

INHERITANCE OF EYE-COLOR IN MAN

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It has been claimed that human eye-color is inherited as a unit character according to Mendel's law and that brown eyes are dominant over blue. Davenport¹ and Hurst² have given the most extensive data intended to prove this point.

Davenport gives eye-color of grandparents, parents, and children of twenty-eight families and considers the data sufficient evidence that brown eyes behave as dominant over blue and grey eyes. Further he claims that grey eyes are dominant in blue-grey matings. These conclusions are not convincing because the investigator has been forced to substitute a hypothetical eye-color for the color actually recorded or to "doubt whether the term is used with precision" in order that his results may conform to the Mendelian formula. As an illustration of the method employed by Davenport we may consider the evidence he gives for recessiveness of blue eye-color. He states that in blue-blue matings sixty-nine of the offspring have blue eyes and six blue-grey or grey. In four families he says all the children are blue-eyed. In looking over the table, however, we see that of the sixty-nine blue-eyed offspring only forty are classed as blue-eyed without hypothesis or doubt as to the validity of the observations. Of the four families with three generations of blue eyes only, two have hypothetically blue eyes.

In the present study a new method, which requires data of only two generations—parents and children—has been used to test the Mendelian hypothesis for the inheritance of eye-color. Let us assume, as Davenport and Hurst have done, that brown eye-color is dominant over blue in the usual Mendelian sense. Classifying eyes as either blue or brown there are, of course, six possible matings: homozygous brown with homozygous brown, homozygous brown with heterozygous brown, heterozygous brown with heterozygous brown,

¹ Davenport, C. B. 1907. Heredity of Eye-color in man. *Science*, N. S., 26 : 589.

² Hurst, C. C. 1908. On the inheritance of eye-color in man. *Proc. Roy. Soc.*, 80: 85.

homozygous brown with blue, heterozygous brown with blue, and blue with blue. In order to test for Mendelian ratios those families only must be used in which blue-eyed children appear; that is the parents must both be either heterozygous brown-eyed, both blue-eyed, or one heterozygous brown-eyed and the other blue-eyed. Although in the population there will also be families with only brown-eyed children, as a result of heterozygous matings, these cannot be used, since there is no way of judging whether they are of heterozygous or homozygous origin. As soon as homozygous brown are included the distribution of eye-color will depend on the composition of the population. We cannot obtain the 3 : 1 ratio typical for Mendelian inheritance in heterozygous brown-brown matings, when we include in our data families with only brown-eyed children, because many of these will be of homozygous origin. The larger the number of families of homozygous origin included, the more the ratio will be disturbed. The same, of course, holds true in heterozygous brown-blue matings, where the typical 50 : 50 ratio would not be obtained if brown-eyed children of homozygous origin were included. For this reason it is necessary to exclude all families with only brown-eyed children.

TABLE I
DISTRIBUTION OF EYE-COLOR AMONG BOHEMIANS *in per Cent*

Observers	Eyes, Color					Total		Total Number of Observations
	Brown	Brown-grey	Grey	Blue-grey	Blue	Brown	Blue	
MF.....	48	—	13	—	39	61	39	237
MJ.....	41	1	15	2	41	57	43	528
TM.....	58	—	7	—	35	65	35	259
G.....	66	—	4	—	30	70	30	358
B.....	41	13	1	13 ¹	32	55	45	599
MB.....	48	—	23	—	29	71	29	456

I have analyzed three different populations, Italians, Bohemians, and East European Jews from this point of view. The material was collected in New York in 1908-09 in connection with work for the Immigration Commission. The observers were the same in all three cases. The accompanying tables (Tables I and II) show that the classification as to the color of the eyes is consistent and further that it is

¹ In this case it might be better to include blue-grey with brown. However the number of families which could be used for determining the probability for the occurrence of blue-grey eye-color was so small that the classification does not influence the result.

justifiable to class grey and brown-grey eyes with brown, and blue-grey with blue. Among the Italians the percentage of brown eyes is so great that it is not necessary to list the observations for the whole population, as has been done for the Bohemians and Jews.

TABLE II
DISTRIBUTION OF EYE-COLOR AMONG EAST EUROPEAN JEWS *in per Cent*

Observers	Eyes, Color					Total		Total Number of Observations
	Brown	Brown-grey	Grey	Blue-grey	Blue	Brown	Blue	
L.	40	7	29	5	18	76	23	156
MF.	66	—	13	—	21	79	21	356
SF.	68	—	14	—	14	82	14	46
F.	62	—	9	—	29	73	29	345
F. & Rap.	87	—	7	—	7	94	7	56
R.	67	—	17	—	17	84	17	93
S.	65	—	19	—	15	84	15	1440

If for one particular type of mating p represents the probability for brown eyes and q for blue eyes and n the number of children in a family; then nq will represent the average number of blue-eyed children per family. To test the theory we must however, as has been explained above, exclude families with only brown-eyed children. The probability that in a family with n children all will have brown eyes is p^n , therefore excluding these, $n(1 - p^n)$ will be the total number of children in the population. Consequently the probability for blue eyes in the whole series will be $\frac{nq}{n(1 - p^n)}$ or $\frac{1 - p}{1 - p^n}$.

In heterozygous brown-brown matings p for the whole population equals $3/4$. In families of two children p^n would equal $(3/4)^2$ and $\frac{1 - p}{1 - p^n}$, the value wanted in order to test the theory, would equal $\frac{1 - 3/4}{1 - 9/16}$. We thus obtain the following series of theoretical values on the assumption that we are dealing with Mendelian inheritance of a single unit factor:

n	2	3	4	5	6	7	8
$\frac{1 - p}{1 - p^n}$	57	43	37	33	30	29	28

The following tables III and IV give, in per cent, the actual observed values for blue eyes.

TABLE III
HETEROZYGOUS BROWN $\times$ HETEROZYGOUS BROWN
Per Cent of Brown

<i>n</i>	2	3	4	5	6	7	8
Theoretical.....	57	43	37	33	30	29	28
Observed:							
Jews.....	50	52	36	25	16	14	—
Bohemians.....	68	42	43	30	—	29	—
Italians.....	70	43	25	36	17	—	—
Hurst.....	50	33	25	40	27	—	33

TABLE IV
HETEROZYGOUS BROWN $\times$ BLUE
Per Cent of Brown

<i>n</i>	2	3	4	5	6	7	8	9
Theoretical.....	67	57	53	52	51	50	50	50
Observed:								
Jews.....	59	60	72	40	—	—	25	—
Bohemians.....	68	52	58	53	33	—	—	—
Italians.....	63	67	38	20	—	—	25	—
Hurst.....	56	56	56	56	54	43	63	51

Tables V and VI give the actual observed values for the different populations. At the foot of the tables are given the total percentage of brown eye-color resulting when the four different populations are combined, and for comparison the theoretical values on the assumption of Mendelian inheritance. As will be seen from the tables the totals are calculated by dividing the total number of cases of blue eyes in each column, numerator of the fraction, by the total number of children recorded, denominator.

TABLE V
HETEROZYGOUS BROWN $\times$ HETEROZYGOUS BROWN
Observed Values

<i>n</i>	2	3	4	5	6	7	8
Jews.....	10/20	22/42	13/36	5/20	4/24	1/7	—
Bohemians.....	34/50	15/36	17/40	6/20	—	2/7	—
Italians.....	7/10	13/30	5/20	9/25	1/6	—	—
Hurst.....	1/2	2/6	3/12	2/5	8/48	—	2/8
Total.....	52/82	52/134	38/108	22/70	13/78	3/14	2/8
Per cent brown.....	65	39	35	32	17	21	25
Theoretical per cent.....	57	43	37	33	30	29	28

TABLE VI
HETEROZYGOUS BROWN $\times$ BLUE
Observed Values

<i>n</i>	2	3	4	5	6	7	8	9
Jews.....	13/22	20/33	20/28	4/10	—	—	2/8	—
Bohemians.....	41/60	22/42	14/24	8/15	2/6	—	—	—
Italians.....	5/8	10/15	6/16	2/10	—	—	2/8	—
Hurst.....	9/16	10/18	18/32	25/45	29/54	12/28	5/8	23/45
Total.....	68/106	62/108	58/100	39/80	31/60	12/28	9/24	23/45
Per cent brown.....	64	57	58	45	52	43	38	51
Theoretical per cent.....	67	57	53	52	51	50	50	50

From these tables it might be argued, especially because of the rather small number of cases, that the observed values correspond fairly well with expected values for Mendelian inheritance. A few other points should, however, be taken into consideration. The following table, Table VII, gives the occurrence of brown eyes in blue-blue matings.

TABLE VII
BLUE $\times$ BLUE
Observed Values

<i>n</i>	2	3	4	5	6	7
Jews.....	2/6	1/6	6/16	—	—	1/14
Bohemians.....	3/22	8/80	2/4	—	—	—
Italians.....	4/12	—	1/8	—	—	—
Hurst.....	0/12	0/6	0/12	0/5	0/6	0/14
Total.....	9/52	7/92	9/40	0/5	0/6	1/28
Per Cent blue.....	83	92	77	100	100	96
Theoretical per cent.....	100	100	100	100	100	100

There are here among the children of two blue-eyed parents 12 per cent with brown eyes. This might, of course, be due to an error in observation. The eyes of these parents may have had some brown and really belong to the brown-eyed class. If this is the case we must assume that the same error was made in the other matings and we might have up to 12 per cent more brown eyes than observed. This would bring the percentage of brown eyes much higher than should be the case in Mendelian inheritance.

From Table V it seems as though in families with two children the observed percentage of blue-eyed children is higher than should be expected in Mendelian inheritance of a unit factor, while for families

with a larger number of children it is too low. More material is necessary to determine whether this result is significant, or merely accidental. It might be possible, for instance, to assume that the ancestry had some influence on the eye-color of the children and not the immediate parents alone. In excluding families with only brown-eyed children, as has been done in this paper, a larger percentage of families with two children have been excluded than with more than two children. This may have brought about a selection so that the distribution of eye-color in the ancestry of the different groups is not alike.

It is not claimed that the data here presented prove or disprove the Mendelian inheritance of eye-color. An attempt has been made to show that the previous studies which have claimed Mendelian inheritance as a unit factor are unsatisfactory and a different method of treating such problems has been pointed out. This method has the advantage that only two generations are necessary, parents and children, and not, as generally, at least three generations in order to determine the homozygosity or heterozygosity of the parents.