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THE VISUAL ACUITY OF SOME  
PASSERINE BIRDS

BY

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WITH 17 TABLES AND 13 FIGURES

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## Contents.

	Page
I. Introduction .....	3
II. The author's investigations .....	6
1. Determination of the minimum separabile .....	6
2. The morphological visual acuity .....	17
3. The width of the pupil at different levels of illumination .....	22
III. Discussion .....	24
1. The maximum visual acuity of the birds .....	24
2. The dependence of visual acuity on illumination .....	29
3. The biological and ecological significance of the results .....	30
Summary .....	33

### I. Introduction.

In 1907 ALEXANDER-SCHÄFER published the first investigation on the visual acuity of animals. This study was, however, only based on a histological examination of the eyes, assuming that every receptor in the central part of the retina is able to produce a visual sensation that differs from that of the adjacent receptors. The first experimental determination of the visual acuity of animals was carried out by JOHNSON (1914, a, b, 1916 a, b). He worked with monkeys and chicken with a training method, a method that at least concerning the higher vertebrates has been the dominating one also in later studies on this subject. Another method of determining the visual acuity of animals was used by HECHT and WOLF (1929) who studied the honey bee by using the optomotoric reactions produced by moving patterns of black and white stripes. Both methods have later been used in determinations of the visual acuity of different animals (cf. Tab. XV and XVI, p. 27—28).

Generally speaking the term visual acuity covers several different visual performances. As already pointed out by HERING (1899) a clear definition must be established before an investigation of the visual acuity is made. HERING stated that the resolving power of the eye cannot be measured by determining the ability of the eye to discriminate differences in the position

of two objects, neither in a plane visual field nor with stereoscopic vision. But visual acuity must be defined (by analogy to the resolving power of an optical instrument) as the ability of the eye to discriminate two points or lines from each other in a plane visual field. A wider definition is given by GUILLERY (1929) who says (p. 751):

»Ganz allgemein kann man die Sehschärfe bezeichnen als die Feinheit der räumlichen Wahrnehmung im ebenen Sehfeld«.

HOFMANN (1920) defines visual acuity in the same manner. Unlike HERING, HOFMANN and GUILLERY do not restrict the visual acuity only to the ability of the eye to discriminate between two points but also refer to it the ability of the eye to discriminate small single points or lines. Yet HOFMANN (1920) calls the latter form »Punktsehschärfe«. For the sake of a better distinction in the definitions the term »minimum separabile« has been created for that acuity that depends on the discrimination of two points and the term »minimum visible« for that acuity that depends on the discrimination of one single point or line. These terms are commonly accepted, irrespective of the way in which the visual acuity is defined.

The test objects used to study the minimum visible or minimum separabile consist in their simplest form of one or two points. The point or points may, however, be replaced by lines or systems of lines without any principal difference. Thus minimum visible is determined by the visibility of single lines, while minimum separabile expresses the visibility of two or several lines at a distance equal to their own width from each other. The values obtained depend to some extent on the kind of test object used, as a rule the latter type of objects give a little higher numbers for the visual acuity (GUILLERY 1929, ROELOFS and BIERENS DE HAAN 1922). This is apparently caused by some kind of summation of the excitation in the retina.

Both minimum separabile and minimum visible are influenced by numerous factors. GUILLERY (1929) divides them in physical, physiological and psychological factors, by analogy with what is true for all visual performances. With the aid of the laws of optics and especially the geometrical optics the size and qualities of the retinal image may be calculated. Thus the properties of the refracting system of the eye determine the character of the retinal image. The physical factors then could be called anatomical factors, because the character of the retinal image is directly determined by the structure of the eye.

Physiologically visual acuity is influenced by the state of adaptation and stimulation in the retina and by its ability to discriminate stimuli of different intensity from each other. The size of the pupil may also be referred to the physiological factors, although it is of importance also for the acuity of the retinal image and so as well may be placed among the physical factors.

In spite of the fact that one always is trying to get more or less exact information about the discriminating ability of the eye itself, GUILLERY (1929) points out that even at the most simple examinations of the visual sense in man the influence of judgment, experience and training can never be excluded, a statement that is valid for all determinations of sense-physiological data using psycho-physical methods.

This classification is of course not ideal. The factors determining visual acuity cannot be wholly separated from each other because they influence each other and co-operate to a certain extent.

Birds are known to orientate mainly with the aid of their eyes. The flight and their way of finding their food demand very acute vision. Anatomical and histological investigations support this view; it has been stated that the birds have a high visual acuity, in the birds of prey perhaps the best of all animals, including man. This is confirmed by field-ornithological observations. The only investigations on the visual acuity of birds, however, done are studies on the chicken (JOHNSON 1914 a, b) and the domestic pigeon (HAMILTON and GOLDSTEIN 1933, GUNDLACH 1933, CHARD 1939). Hence our knowledge is restricted to species that in this respect probably do not have the best performance ability. An investigation of the visual acuity of other birds may therefore be justified. For this purpose the small song birds are very suitable and of interest since it has been stated (Von BUDDENBROCK 1937) that they might be expected to have about the same visual acuity as man. Histological investigations have suggested that these birds may have a comparably high degree of visual acuity by comparison with other birds. This of course may be said only about the minimum separabile, where the structure of the retina and of the optical system of the eye definitely limits the performances. The very good intensity discrimination of birds, as demonstrated by MEIJKNECHT (1941) for the song-thrush and the owl *Athene noctua* also support the view of a good visual acuity. For both the minimum visible and the minimum separabile are influenced by the intensity discrimination as pointed out by GUILLERY (1929).

In the present study an attempt has been made to determine the minimum separabile for some passerine birds by means of a training method and to compare the results obtained with the data found in a histological examination of the birds' eyes as well as with the results obtained from rough measurements of the width of the pupil at different intensities of light.

The author is highly indebted to Prof. Pontus Palmgren for valuable advice and criticism during the work. Thanks are also due to Mr. Aro at AB Tilgmann OY for supplying the finest test patterns for the experiments and to the British Council for linguistic revision of the manuscript.

## II. The author's investigations.

### 1. Determination of the minimum separabile.

#### A. Material and procedure.

*Bird material.* The training experiments were started (Dec. 1946) with 14 individuals representing 10 different species. However, results were obtained only with 7 birds, all of different species (*Turdus merula*, *Turdus pilaris*, *Erithacus rubeculus*, *Alauda arvensis*, *Emberiza citrinella*, *Emberiza schoeniclus*, *Fringilla coelebs*). This small number was partly caused by the fact that some birds were relatively difficult to keep alive under the prevailing difficult feeding situation, owing to the low quality of the meat obtained for this purpose. Thus 4 birds died before any results had been obtained. Three of the remaining birds were found to be very difficult to train and were therefore given up.

On the days when the birds were not trained they were kept together in common cages in the bird room of the Zoological Institute. The thrushes were fed with boiled potatoes and peas, cowberries, fish and meat. The finches, the sparrows and the lark got different kinds of seed and bread soaked in milk. The smaller insectivorous birds were fed with meat, occasionally they got ants eggs and some mealworms. All birds were given every second day in their food one or two drops of the vitamin A concentrate «Vitol» (Orion) to prevent A-avitaminosis. In spite of this during January and February 1947 there occurred symptoms of A-avitaminosis in the robin. This, however, was cured through a great increase in the vitamin A dosis. The bird apparently fully recovered and did not later show any signs of a deficient diet. It is of course possible that this A-avitaminosis has influenced the vision of the robin, since it is a well known fact that scotopic vision is particularly impaired by lack of vitamin A (cf. e.g. DETWILER 1943). JOHNSON (1943) has shown on rats that the external segments of the rods degenerate during extreme lack of vitamin A, but that full recovery is obtained after a period of vitamin A treatment. It therefore seems probable that during the time when the determinations were made the vision of the robin was not influenced by the earlier lack of vitamin A.

The birds used for the investigation were caught in the autumn 1946 at the lighthouse on Söderskär during the migration.

*The training apparatus.* Since it is difficult to train invertebrates the method based on the optomotoric reactions is more suitable for them. But in case of vertebrates where attainment of the maximum visual acuity demands fixation of the object, the training method seems to be the best. In this the animals are forced to take part actively when they make their choice.

Both of the methods, mentioned above, are based on observations of differences between the behaviour of the animals when they are able to discriminate the pattern and when they are not, assuming that the change in be-

haviour takes place at the actual limit of their vision. However, von BUDDENBROCK (1937) points out that this cannot with certainty be said (p. 1):

»Wenn also ein Tier auf einen Reiz nicht anspricht, so ist damit keineswegs bewiesen, dass seine Sinnesorgane ihn nicht perzipiert haben».

The values obtained are then always to some extent uncertain. The error produced is probably neither absolutely nor relatively of the same magnitude for all animals, but must be assumed to be very variable which in turn makes a comparison between different animals more unreliable.

The determination of the visual acuity with the birds mentioned above was based on the training method. The apparatus used was built up in the dark-room of the Zoological

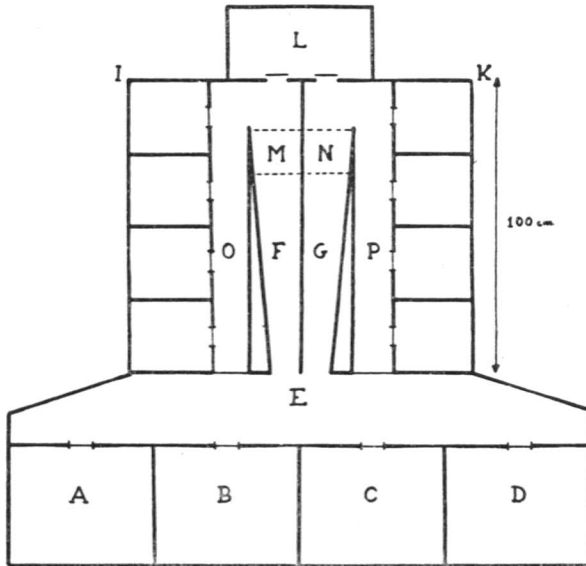


Fig. 1. Plan of the training apparatus as seen from above.

Institute, a room of the size  $4.30 \times 3.10$  m. In Fig. 1 a plan of the apparatus is seen. A, B, C and D are cages ( $40 \times 50 \times 60$  cm). From these a small opening ( $14 \times 10$  cm) that could be shut by a door led to E. The doors were fastened to the upper edge of the opening so that the birds in the cages A, B, C and D could not push out through them. From E two corridors F and G led to the small feeding cages to which the birds came from O and P. In the wall I—K two windows were placed so that they they could be seen from E at the beginning of each corridor. In these windows ( $8 \times 6.5$  cm) the test patterns were placed and were illuminated from behind from L (see also Fig. 10, Pl. I, and 2). In the corridors two squares of cardboard (M and N, Fig. 1) could be raised by a string thus stopping the bird when needed. The small feeding cages, opening to O and P, were of the size  $30 \times 30 \times 20$  cm and provided with doors of the same design as for the big cages A, B, C and D. At the end of the corridors O and P there were doors that were usually shut but through which the birds could be passed back to the big cages.

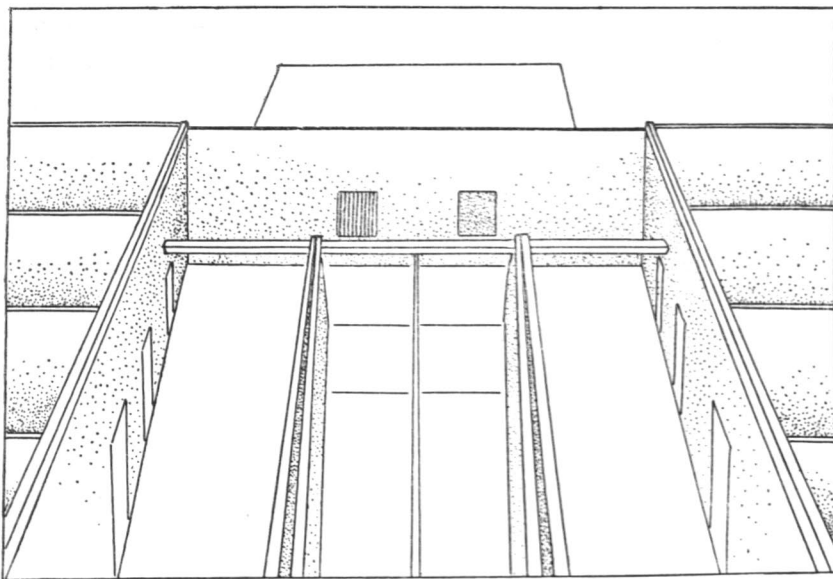


Fig. 2. The training apparatus. The two passages and the test objects.

The walls of the corridors and the cages were made of cardboard and the ceiling of fine fishing net. In the big cages the upper part of the wall facing E was covered with netting but also with transparent paper to prevent the birds seeing what was going on in other parts of the apparatus. Fig. 10 (Pl. I) gives a view of the apparatus from the door of the room and Fig. 2 the back part of the corridors F and G (Fig. 1) with the test objects and the small feeding cages. The doors to all the cages and the «shutters» M and N were manoeuvred by means of threads that passed through a hole in the wall (Fig. 10, Pl. I) to another room. This hole was simultaneously used for observation during the experiments, so that the observer was invisible for the birds.

The test patterns were photographed on to ordinary  $9 \times 12$  photographic plates. They consisted of vertical line patterns in which each black vertical line was separated from its neighbour by a transparent space of width equal to the vertical line. 15 different widths were used, from lines of 10 mm width down to 0.1 mm. As negative objects plain exposed photographic plates were used with the same average transmission as that of the

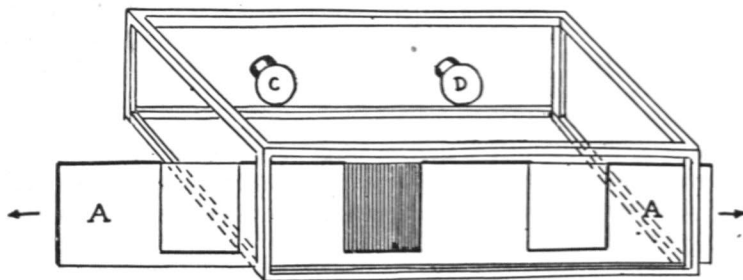


Fig. 3. The illuminator with the frame (A—A) for the test objects. D and C are bulbs.



pattern. This was not determined by any measurements as no exact methods were available. Instead a great number of plates were exposed and the ones with the same brightness for the human eye as that of the patterns were chosen. This source of error was eliminated in the experiments by using, irregularly alternating, darker and lighter plates than the patterns.

The test objects were placed in a frame provided with three openings (Fig. 3: A) that could be moved in the illuminator in direction of the arrows, so that the test objects were seen through the windows in either of the two corridors F and G (Fig. 1). The design of the illuminator can be seen from Fig. 3. Two bulbs C and D illuminated the test objects from behind; between the lamps and these milk glass filters were used to get an even distribution of light over the whole surface of the objects.

*The illumination.* In the apparatus described above the illumination factor may be divided into two components, the illumination of the test objects being independent of the illumination in the room. The latter was made as even as possible by covering the walls of the dark-room with white paper. Over the apparatus, about 1.5 m from the floor a ceiling of transparent paper was built (Fig. 10 Pl. I). Over this ceiling 5 lamps were hung so that an equal illumination on all parts of it was obtained. In this way the apparatus was evenly illuminated without shadows. The lamps were connected to the mains (125 V D. C.). The variations of the output voltage of course then caused slight variations in the illumination but the differences were not too big. Measurements showed that the voltage generally was between 124—126 V (28 measurements at different times of the day).

The experiments were made in 6 different intensities. These were obtained by changing the lamps over the transparent ceiling to different strengths. The illumination of the test objects was adjusted with the aid of filters and by changing lamps so that it was a little brighter than the surrounding wall of the apparatus. The illumination measurements were performed with the aid of a photo-electric cell (AEG — range 1—100 and 1—1000 Lux) which was kindly supplied by the «Statens tekniska forskningsanstalt». The measurements were carried out in the big cages, where the birds usually were sitting, in all directions and also upwards, and an average was taken. In all four cages approximately the same values were got. In addition the illumination was measured in the opening of the corridors with the test objects. Finally the brightness of the test objects was determined separately, extinguishing all other lights and the light coming from only one of the windows being measured from a certain distance. From the values obtained the brightness of the test object in millilamberts was calculated.

The values obtained are given in table I. The illumination in the big cages A and D and on the other hand B and C (Fig. 1) were slightly different, the average value is given in table I. This is of importance only for the state of adaptation of the eye, which is of a small significance for the vision in retinae of the type that these birds possess (GRANT 1936, 1947). The illumination at the opening of the two corridors is more important and these values have accordingly been given in curves 4—7 and tables III—X. The brightness

Table I.

No.	Illumination in Lux in big cages	Illumination in Lux at opening of corridor	Brightness of test objects, millilamb.
I	48.0	42.5	6.0
II	29.8	33	2.7
III	5.2	4.5	0.48
IV	2.0	1.5	0.14
V	(0.15)	(0.15)	(0.02)
VI	(0.07)	(0.07)	(0.01)

(Indirectly determined values in brackets.)

of the test objects was of the same relative magnitude (table I). The brightness again determines the contrast between the lines and the bright background when assuming that the lines themselves are totally black. The brightness of the background is then twice as much as the average brightness of the test object. In the present experiments the illumination of the surroundings and the illumination of the test object were thus changed to an equal amount and always maintained their relation to each other.

The lowest illumination values were determined indirectly since the instrument available was not sensitive enough. This was possible when the relative strengths of the lamps in relation to each other as determined at the Physical Laboratory of the University was known.

*The training method and the course of the experiments.* The training and later on the experiments were carried out in the following way:

In each of the big cages (A, B, C, D, Fig. 1) a bird was placed. In these cages they had only a cup of water. After some starvation (3—4 hours, for the thrushes often overnight) the door was opened and the bird had to walk out from the cage, choose the positive corridor at E, and find its food in one of the feeding cages the door of which had been opened. When the bird had got some food it was driven back to the big cage. If the wrong corridor was chosen the «shutter» (M and N, Fig. 1) in the corridor was raised and the bird was scared. By changing irregularly the place of the positive test object a preference of one of the two passages was avoided. When the training was completed the positive test object was changed into one with somewhat finer lines and this procedure repeated till the bird could not any more make a proper choice from the beginning of the corridors, from which the distance to the test objects was exactly one meter.

Four different birds could be used simultaneously, one in each of the big cages. The experiments could then be performed so that all in turn got a run, as they always found their food in different feeding cages.

As mentioned before training was started with 14 different birds. These were divided into three groups and were trained every third day. Later on, when the number of birds was smaller each bird was trained every second day. This of course delayed the training but it should be noted that the condition of the birds was better maintained when they always got one day of rest, with enough food, after the experiments.

The training was started at Dec. 10th 1946. In the beginning the birds had to be chased to the feeding cages. After some 40 runs they had learnt to seek their food in the feeding cages and the training on the test objects was started. During the training period the highest illumination (42.5 Lux) was used and the 2.8 mm test object. The control (grey glass plate) was irregularly varied with respect to its brightness (cf. p. 9) so that no regularly occurring brightness difference between the grating pattern and the control could confuse the experiments. This was a matter of importance since it has been found with the domestic hen that they usually try to solve a difficult task with the aid of an easier one and thus first learn the more simple alternative if several present (KROH 1926, KROH, GÖTZ, SCHOLL and ZIEGLER 1927). This is probably true for other birds also. As training on brightness is an easier task than training on a lined test pattern, the brightness factor must be carefully eliminated in experiments of the type used in the present work.

The results of the runs both during the training and during the experiments were marked in tables. These also show which corridor was the positive one together with the fineness of the pattern used. A correct choice was marked with + and a wrong one with —. Uncertain cases when the bird for example walked some steps into one of the corridors and then turned back again, were rejected.

The speed of learning varied. In table II the number of runs before a positive result was got are given. That such a great number of runs was needed was partly due to the fact that the surroundings were somewhat noisy, a fact which obviously disturbed the birds. The robin, which needed much more training than the other birds, learned very quickly to find its way to the feeding cages but moved so quickly that it probably did not observe the test objects properly.

Table II.

*Total number of runs before training was complete.*

Turdus merula .....	185	Emberiza schoeniclus .....	170
Turdus pilaris .....	167	Erithacus rubecula .....	374
Alauda arvensis .....	184	Fringilla coelebs .....	286
Emberiza citrinella .....	256		

The training was thought to be successful when in a series of 20 subsequent runs 80—100 % positive choices were obtained. The maximum percent of positive choices was, however, quite individual; thus the chaffinch, the skylark and the thrushes from the beginning made only few errors while the other birds only occasionally did more than 70—80 % positive choices. This of course makes the results for the latter more uncertain which should be taken into account when considering the results. A strictly mathematical criterion of the stage at which the birds could be said to have learned the task seemed rather out of place, individual differences between the birds playing a great role.

## B. The results.

When positive results were obtained in the training, the experiments were started. This was done at different times for different birds, depending on the fact that all birds did not equally well learn their task, as is seen from table II. During the experiments the observer was always hidden from the birds, observing their reactions through the hole in the wall. This hole was built so that the birds could not be seen when they made their choice, they were seen only then when they already walked along one of the corridors. In this way the risk was eliminated, that the observer unconsciously could have influenced the choice.

When the experiments at one illumination intensity had been carried so far that the test pattern used gave a negative result and thus the limit for discrimination was determined, the intensity of illumination was changed and the experiments repeated, starting with a pattern with relatively wide lines in order to check the training of the birds. Visual acuity was determined in this manner for 6 different intensities.

The experiments lasted from Dec. 10th 1946 to July 28th 1947 including training period, every day except Sundays. On an average each bird made 12—15 runs a day, with 4 birds 50—60 runs a day were got, the greatest number being 120.

The results are given in tables III—IX for each bird separately. From the tables can be seen the number of positive and negative choices at each intensity of light and width of the lines. On the basis of these numbers a probability value has been calculated from the formula (BONNIER & TEDIN 1940, p. 229):

Table III. *Turdus merula*.

Visual angle	Width of lines, mm	42.5 Lux			33 Lux			4.5 Lux			1.5 Lux			0.15 Lux			0.07 Lux		
		+	-	t	+	-	t	+	-	t	+	-	t	+	-	t	+	-	t
9'40"	2.8	15	1	<.001							7	2	.09	6	1	.03	5	0	.03
7'20"	2.2	8	1	.02							5	1	.10	6	1	.03	10	3	.05
6'10"	1.8	11	4	.08							6	3	.30	8	3	.14	5	1	.10
4'40"	1.35	6	2	.16				6	1	.03	15	7	.08	7	5	.35	6	2	.16
3'50"	1.1	5	1	.10	7	0	.009	6	0	.02	5	0	.03	6	2	.16	11	4	.08
3'07"	0.9	7	3	.21	4	1	.19	6	0	.02	5	0	.03	8	1	.02	5	1	.10
2'38"	0.75	16	6	.04	4	1	.19	14	4	.02	5	0	.03	6	1	.03	6	1	.03
1'55"	0.55	50	11	<.001	10	1	.009	14	7	.14	5	0	.03	5	1	.10	4	4	.99
1'20"	0.4	10	1	.009	5	1	.10	4	0	.05	5	0	.03	3	4	.70			
0'40"	0.2	4	5	.72	3	4	.70	1	4	.19	2	3	.67						

$$\chi^2 = \frac{m^2}{m+n} + \frac{n^2}{m+n} - (m+n)$$

where m = the number of positive choices and n = the number of negative ones. The probability value t was got from the tables of BONNIER and TEDIN (1940). t gives the probability for the distribution of positive and negative choices being only a matter of chance. Thus high values (near 1) for t indicate that the birds were not able to see the grating.

Table IV. Turdus pilaris.

Visual angle	Width of lines, mm	42.5 Lux			33 Lux			4.5 Lux			1.5 Lux			0.15 Lux			0.07 Lux		
		+	-	t	+	-	t	+	-	t	+	-	t	+	-	t	+	-	t
9'40"	2.8	18	1	<.001							5	1	.10	6	0	.02	5	0	.03
7'20"	2.2	5	2	.25							11	1	.008	7	1	.04	8	0	.006
6'10"	1.8	7	3	.21							6	0	.02	11	2	.01	10	4	.11
4'40"	1.35	5	0	.03				7	2	.09	6	1	.03	6	2	.16	7	3	.21
3'50"	1.1	4	1	.19	8	0	.006	5	0	.03	5	0	.03	9	1	.01	9	3	.09
3'07"	0.9	24	2	<.001	9	1	.01	9	0	.003	7	1	.04	10	5	.19	6	2	.16
2'38"	0.75	13	3	.01	8	1	.02	9	1	.01	6	0	.02	6	2	.16	3	7	.21
1'55"	0.55	7	1	.04	9	1	.01	5	1	.10	8	1	.02	3	4	.70			
1'20"	0.4	4	6	.51	6	0	.02	6	1	.03	6	1	.03						
0'40"	0.2				1	6	.03	2	3	.67	1	6	.03						

Table V. Alauda arvensis.

Visual angle	Width of lines, mm	42.5 Lux			33 Lux			4.5 Lux			1.5 Lux			0.15 Lux			0.07 Lux		
		+	-	t	+	-	t	+	-	t	+	-	t	+	-	t	+	-	t
20'42"	6.0												8	2	.06	5	1	.10	
13'48"	4.0										7	1	.04	6	0	.02	11	2	.01
9'40"	2.8	11	0	<.001							13	7	.19	6	2	.16	8	4	.19
7'20"	2.2	9	1	.01							14	5	.04	7	1	.04	6	2	.16
6'10"	1.8	15	6	.05							9	4	.18	14	5	.04	5	2	.25
4'40"	1.35	10	3	.05				8	0	.006	5	1	.10	9	8	.83	2	3	.67
3'50"	1.1	5	1	.10	11	2	.01	7	3	.21	5	1	.10						
3'07"	0.9	6	2	.16	16	3	.005	25	7	.002	5	1	.10						
2'38"	0.75	14	6	.08	12	6	.17	12	6	.17	5	1	.10						
1'55"	0.55	11	8	.48	6	1	.03	5	1	.10	5	0	.03						
1'20"	0.4				5	1	.10	5	1	.10	5	1	.10						
0'40"	0.2				6	4	.51	2	3	.67	2	4	.41						



Table VIII. *Emberiza schoeniclus*.

Visual angle	Width of lines, mm	42.5 Lux			33 Lux			4.5 Lux			1.5 Lux			
		+	-	t	+	-	t	+	-	t	+	-	t	
34'24"	10.0											9	3	.09
27'36"	8.0											5	10	.19
20'42"	6.0													
13'48"	4.0								8	3	.14			
9'40"	2.8	16	7	.06					11	9	.67			
7'20"	2.2	4	1	.19					2	1	.60			
6'10"	1.8	10	6	.31	39	23	.04							
4'40"	1.35	8	2	.02	11	5	.14							
3'50"	1.1	7	4	.39	8	4	.19							
3'07"	0.9	9	9	.99	4	4	.99							

Table IX. *Erithacus rubeculus*.

Visual angle	Width of lines, mm	42.5 Lux			33 Lux			4.5 Lux			1.5 Lux			0.15 Lux			0.07 Lux				
		+	-	t	+	-	t	+	-	t	+	-	t	+	-	t	+	-	t		
20'42"	6.0												6	1	.03						
13'48"	4.0												7	3	.21		7	3	.21		
9'40"	2.8	19	11	.16				11	6	.22	15	8	.16	11	5	.17	6	1	.03		
7'20"	2.2	5	0	.03				14	5	.04	14	6	.08	5	0	.03	5	1	.10		
6'10"	1.8	17	11	.26	15	6	.05	7	3	.21	21	5	.003	7	3	.21	5	1	.10		
4'40"	1.35	8	4	.19	10	2	.02	7	3	.21	6	1	.03	6	3	.30	9	4	.18		
3'50"	1.1	30	38	.35	7	6	.83	4	4	.99	4	4	.99	3	4	.70	10	4	.11		
3'07"	0.9																6	1	.03		
2'38"	0.75																9	3	.09		
1'55"	0.55																4	5	.72		

Table X. Visual acuity in terms of visual angle for different illuminations.

Illumination in Lux	42.5	33	4.5	1.5	0.15	0.07
<i>Turdus merula</i> .....	1'20"	1'20"	1'20"	1'20"	1'53"	2'38"
<i>Turdus pilaris</i> .....	1'53"	1'20"	1'20"	1'20"	2'38"	3'07"
<i>Alauda arvensis</i> .....	2'38"	1'20"	1'20"	1'20"	6'10"	6'10"
<i>Emberiza citrinella</i> .	3'07"	4'40"	13'48"	34'24"		
<i>Emberiza schoeniclus</i>	3'50"	3'50"	13'48"	34'24"		
<i>Erithacus rubeculus</i> .	4'40"	4'40"	4'40"	4'40"	4'40"	2'38"
<i>Fringilla coelebs</i> .....	1'20"	1'20"	1'20"	1'20"	2'38"	3'07"

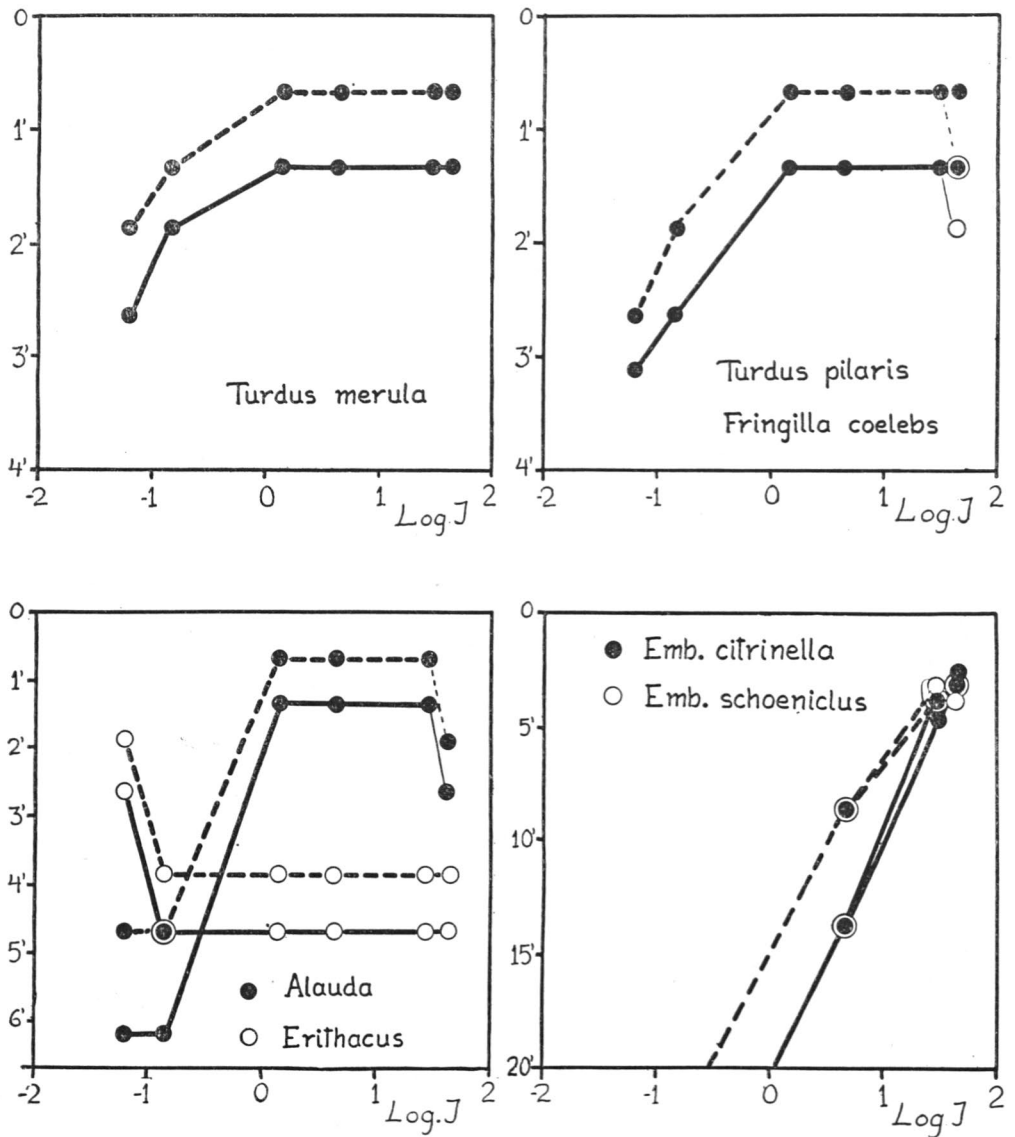


Fig. 4—7. Graphs giving the last positive (lines in full) and first negative values (broken lines) as a function of the logarithm of illumination. Ordinates minutes of arc (values calculated from the width of the grating as seen from 1 m distance).

The probability for each determination does not, however, give a correct picture of the reliability of the whole procedure. When, for instance, the same value for the visual acuity has been obtained for some birds at four intensity levels, this of course makes at least these values more certain. With the yellow-hammer and the reed-bunting rather unreliable results were obtained — a greater number of runs ought to have been made.



But that would have meant a great loss of time also for the experiments with the other birds. To carry out an extensive number of runs only with the critical test patterns again seemed difficult as the tests at critical values soon affect the training adversely.

Table X gives a summary of the values for the visual acuity obtained, based on the minimum width of the lines in the test pattern that gave positive results. As could be expected the visual acuity sinks with decreased intensity of illumination. Only the skylark and the fieldfare gave a somewhat lower value in the brightest light. (It is to be noted that, for example, the acuity 1'20" is higher than 1'53" although the numerical value is lower). This may be due to the fact pointed out by SPENCE (1934) experimenting with chimpanzees, that a certain amount of additional training is necessary for the animal before maximum values are obtained. For the robin a constant value was got for the acuity in the five strongest illuminations, while a considerably higher one was obtained in the weakest illumination. This may be associated with the fact that the robin in nature usually lives in places where the illumination is weak. The size of the eye too suggests that it may be more adapted for scotopic vision. The highest illumination used was not, however, so high that one would in any case expect that the bird had been blinded. It is more likely that the bird did not react properly except in the lowest illumination when its reactions were considerably slower than before. This is the more probable explanation considering that the robin by no means ought to possess an especially low visual acuity as compared with other birds (LACK 1946). It was also quite obvious that the other birds were more affected by the weak illumination than the robin, in the illumination 0.15 Lux the yellow-hammer and the reedbunting could not be forced to make any runs at all.

In addition it should be pointed out that the values given in table X for the visual acuity only give the upper limit for the interval in which the true values lie. The blackbird, for instance, reacted positively for the width 0.4 mm and negatively for 0.2 mm. Obviously, the real limit must then lie between these values. In figures 4—7 graphs of the results are given. For each bird two curves are drawn, one for the last positive and one for the first negative values. The true values for the visual acuity must then lie between both curves.

## 2. The morphological visual acuity.

The limit, due to the anatomical structure of the eye, for the resolving power in case of minimum separabile, can be calculated if the refractive errors of the eye are neglected. And even if they are taken into account we know that the refractive errors probably do not limit the visual acuity. HARTRIDGE

(1918) points out that for the human eye the retinal mosaic is just of the fineness that the refractive system allows.

If the refractive errors are neglected, minimum separabile may be said to depend on two factors:

1. The focal distance of the refractive system or, more correctly, the distance of the posterior nodal point from the retina (cf. HARTRIDGE 1950).

2. The diameter of the photoreceptors in the retina, assuming that each receptor may deliver a separate sensation — the correctness of such an assumption will be discussed later.

The factors co-operate so that the absolute limit for the acuity is got when the retinal image — in this particular case the image of the lines from the test pattern — is so small in relation to the receptors that they all get the same amount of light and thus pattern discrimination is rendered impossible. This is the case when the image of the lines on the retina have a width = half the diameter of a single receptor (cf. WILCOX and PURDY 1933). This is, however, only theoretically true. Usually the angle formed when a single receptor is seen from the nodal point has been taken as a measure of the morphological acuity. For the human eye the morphological acuity as determined in this way is in quite a good agreement with the values for minimum separabile (POLYAK 1941).

#### A. The nodal point distance.

The distance of the posterior nodal point from the retina was determined by a method used by ALEXANDER-SCHÄFER (1907) and EHRENHARDT (1937). The method involves a determination of the size of the retinal image of an

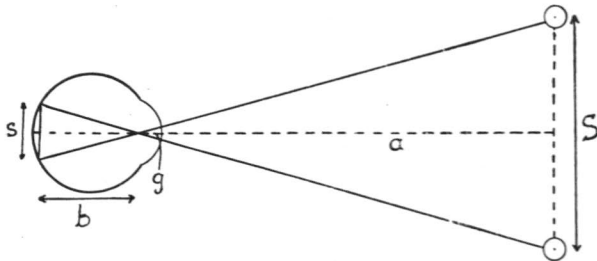


Fig. 8. Schematic illustration of the way of determining the nodal point distance. Full explanation in text.

object at a known distance from the eye, as seen in Fig. 8.  $S$  and  $a$  are known and  $s$  is measured,  $g$  is small and may be neglected. From this  $b$  may be calculated. The difference between the two nodal points of the refracting system may also be neglected.

Table XI.

Dimensions of the eye and nodal point distances for the birds investigated.  
The values in the fourth column refer to single measurements.

	Diameter of the eye, mm.	Length of the eye, mm.	Diam.: length	Nodal point distance mm.	Average nodal point distance
Turdus merula .....	13.4	11.2	1.195	6.96 6.69 6.81	6.82
Turdus pilaris .....	13.7	11.0	1.245	7.32 6.51	6.91
Turdus musicus .....	11.5	9.5	1.210		(4.88)
Alauda arvensis .....	9.8	8.2	1.195	3.73 3.37 3.68	3.56
Emberiza citrinella .....	8.6	6.7	1.282	2.95 2.66 2.40	2.67
Emberiza schoeniclus .....	8.0	6.9	1.158	2.84 2.96 2.96 3.12	2.99
Erithacus rubecula .....	10.4	8.1	1.282	4.34 5.21 4.53	4.69
Fringilla coelebs .....	8.9	7.3	1.220	4.74 4.68 5.28	4.90
Fringilla montifringilla .....	8.0	7.0	1.114		(3.36)
Pyrrhula pyrrhula .....	8.9	7.2	1.232		(3.73)
Parus atricapillus .....	7.8	6.5	1.199		(3.28)

A determination of the nodal point distance was made on the birds that had given results with the training method. The birds were anaesthetized with chloroform and decapitated. The left eye was cut out without damaging it and placed on a piece of cotton wool soaked in Ringer's solution. The eye was then mounted in front of a microscope horizontally placed. In front of the eye two 100 W bulbs were placed at a distance of approximately 3 meters and 1—2 meters from each other. Cutting away a piece of the sclera with great caution the images of the bulbs on the retina could be seen in the microscope and their distance apart measured by means of a micrometer eyepiece. The determination was repeated three times with different distances between the bulbs. To prevent the eye from drying it was now and then moistened with Ringer's solution.

In table XI the values obtained are given and the calculated values for the nodal point distance. The dimensions of the eye are also given.

In connection with the histological examination of the retina some other birds were shot to get a somewhat bigger material. For these eyes the nodal point distance was not determined, but the dimensions of the eye measured. Out of these values an approximate nodal point distance was calculated based on what was known from the other eyes assuming that the proportion between the eye axis and the nodal point distance is about the same for all passerine birds. The calculated values are given in the table in brackets. The average proportion between the eye axis and the nodal point distance for the experimentally determined values is 2.38 — from this the other values have been calculated.

The main error in the measurements is probably due to the damage that has been caused to the eye when it has been excised. For the yellow-hammer and the reedbunting especially the values for the nodal point distance seem rather small, considering that the size and shape of the eye is about the same as for the other birds. One may, however, ask if it is only an accident that the lowest values for the visual acuity have been obtained with these birds.

#### B. The diameter of the retinal elements.

For this purpose sections of the retina were made of all birds mentioned in table XI. From the birds of which the nodal point distance was determined the right eye was fixed.

The sections were prepared in the following way:

The eye was cut into half through the equator, the vitreous removed and the back part with the retina was fixed in Bouin's solution for 24 hours. Then the fixed eyes were changed into 70 % alcohol (1—2 days) and through alcohol-butylalcohol to butyl-alcohol and imbedded in paraffin. Before that the peripheral parts of the retina were cut away so that only a rectangular piece with the fovea in the middle remained. The hard sclera was scratched away from the paraffin blocks and the remaining piece of retina was imbedded once more. 5 and 10  $\mu$  sections were taken at right angles to the surface of the retina. The sections were stained with Mayer's haemalun and eosine, some of them also with Delafield's haematoxylin and eosine.

In figures 11—13 (Pl. I and II) microphotographs of some of the sections are shown. Figures 11 and 12 show the foveae of *Erithacus rubeculus* and *Emberiza schoeniclus*. The fovea was deepest in the robin, the foveae of the other birds being quite similar to that of the reedbunting shown in Fig. 12. Only one fovea was found in all birds investigated.

The shrinking of the retinae at the fixation and imbedding in paraffin was determined by measuring the fixed parts before and after the preparation. The values obtained are given in % in table XII.

The receptors were counted at 920  $\times$  magnification with an oil immersion lens and a micrometer eyepiece previously calibrated. Only the fovea was used for the counting.

Table XII.

The results from the determination of the morphological acuity.

	Nodal point distance	Diameter of receptors in $\mu$ , uncorr.	Shrinking %	Diameter of receptors in $\mu$ , corr.	Morphol. acuity
<i>Turdus merula</i> .....	6.82	$2.94 \pm 0.05$	10.4	$3.28 \pm 0.05$	1'39"
<i>Turdus pilaris</i> .....	6.91	$2.25 \pm 0.04$	3.2	$2.32 \pm 0.04$	1'10"
<i>Turdus musicus</i> .....	(4.83)	$2.06 \pm 0.02$	17.5	$2.50 \pm 0.02$	1'47"
<i>Alauda arvensis</i> .....	3.56	$1.82 \pm 0.05$	11.1	$2.05 \pm 0.05$	1'56"
<i>Emberiza citrinella</i> ...	2.67	$1.75 \pm 0.04$	20.4	$2.20 \pm 0.05$	2'50"
<i>Emberiza schoeniclus</i> .	2.99	$2.05 \pm 0.03$	26.0	$2.75 \pm 0.04$	3'11"
<i>Erithacus rubecula</i> ..	4.69	$2.62 \pm 0.05$	16.3	$3.19 \pm 0.06$	2'20"
<i>Fringilla coelebs</i> .....	4.90	$2.13 \pm 0.04$	7.2	$2.29 \pm 0.04$	1'37"
<i>Fringilla montifringilla</i>	(3.36)	$2.14 \pm 0.04$	19.7	$2.65 \pm 0.05$	2'43"
<i>Pyrrhula pyrrhula</i> .....	(3.73)	$1.73 \pm 0.02$	14.0	$2.01 \pm 0.02$	1'52"
<i>Parus atricapillus</i> .....	(3.28)	$1.58 \pm 0.02$	24.5	$2.09 \pm 0.03$	2'12"

The number of receptors at focus level over  $64 \mu$  was counted for each retina from 10 different sections.

The results are given as an average value in table XII, as well as the corrected values when the shrinking has been taken into account.

The values obtained agree fairly well with earlier values for the diameter of the receptors: FRANZ (1934) mentions that in *Motacilla alba* 120,000 receptors are found per sq. mm extrafoveally which gives a diameter of  $2.9 \mu$ . SLONAKER (1918) gives for *Passer domesticus* foveally 400,000 per sq. mm which means about  $1.6 \mu$ . In these cases nothing, however, is said about the shrinking of the sections, if it has not been taken into account the values of course are somewhat too small. Or the values may somehow have been determined from fresh material.

### C. The morphological visual acuity.

As pointed out before (p. 17) the experimentally determined values for minimum separabile ought to be the same as the morphological acuity. This is of course true only theoretically as many other factors are at work in actual practice, especially in experiments with animals.

In table XII the calculated values for the morphological acuity of the different eyes are given. The results must be said to be rather approximate considering the variability that occurred when the nodal point distance was determined.

### 3. The width of the pupil at different levels of illumination.

The size of the pupil in different intensities of light was determined for all 7 birds that had been used for the training experiments. In addition the second skylark was used. The measurements were performed in the following manner:

The bird was placed in a cage (40 × 50 × 60 cm) the walls of which were covered with white paper. The ceiling of the cage was covered with transparent paper. Over the cage a lamp was hung that could be fixed at certain heights. The papering in the cage made it possible to produce an even illumination from all directions. By the use of different lamps and adjusting the height of them 9 different intensities were obtained. They were measured with the same instrument as was used for the other measurements (p. 9). At the three lowest levels an indirect method was employed based on a comparison between the intensity of light in the cage and at a certain fixed point nearer the lamp when a stronger bulb was used.

The birds were kept 30 minutes in the cage for adaptation. The measurements were performed in the cage (one side of it taken away) with the aid of a nonius gauge under a magnification glass. Care was taken that the procedure always was reproduced in the same manner.

Table XIII.

Diameter in mm. and area in mm<sup>2</sup> of pupil at different intensities of light.

	158 Lux		38 Lux		26 Lux		11 Lux		6.2 Lux	
	D	A	D	A	D	A	D	A	D	A
Turdus merula .....	3.85	11.6	4.07	12.9	4.12	13.3	4.25	14.2	4.37	15.0
Turdus pilaris .....	3.07	7.1	3.47	9.4	3.40	9.1	3.55	9.9	3.80	11.3
Alauda arvensis .....	2.24	3.9	2.38	4.4	2.40	4.5	2.51	4.9	2.53	5.0
(average for 2 birds)										
Emberiza citrinella .....	2.37	4.4	2.52	5.0	2.67	5.6	2.73	5.9	2.72	5.8
Emberiza schoeniclus .....	2.12	3.5	2.28	4.1	2.30	4.2	2.32	4.2	2.37	4.4
Fringilla coelebs .....	2.08	3.4	2.12	3.5	2.20	3.8	2.20	3.8	2.32	4.2
Erithacus rubeculus .....	2.90	6.6	3.12	7.1	3.27	8.4	3.35	8.8	3.45	9.4

	3.0 Lux		0.75 Lux		0.4 Lux		0.2 Lux	
	D	A	D	A	D	A	D	A
Turdus merula .....	4.47	15.7	4.52	16.1	4.55	16.2	4.53	16.1
Turdus pilaris .....	3.88	11.8	3.93	12.1				
Alauda arvensis .....	2.54	5.1	2.56	5.2	2.57	5.2		
(average for 2 birds)								
Emberiza citrinella .....	2.75	5.9						
Emberiza schoeniclus .....	2.32	4.2						
Fringilla coelebs .....	2.30	4.2	2.35	4.3				
Erithacus rubeculus .....	3.53	9.8	3.55	9.9	3.57	10.0		

Such a method, although not quite satisfactory, had to be used since it was impossible to distinguish the pupil with other finer methods even at relatively high levels of illumination. This was caused by the fact that the iris of diurnal birds is so pigmented that it is very difficult to see the borders of the pupil (cf. ERHARD 1924). The accuracy of the measurements was  $\pm 0.1$  mm, bigger deviations in a series were hardly ever obtained. Rapid variations in the size of the pupil due to blinking also made the measurements more difficult. Of course a photographic method using infrared light as used by WAGMAN and GULLBERG (1942) on man would have been the best but such a method was out of question with the resources available.

Trying to measure the absolute size of the pupil making observations through the cornea gives somewhat erroneous results due to refraction particularly in the front surface of the cornea. The error is, however, always of about the same magnitude and has the same direction for all measurements. Thus it can be neglected when as here aiming at a determination of the relative size of the pupil at different intensities.

Three measurements were made for each intensity and each bird and an average was calculated. The results can be seen in table XIII in which also the area of the pupil is given, this being the determining factor for the amount of light passing into the eye.

At the lowest illuminations the measurements were impossible to perform with some birds as the pupil could not be seen at all.

In Fig. 9 are given the average curves for the area of the pupil as a function of the intensity of light for (1) *Turdus pilaris*, *Turdus merula*, *Fringilla*

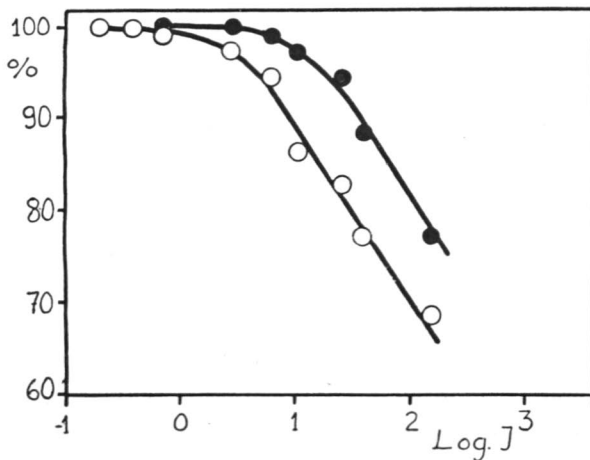


Fig. 9. Average area of pupil in percents of maximum for 1. *Turdus merula*, *Turdus pilaris*, *Fringilla ccelebs*, *Erithacus rubeculus* (circles) and 2. *Emberiza citrinella* and *Emberiza schoeniclus* (filled circles) as a function of the logarithm of illumination.

*coelebs* and *Erithacus rubeculus* and (2) *Emberiza citrinella* and *Emberiza schoeniclus*. These two groups are based on the results obtained with the training method. The birds in the first group were comparably little influenced by decreasing illumination while the birds of the second group seemed to suffer from it quite strongly. As seen from the figure the birds of the second group dilate their pupil maximally at a higher level of illumination than those of the first group. This indicates that weak illumination is more unfavourable for the vision of the birds of the second group which is in agreement with what was found with the training method.

### III. Discussion.

#### 1. The maximum visual acuity of the birds.

##### A. Comparison of the present results.

The relation between experimentally determined values for minimum separable and the morphological acuity is valid only if it may be stated that each receptor is able to produce a separate sensation. POLYAK (1941) shows that for man and the higher apes there is no doubt of the existence of isolated neural pathways from the fovea. He assumes on these grounds that each receptor is a functional unit, a conclusion already drawn by CAJAL (1894) on the basis of investigations on among others birds. POLYAK (op. cit.) makes a comparison between the human visual acuity and the morphological acuity in different parts of the retina. Both curves join in the fovea, more peripherally the morphological acuity is higher which must be due to the convergence of the receptors towards a small number of ganglion cells. In the human fovea we may thus on good grounds accept the view that the receptors are single functional units although certainly not in that sense isolated from each other that they cannot have an influence on neighbouring receptors through horizontals and amacrine cells. On histological evidence presented by CAJAL (1894) this may also be said to be true for diurnal birds. A comparison made by WALLS (1942) also illustrates the same principle: the number of ganglion cells and receptors is the same in the fovea of several birds investigated.

The values for the experimentally determined visual acuity in the present work can then be compared with the values for the morphological acuity. The values obtained are given in table XIV. For the results from the training experiments the interval is given in which the true value ought to be (p. 17).

When the possible errors of both methods are taken into account there seems to be a good agreement. For three of the birds the morphological value is higher than the experimentally determined one but the difference is so small



Table XIV.

	Training experiments	Morphol. acuity
Turdus merula .....	1'20" — 0'40"	1'39"
Turdus pilaris .....	1'20" — 0'40"	1'10"
Alauda arvensis .....	1'20" — 0'40"	1'56"
Emberiza citrinella .....	3'07" — 2'38"	2'50"
Emberiza schoeniclus .....	3'50" — 3'07"	3'11"
Fringilla coelebs .....	1'20" — 0'40"	1'37"
Erithacus rubeculus .....	2'38" — 1'53"	2'20"
Average .....	2'08" — 1'28"	1'58"

that it may be due to errors in the measurements. The average morphological acuity for all 7 birds falls within the averaged interval for the minimum separabile. However, the training results give a surprisingly high acuity considering that it cannot be expected that the birds perform their very best in the experiments. This may possibly be due to the theoretical possibility pointed out by WILCOX and PURDY (1933) that the diameter of the receptors is not the right measure for the morphological acuity (p. 18). This may be true considering the high discrimination ability of the birds' retina both in case of brightness discrimination (MEIJKNECHT 1941, DICE 1945) and in flicker experiments as expressed by the high fusion frequency (GRANIT 1936, CROZIER and WOLF 1944, a, b, c).

#### B. Comparison with earlier values for the visual acuity of birds.

The first determination of the visual acuity of birds was made by JOHNSON (1914) on chicken. He obtained the value 4'14" (VON BUDDENBROCK 1937). As the work of JOHNSON has been unavailable it is impossible to say how the determination has been done. However, it is not impossible that the domestic hen really has a low visual acuity. Already SLONAKER (1897) and FRANZ (1909) assume that the gallinaceous birds possess the lowest visual acuity among all birds due to their minute fovea. This has also been pointed out by ROCHON-DUVIGNEAUD (1943).

HAMILTON and GOLDSTEIN (1933) determined the visual acuity of pigeons through a training method based on two test objects with the lines differently orientated and obtained the value 2'42". Only one intensity of light was used. The determination was carried out at 31, 66 and 107 cm distance from the test object, the best values for the acuity being obtained from 107 cm. At 31 cm the value was 3'48". Such a decrease in the visual acuity with decreasing distance to the test object has also been observed in man (LUCKIESH and MOSS 1941) although not so marked as in this case. A good agreement with

HAMILTON and GOLDSTEIN's values was obtained by CHARD (1939) also with pigeons. He got the maximum value  $2'42''$  from 1 m distance and found a decrease in the acuity when the distance was smaller than that. This may only be caused by the retinal image losing some of its sharpness when the eye is more strongly accommodated.

GUNDLACH (1933) trained homing pigeons to discriminate between two 20 feet pathways at the end of which the test objects were placed. The experiments were carried out during  $2\frac{1}{2}$  years. The results indicate that even with a pattern giving the acuity  $0'23''$  mainly positive results were obtained. Test objects that would have given a fully negative response were never used, although he obtained a higher percentage of error for the finest object but without any decisive difference from the results with the patterns with wider lines. Thus the results do not seem reliable especially considering the great difference with respect to the results of HAMILTON and GOLDSTEIN (1933) and CHARD (1939). CHARD assumes that the determination made by GUNDLACH is not reliable and that he selected the best experimental series and thus eliminated the negative results. CHARD points out that his birds tested by the procedure adopted by GUNDLACH would certainly have given similar results.

According to SLONAKER (1897) the pigeon's fovea is not very deep, about one half of the total thickness of the retina. This is confirmed by FRITSCH (1911) and CHARD and GUNDLACH (1938). It is thus shallower than the fovea of most other birds (CHIEVITZ 1891, SLONAKER 1897, FRANZ 1909, KAHMANN 1936) a circumstance which generally has been assumed as being related to a lower visual acuity. SLONAKER (1897) mentions that the cones in the retina of pigeons have a diameter of  $1-5\ \mu$ , for the rods the same value is  $2.6-3.3\ \mu$ . According to MENNER (1929) the receptors measure extrafoveally  $4.3\ \mu$  and the diameter of the eye is 17 mm (KAJIKAWA 1923: 17 mm, CHARD and GUNDLACH 1938: 13.5 mm). The eye of the pigeon is then somewhat bigger than that of the thrushes used in the present work. As these have a nodal point distance of about 7 mm, for the pigeon 8 mm may be taken as a rough estimate. If these values are used for a rough calculation (the cones  $1-5\ \mu$ ) we get  $0'26''-2'10''$ .

In table XV all known values for the visual acuity of birds have been collected, some of them are based only on a calculation from the values given by different authors. As may be expected the Accipitres seem to possess the best acuity although the values mentioned in the table probably do not give their maximum capacity. POLYAK (1941) mentions that the foveal receptors of the Golden Eagle have a diameter of  $0.3\ \mu$  which would give an acuity of about  $5''-10''$ .

Only the diurnal birds have been taken into account, for nocturnal birds enough values are not found in the literature. It may, however, be assumed that their visual acuity is not as good as that of the diurnal birds, since the

Table XV.

Experimentally determined and calculated values for the minimum separabile of birds in general.

	Training results	Morph. acuity	
Turdus merula .....	1'20"	1'39"	
Turdus pilaris .....	1'20"	1'10"	
Turdus musicus .....		(1'47")	
Alauda arvensis .....	1'20"	1'56"	
Emberiza citrinella .....	3'07"	2'50"	
Emberiza schoeniclus .....	3'50"	3'11"	
Fringilla coelebs .....	1'20"	1'37"	
Fringilla montifringilla ...		(2'43")	
Erithacus rubeculus .....	2'38"	2'20"	
Pyrrhula pyrrhula .....		(1'52")	
Parus atricapillus .....		(2'12")	
Gallus domesticus .....	4'14"		JOHNSON (1914)
Columba livia domestica ..	2'42"		HAMILTON and GOLDSTEIN (1933), CHARD (1939)
» » » .....	0'23"		GUNDLACH (1933)
» » » .....		0'26" — 2'10"	SLONAKER (1897), WALLS (1942), KAJIKAWA (1923), CHARD and GUNDLACH (1938).
Passer domesticus .....		(1'42")	SLONAKER (1918)
Motacilla alba .....		1/5 of the human	FRANZ (1934)
Falco subbuteo .....		(0'21")	ROCHON-DUVIGNEAUD (1943)
Buteo buteo .....		(0'17")	ROCHON-DUVIGNEAUD (1943)
			ALEXANDER-SCHÄFER (1907)

retina seems more adapted to summation than discrimination. FRANZ (1934) mentions that the Great Horned Owl extrafoveally has 56,000 receptors and only 3,600 ganglion cells per sq. mm. This must mean that there is a considerable convergence which certainly does not promote acuity. The diameter of the receptors would be on these grounds about 4  $\mu$  — quite a big value as compared with the diurnal birds although this value is taken extrafoveally.

That the visual acuity of birds is relatively higher than of other animals, except the primates, is evident from table XVI, where all available data for the visual acuity of different animals have been collected. Values for the morphological acuity have not been taken into account. The superiority of the birds in comparison with the mammals is very marked. The values for the invertebrates are of a quite different magnitude, the relatively high visual acuity of the honey bee is, however, noteworthy.

Table XVI.

Experimentally determined values for the visual acuity of animals

Homo .....	0'26"	SPENCE (1934)
Chimpanzee .....	0'28"	SPENCE (1934)
Rhesus macacus .....	0'40"	WEINSTEIN and GREYER (1940)
Felis domestica .....	5'30"	SMITH (1936)
Mus rattus .....	26'00"	LASHLEY (1930)
Mus rattus alb. ....	52'00"	LASHLEY (1930)
Opossum .....	11'00"	WARKENTIN (1937)
Aves .....	0'10" — 4'14"	
Rana temporaria .....	6'53"	BIRUKOW (1937)
Lacerta agilis.....	11'28"	EHRENHARDT (1937)
Alligator .....	11'00"	WARKENTIN (1937)
Phoxinus laevis .....	10'50"	BRUNNER (1934)
Drosophila .....	9°17'	HECHT and WALD (1934)
» .....	4°15'	VON GAVEL (1939)
Apis mellifica .....	0°59'	HECHT and WOLF (1929)
Uca pugnax .....	3°52'	CLARK (1935)

C. *The physiological background for the high visual acuity of the avian eye.*

Visual acuity of the eye is limited by a great number of factors. One may then ask if there are any special arrangements in the bird eye by which some of these factors are eliminated.

The nuclear layers of the avian retina are very extensive. CHARD and GUNDLACH (1938) point out that the retina of the pigeon is nearly twice as thick as that of man and that this is due to the great number of nervous elements present. This probably makes the retina more apt for discrimination of detail (DETWILER 1943).

The coloured oil droplets in the cones absorb the short wavelengths since they are placed so that the light must pass them before the distal parts of the cones are reached. POLACK (1923) has pointed out that this may be a method of eliminating the chromatic aberration of the eye, thus making the retinal image more acute. If the blue part of the spectrum that is refracted more strongly than the long wave-lengths, is eliminated the chromatic aberration of course must be smaller. Such internal filters are known also from other animals (WALLS 1942) but are never so well developed as in the birds.

A well developed fovea was already by SLONAKER (1897) assumed to be a sign of high visual acuity. According to KAJIKAWA (1923) there are three types of foveae, the most extreme being the one where the retinal layers have been greatly reduced. This is the type found in diurnal birds. In mammals, except the primates, there is only an area centralis (KAHMANN 1936, WALLS 1942).

Among the birds there may be even two foveae present (SLONAKER 1897, FRANZ 1909, KOLMER 1924, KAHMANN 1936).

The reduction of the retinal layers in the fovea has generally been said to give the incident light a free passage to the receptors. KAJIKAWA (1923) mentions that the retina, although transparent, is never as clear as the vitreous and that a deep fovea thus presents the best conditions for acute vision. WALLS (1937, 1940, 1942) criticizes these views and states that a fovea with such a function would be of quite another shape. He then suggests that the fovea may play a role as a mechanism for promoting the visual acuity by a magnification of the retinal image. Measurements of the refraction index of the vitreous and the retina made by VALENTIN (1879 a, b) show that there really is a small difference and that thus a refraction at the surface may take place. WALLS (1940) calculates that the magnification of the retinal image in the fovea may be linearly about 13 %.

## 2. The dependence of visual acuity on illumination.

In all animals hitherto investigated the visual acuity has been seen to decrease with decreasing intensity of light. This has also been the case in the present work and to a different extent for different birds. We may then ask whether there are any perceptible differences in the structure and function of the eye that would support the results obtained.

The birds used here must all be said to be diurnal, although differences in their daily rhythm and habits occur (cf. p. 31). When the minimum separable was determined for these birds it was found that the robin and the blackbird were only to a small extent influenced by a decrease in illumination whereas the yellow-hammer and the reedbunting were quite strongly affected. The chaffinch and the fieldfare may be said to have been somewhat stronger affected by weak illumination than the robin and the blackbird but the difference is fairly small.

As the functional task of the pupil is to admit so much light to the retina that the best discrimination is achieved one may ask if there is any correlation between the size of the pupil at different levels of illumination and the results obtained for the visual acuity. As seen from Fig. 9 the yellow-hammer and the reedbunting show a tendency to dilate the pupil more strongly than the other birds. This would mean that the latter birds are better equipped for dim light vision and need not use the maximum capacity of the eye at a certain level of illumination where the first group already has to do so.

Calculating the relative amount of light falling on each receptor provides us with information about to what extent the optical system of the eye is adapted to dim light vision.

Table XVII.

Relative amount of light falling on each receptor when the pupil is maximally dilated.

Erithacus rubeculus.....	5.9	Fringilla coelebs .....	1.3
Turdus merula .....	4.9	Emberiza citrinella .....	5.4
Alauda arvensis .....	2.5	Emberiza schoeniulus .....	4.6
Turdus pilaris .....	1.8		

The formula

$$v = \left( \frac{d \times s}{f} \right)^2$$

has been used for this purpose.  $f$  = the nodal point distance,  $s$  = the diameter of the receptors and  $d$  = the maximum diameter of the pupil. The results are given in table XVII. If the yellow-hammer and the reedbunting are omitted there is a series beginning with the robin and ending with the chaffinch — the highest values indicating better qualifications for vision in dim light. These values also agree with the training results at least so far that they demonstrate the difference between the robin and the blackbird and on the other hand the skylark, the fieldfare and the chaffinch, that gave approximately the same values in the training experiments. Thus the difference in behaviour between these birds may partly be caused by slight differences in the structure of the eye. It must, however, be kept in mind that the retinal direction effect found by STILES and CRAWFORD (cf. summary by HARTRIDGE 1950) is not accounted for, the conclusions must thus be regarded with some caution. As to the yellow-hammer and the reedbunting it is difficult to say if the values are significant. However, it is hardly probable that the experimental errors have been so big that the true values would be smaller than those for the skylark, the fieldfare and the chaffinch. Thus we must conclude about the two *Emberiza* that although they seem to be in some respects better equipped for dim light vision than some of the other birds used, some factor, possibly a certain insensitivity of the retina as indicated by the pupil width measurements limits their ability to such an extent that visual acuity highly decreases with decreasing illumination.

### 3. The biological and ecological significance of the results.

The high performance ability of the avian eye has been known long before any experimental investigations have been made (cf. WALLS 1942). Many field-ornithologists have found that the birds' vision is superior to their own and this superiority has as a rule been referred to a higher visual acuity. It is true that the mode of living of the diurnal birds demands a high visual acuity. ROCHON-DUVIGNEAUD (1943), however, points out that the performances may

not always be a function of the visual acuity as expressed by the minimum separabile. He makes an analysis of some observations both on birds of prey and on smaller birds and comes to the conclusion that they do not necessarily demand an acuity superior to that of man. Very small objects, moving on the ground, are however detected by the birds but that can be said to be a function of minimum visible more than minimum separabile. The probable role played by the pecten in the detection of moving objects (MENNER 1935, 1938, CROZIER and WOLF 1944 a, b, c) must also be taken into account. But this is never able to produce a higher minimum separabile. Experiments carried out by SCHMID (1938) show that peregrine falcons are able to see moving objects invisible for the human eye even with field-glasses with  $8\times$  magnification. ROCHON-DUVIGNEAUD (1943) mentions some cases when small song-birds have been able to detect insects much better than man. But such observations do not allow any conclusions to be made about the minimum separabile, they only indicate that the minimum visible is higher than in man, which does not at all seem improbable considering that the intensity discrimination in birds probably is better than that of man (MEIJKNECHT 1941).

As birds in general may be said to orientate mainly with the aid of their eyes it may be of interest to find out whether the results obtained can be correlated with characteristic differences in the behaviour and habits of different birds.

*Feeding:* In this respect the highest visual acuity ought to be possessed by the diurnal birds of prey and the insectivorous birds, especially by those that catch their prey during flight. Birds feeding on seeds probably need not have such high acuity, they can find their food without detecting it from a great distance. Of the birds used in the present work the blackbird, the fieldfare and the robin must be regarded as the most typically insectivorous, whilst the skylark and the chaffinch also feed on seeds. But the yellow-hammer and the reed-bunting are typical granivorous birds. From this point of view the low visual acuity obtained for the latter birds seems to be just what can be expected. Definite conclusions cannot, of course, be made as only one bird of each species has been used.

*The diurnal rhythm:* The birds used in the experiments must all be regarded as diurnal animals. They do, however, show differences in their diurnal rhythm as e.g. recorded by the different awakening times in the morning. This can approximately be determined by observing the time for the first song. Such a method does not, however, give quite correct results since in nature there may be considerable differences in illumination depending on the place where the bird spends the night. The skylark and on the other hand the robin in this respect probably represent two extremes. PALMGREN (1944) found that the robin was very sensitive to changes in the illumination with respect to the

awakening and sleeping time. He claims that the change in illumination from day to day due to different weather has a direct influence.

For a discussion of the factors influencing the time for the first song see e.g. PALMGREN (1932), NICE (1939), KLOCKARS (1941).

If the awakening time cannot be regarded as determined only by the illumination it may, however, be stated that the light must play a decisive role for the time when the activity in the morning is started although this relationship is to some extent obscured by the influence of certain weather factors.

Of the birds used the blackbird and the robin have generally been found to start their singing relatively early which is quite what can be expected (PALMGREN 1932, BÖÖK 1933, PAATELA 1938, KLOCKARS 1941). The yellow-hammer also wakes up quite early but seems to be, according to BERGMAN (1950) incapable of activity that demands more acute vision in the prevailing low illumination early in the morning.

Ornithologists generally divide the song-birds into daysingers and night-singers (PALMGREN 1932) and refer the yellow-hammer and the chaffinch to the former group and the blackbird and the robin to the latter.

*The migration:* It may be stated that the birds that migrate by night ought to have a better dim light vision than those that migrate during the day. Although the migratory birds cannot be divided into two distinct groups in this respect there are two types that either prefer the night or daylight for their migration. Of the birds used here the blackbird and the robin mostly migrate by night. On the other hand the chaffinch, the skylark, the yellow-hammer and the reed-bunting migrate during daylight while the fieldfare may do so too or as well in the night. GROEBBELS (1932) claims that the differences in migration are caused by differences in the metabolism due to the kind of food the birds in question are specialized for. Contrary to this PALMGREN (1936) comes to the conclusion that the main reason must be sense-physiological as to its nature. Whatever the case may be it, however, seems natural that migration in the night demands more acute vision in the dark as compared with migration during the day. This conception is quite in agreement with the present results where the blackbird and the robin actually gave the best values in weak illuminations.

The numbers given by HÖRRING (1911—1927) concerning the number of birds each year killed during migration in the night at the Danish light-houses are in this connection of some interest. For the birds used in this work the following numbers taken from the years 1911—1927 are given:



<i>Turdus merula</i> .....	1,048 ind.
<i>Turdus pilaris</i> .....	1,438 »
<i>Erithacus rubeculus</i> .....	1,914 »
<i>Fringilla coelebs</i> .....	203 »
<i>Alauda arvensis</i> .....	10,494 »
<i>Emberiza citrinella</i> .....	14 »
<i>Emberiza schoeniclus</i> .....	162 »

The numbers given naturally ought to be compared with the total number of birds of each species migrating during the night. As this cannot be done it is difficult to make any definite conclusions about differences occurring between different birds. However, the great number of killed skylarks is very striking and cannot possibly be caused by such great differences in the number of migrating birds. It seems more natural to think about this being caused by the evidently relatively bad dim light vision possessed by the skylark as indicated by the present results.

### Summary.

1. In the introduction a short review is given of previous investigations on the visual acuity of animals.

2. The visual acuity (minimum separabile) was determined for 7 different birds (*Turdus merula*, *Turdus pilaris*, *Erithacus rubeculus*, *Alauda arvensis*, *Fringilla coelebs*, *Emberiza citrinella*, *Emberiza schoeniclus*) by a training method. This was based on training the birds to discriminate between a minimum separabile-pattern (grating) and a grey object of the same brightness. The pattern was the positive object. The birds had to find their food in small cages to which they passed through either of two passages at the ends of which the test objects were placed. After 150—400 runs positive results were obtained.

3. The determination was carried out at 6 different illuminations by making the pattern finer and finer until the birds did not react positively any more. The maximum acuity of *Turdus merula*, *Turdus pilaris*, *Alauda arvensis*, and *Fringilla coelebs* lies between 1'20" and 0'40", of *Erithacus rubeculus* between 2'38" and 1'55", of *Emberiza citrinella* between 3'07" and 2'38" and of *Emberiza schoeniclus* between 3'50" and 3'07". The decrease in visual acuity with decreasing illumination was most marked for the *Emberiza*-species' and smallest for *Erithacus* and *Turdus merula*.

4. The morphological acuity (the resolving power of the eye) was determined for the birds used, through a determination of the nodal point distance

from the retina and the diameter of the receptors in the fovea. The values obtained show a good agreement with those of the training experiments (Table XIV).

5. The size of the pupil was measured at different illuminations (Table XIII).

6. A comparison of the visual acuity of birds with that of other animals shows that the birds are superior to most of them except the primates that give about the same values (Table XVI).

7. The decrease in visual acuity in comparison with the size of the pupil at different levels of illumination is discussed. The birds that show the most marked decrease seem to use the highest pupil width at a higher level of illumination in comparison with the other birds. Some correlation is also found between the decrease in visual acuity and the amount of light falling on a single receptor in the retina.

8. The possible relation of the present results to some ecological and biological differences between the birds used is briefly discussed.

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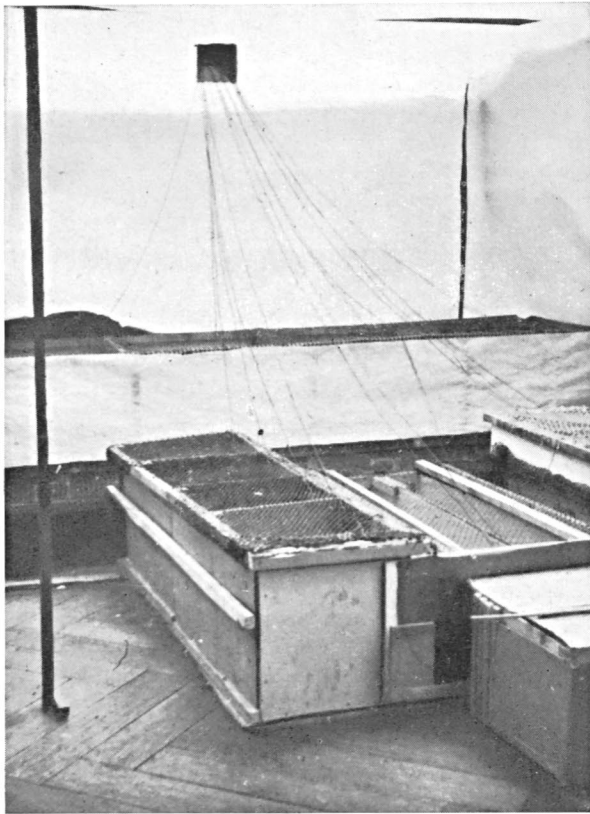


Fig. 10. The training apparatus as seen from the door of the darkroom.

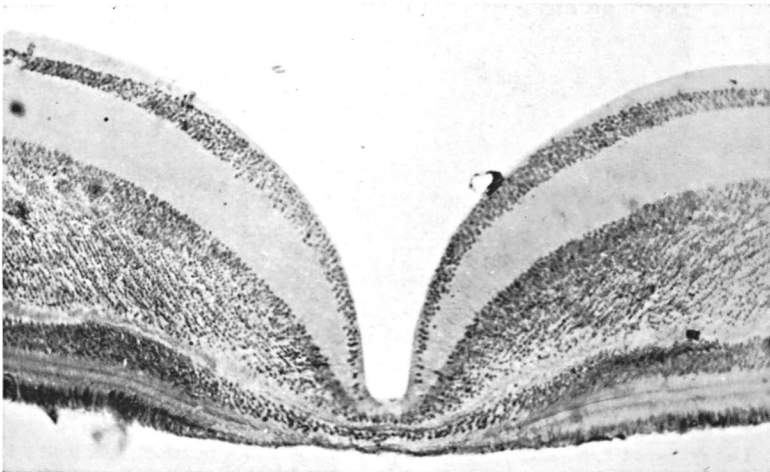


Fig. 11. Section of the fovea of *Erithacus rubeculus*.  $130\times$  magnification. Stained with Delafield's haematoxylin and eosine. Partly depigmented with  $H_2O_2$ .

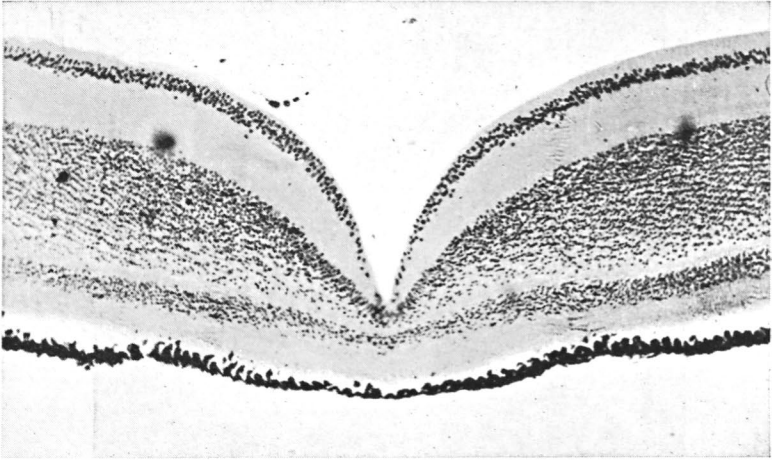


Fig. 12. Section of the fovea of *Emberiza schoeniclus*. 130  $\times$  magnification. Stained with Mayer's haemalun and eosine.

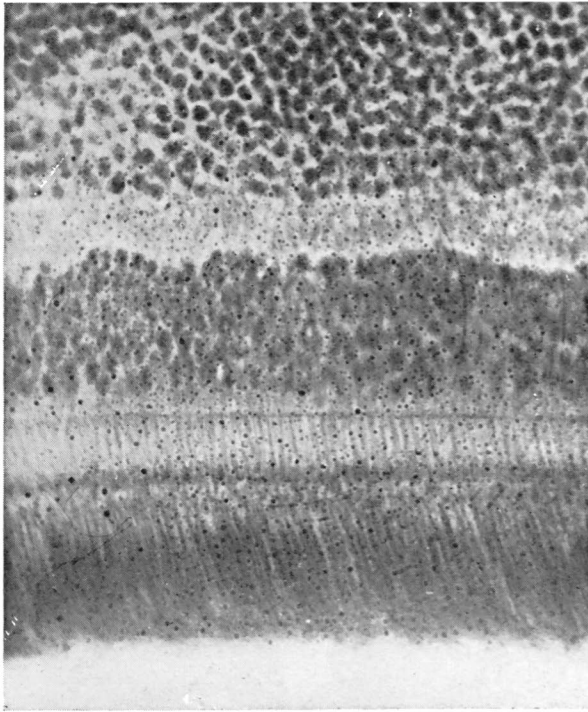


Fig. 13. The retina of *Erithacus* near the fovea. 560  $\times$  magnification. Delafield's haematoxylin and eosine. The receptors can be seen in the lower part of the picture and their nuclei in the following layer above.