placing the stand near the screen and allowing the animals to step through the open holes to the platform, then gradually withdrawing the stand until, in 10 to 15 trials, the distance of 25 cm. is reached. Cards are then placed in position and training in discrimination begun.

TABLE 1

Comparison of the efficiency of the method of jumping and of the discrimination box in the establishment of the same habits in the rat. The figures for the discrimination box represent practice to establish a record of 85% correct choices; those for the method of jumping, a record of 100% correct.

Stimuli	Author	Discrimination box		Jumping		No.
		Trials	Errors	Trials	Errors	Cases
Black vs. white Horizontal vs.	Lashley (4)	128	42	4.3	0.7	33
vertical lines	Lashley (3)	260	98	27.0	6.0	10
Size of circles	Lashley (3)	350-700		37.5	6.5	4
Triangles (H, Figure 2)	Fields (1, 2)	600+	••	28.6	7.8	6

The eye of the rat, both albino and wild is, contrary to Vincent's statements (6), very myopic. The most distant adaptation is about 8 cm. and occasionally a still more nearsighted individual has been observed. Nevertheless, the depth of focus is great and the eye forms fairly distinct images even of distant objects. The evidence for these statements will be presented in a later study of the structure and resolving power of the eye. Since the longer jump seems more effective for the formation of habits of discrimination, it has been adopted for the majority of tests. For questions like the relation of visual acuity to retinal structure, distances within the focal range have been used.

Efficiency of the Method

Errorless discrimination of each of the pairs of patterns represented in Figure 2 has been obtained with relatively little practice, using pigmented animals. In comparison with the results of training by the discrimination box, the method is extremely rapid. Table 1

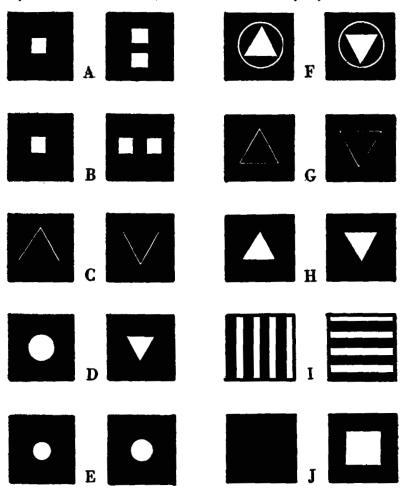


FIGURE 2
PAIRS OF PATTERNS BETWEEN WHICH RATS HAVE BEEN TRAINED TO
DISCRIMINATE
The cards bearing the patterns are six inches square. The patterns are
drawn to scale.

compares the rates for learning of different visual problems which have been tested with both the discrimination box and the jumping method. With the discrimination box a consistent errorless record for pattern discrimination has never been obtained. The figures given, except for black-white discrimination, represent the practice required to reach an accuracy of 80 to 85%, which is actually little better than chance.⁸ The records for the jumping method represent practice preceding 30 or more successive errorless trials, which, under most conditions, is predictive of permanent accuracy.

The variety of discriminations which the rat can make seems almost unlimited, and the directness of adaptation is surprising. Almost all normal animals jump for the single white square (Figure 2, J) without training and several have chosen the horizontal lines in preference to the vertical (Figure 2, I) with no error. Direct transfer, as from H to C or G, is the rule for similar patterns. Of the patterns tested, F, B, and D seem to present the greatest difficulties for the animals.

VALIDITY OF THE METHOD

The marked differences in results attained by this and by previous methods call for a careful analysis of the method for possible non-visual cues. The apparatus itself seems to provide against the common sources of error. The screen framing the patterns is fixed and offers no cues as to the right or left position of the fixed card. The cards fit closely against the back of the screen, the room behind is dimly lighted, and the screen is observed by reflected light, so that leakage of light, so difficult to control in the discrimination box, is ruled out.

Most of the cards bearing the pairs of patterns are interchangeable by rotation, so that either card may be used to present the positive or the negative pattern. Neither this change nor the substitution of new cards has ever disturbed discrimination. The animal must choose between the cards while at least 20 cm. from them. Thus tactile and olfactory cues are effectually ruled out.

There remains only the possibility of cues from the behavior of the experimenter. In training series, the experimenter sets the cards

²The order of alternating stimuli employed by almost all who have used the discrimination box involves more frequent reversals than repetitions of position. With the order which I have used, the most probable chance score, with an animal which has acquired a habit of alternation, is 70% correct.

while the rat eats, then tosses it around the right side of the screen to the stand, and steps back behind the screen where he remains, ignorant of the animal's actions, until it leaps against the screen. I have varied this procedure in many ways but have not succeeded in disturbing the accuracy of discrimination. The following formal tests of the validity of the method have been made.

- 1) Two rats which had served in a long series of tests, each making more than a thousand correct discriminations of various patterns, were blinded by enucleation of the eyes. Before the operation their average time for jumping after return to the stand was less than two seconds. After blinding, neither could be induced to jump. If the stand were placed near the screen they would step through the openings, so long as these were within reach of vibrissae and not closed by cards. With the cards in place the edges of the openings seemed not to be identified. With the stand beyond reach of the screen the animals reached out in every direction but were completely disoriented with respect to the position of the screen. They were tested at frequent intervals for a month after operation. During this time one of them jumped once, after much urging, and missed the screen entirely.
- 2) The openings were closed by fresh white cards, held only by the springs. The room was darkened and the patterns H and I of Figure 2 projected on the cards from a lantern placed above and behind the stand. Four animals previously trained with these patterns painted on the cards were tested. Each made no error in 20 trials.
- 3) Two animals trained on triangles (H) were tested by an assistant who did not know which of the patterns had been positive during training and who set both cards with the springs. No errors were made in these tests.
- 4) Animals trained with lines (I) were returned to the home cage during each setting of the cards and the experimenter hastened from the room after tossing them to the stand. No errors were made in these tests.

Dr. Munn has been kind enough to subject the method to still further analysis. He reports his findings in a note on pages 528-530 of this issue.

In general, no change in the routine of training or in the nonvisual elements of the situations has produced any disturbance in the accuracy of discrimination. On the other hand, any change in the visual pattern results in long hesitation, or inaccurate responses, and only chance scores are obtained with cards bearing identical patterns.

Finally, the most conclusive evidence that the discriminations are based upon visual pattern is the consistent character of the results obtained in tests for thresholds and for central nervous functions. All pigmented animals trained with striations of variable width (Figure 2, I) fail to discriminate when the lines are reduced to a width subtending about 57' of arc at 25 cm. With a shorter jumping distance these same lines are discriminated. With finer lines training to 300 trials does not improve the score above chance. Animals with destruction of the lateral geniculate bodies will not jump. Those with extensive lesions in the area striata jump but do not discriminate patterns. Albinos have a lesser acuity than pigmented animals, as measured by reactions to patterns, and the acuity corresponds closely to the resolving power of the eye, measured directly.

It will not now be profitable to discuss the nature of the rat's vision for patterns. The rôles of distribution of masses of light, of acuity for isolated elements, of the relation of figure and ground, of direction and movement, of configuration, of generalizing relations in the perception of objects are largely unknown even in human vision. I have accumulated a considerable amount of material which still serves only to emphasize the complexity of the problem. However, the method seems rapid and accurate enough to permit of a profitable attack upon questions of the organization of the visual field and of an analysis of the function of central nervous structures in various types of visual response.

SUMMARY

Apparatus requiring the rat to jump from a distance upon the stimulus patterns induces a rapid formation of habits of reacting to the visual elements of the patterns. Controls show that the discrimination cannot be ascribed to non-visual cues.

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LE MÉCANISME DE LA VISION: I. UNE MÉTHODE POUR L'ANALYSE RAPIDE DE LA VISION DES FORMES CHEZ LE RAT (Résumé)

L'appareil qui exige que le rat saute d'une distance sur les formes du stimulus cause une formation rapide d'habitudes de réaction aux éléments visuels des formes. Les contrôles montrent qu'on ne peut attribuer la discrimination à des suggestion non visuelles.

LASHLEY

DER MECHANISMUS DES SEHENS: I. EINE METHODE FÜR DIE SCHNELLE BEURTEILUNG DES FIGUREN-SEHENS BEI RATTEN (Referat)

Ein Apperat, der die Ratte veranlasst aus Distanz auf Reizmodelle zu springen, führt zu einer raschen Gewöhnung, auf visuelle Elemente der Modelle zu reagieren. Nachkontrollen zeigen, dass die Unterscheidung nicht auf nicht-visuelle Zeichen zurückgeführt werden kann.

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