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The Inheritance of Red Hair

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Variations in pigmentation attracted the early attention of the pioneers in human genetics. The inheritance of differences between Negroes and Whites in shade of skin color was first investigated by Davenport (1910), and his findings are frequently cited as a classical example of multiple factor inheritance. In spite of this, the number of genes involved and their interactions are still unknown. Brown eye color was formerly considered to be an example of simple dominance, blue being recessive. We now know that the inheritance of eye color is complex, involving many genes. Color of hair is highly variable, depending upon two types of pigment.

Variations in the amount of melanin are primarily responsible for differences in shade of skin pigmentation, eye color and the various grades of light and dark hair. Red hair results from round or oval pigment granules (Birbeck and Barnicot, 1959) as contrasted with the large irregular granules responsible for brown and black. Although red hair is frequently cited as an example of simple recessive inheritance, this hypothesis does not bear up under careful analysis. Heavy concentrations of melanin completely or partially mask the red pigment. Examination has revealed red pigment in the black hair of some West Africans and Melanesians. Among Whites the expression of red pigment is less likely to be masked on the face than on the scalp, sometimes resulting in a combination of black hair and red beard. The analysis of hair color is further complicated by the common tendency for the hair of many blond and red haired children to become brown as they grow older. Shade of color may become lighter because of exposure to the sun, and it is sometimes difficult to determine whether the color is natural or synthetic.

Neel (1943) analyzed data on the incidence of red hair among the children from 26 families in which both parents were red haired. These data were obtained from family pedigrees on file at the Eugenics Record Office in Cold Spring Harbor, N. Y. There were 101 children with red hair, and 13 with non-red hair, a total of 114. Neel assumed that dark brown and black are epistatic to red hair color, and that 57.5% of the White population possess these dark shades. He further assumed that among the remainder 3% are red haired and 97% are dark brown or lighter. On this basis a gene frequency analysis gave too few non-red offspring if red is dominant, whereas if recessive there should be no blond offspring from red haired parents.

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Although favoring the hypothesis that red hair is recessive, Neel proposed two independent sets of recessive genes being involved, which could account for the non-red offspring from red haired parents.

Reed (1952-53) made an extensive spectrophotometric reflectance curve analysis of red hair in several large families. Although concluding that red hair is a genetical character, he made no proposal as to the mode of inheritance.

The writer has collected data over a period of years on families in which one or more members are red haired, and the relatively high concentration of red hair within families led to undertaking the project herein outlined.

Design of the project

The hypothesis to be tested proposes that a single dominant gene is responsible for red pigmentation of human hair. It is further proposed that various shades of brown and black are epistatic to red. This differs from the hypotheses of other investigators in that here not only black and dark brown, but also lighter shades of brown are assumed to be epistatic to red. Only hair too light to be unmistakably classified as brown is considered to be completely non-epistatic to red. Individuals with light hair are classed as blonds, and include subjects with yellow, flaxen and lighter shades.

Data have been assembled from 22 families and the results are recorded in Tab. 1. Shades other than red or blond among the offspring are noted in parenthesis as dark. Members of each family were observed and interviewed, and no attempt was made to select large families or those having two or more red haired members. When a red haired person was observed individual contacts were made with the subject when feasible and subsequently with other members of his or her immediate family.

If a trait is inherited as a simple recessive, the proportion of recessive offspring among families in which both parents are of dominant phenotype should range between zero and 25%, depending upon gene frequencies. In families where one parent is of dominant phenotype and the other recessive, the proportion of recessive offspring should not exceed 50%. Tab. 1 reveals that the proportion of red haired offspring considerably exceeds these limitations, indicating that its inheritance cannot be explained as a simple recessive.

In order to test this hypothesis it was necessary to obtain an estimate of the ratio of blonds to red haired in the general population. The P. K. Yonge Laboratory School of the University of Florida provided an excellent source for procurement of the desired information. This school includes nursery, kindergarten and the twelve grades through high school. Each teacher has approximately 30 pupils, and each submitted a list of blond and red haired pupils under his or her supervision. Later each class was observed by the writer, and his classification was compared with that of the teachers. Very good agreement was found, although there were a few border line cases where classification was debatable.

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Tab. 1*a*. Hair color within families

	1.	2.	3.	4.
Parents	Dark × Red(light)	Red(beard) × Red(light)	Dark × Dark	Dark × Dark
Offspring	2 Red 1 Blond	1 Red 1 Blond (3 dark)	2 Red 2 Blond	4 Red
	5.	**6.**	**7.**	**8.**
Parents	Dark × Blond	Dark × Red(light)	Dark × Red(light)	Dark × Red(light)
Offspring	1 Red 1 Blond	1 Red	2 Red (2 dark)	4 Red 1 Blond
	9.	**10.**	**11.**	**12.**
Parents	Red(dark) × Red(light)	Dark × Blond	Red × Red	Red × Dark
Offspring	4 Red (2 dark) (2 light)	3 Red	4 Red	2 Blond
	13.	**14.**	**15.**	**16.**
Parents	Blond × Dark	Dark × Red(light)	Dark × Dark	Red × Red(dark)
Offspring	3 Red	2 Red 2 Blond	2 Red 1 Blond	1 Blond (3 dark)
	17.	**18.**	**19.**	**20.**
Parents	Red × Dark	Red × Dark	Red × Blond	Red × Dark
Offspring	2 Red (1 dark)	3 Red	4 Blond	2 Red 1 Blond (1 dark)
	21.	**22.**		
Parents	Dark × Red	Red × Red		
Offspring	4 Red	3 Red		

Tab. 1*b*. Summary

N. of families	Parents	Offspring		
		Red	Blond	Dark
5	Red × Red	12	2	6
4	Non-blond × Blond	7	5	0
13	Red & Dark × Dark	30	10	4
Totals 22		49	17	10

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Gene frequency analysis of the data

At the time of the survey there were 910 pupils in the school. Among these 76 were classified as blonds and 44 as red haired. This gave a ratio of 0.633 blonds to 0.367 red haired. Assuming red to be dominant to blond and hypostatic to dark, $q^2 = 0.633$ and $q = 0.795$. These values are somewhat higher than those obtained by other investigators, principly because of the assumption that all shades of brown are epistatic to red. These gene frequencies form the basis for tests *b*, *c*, *d* and *e* in Tab. 2. The result of test *a* reveals that the proportion of red haired children within the families under consideration exceeds the maximum number to be expected by a highly significant amount, if red is considered recessive to blond. The deviation would be highly significant for *any* frequency of q, and is strong evidence against red hair being recessive to blond.

It is important to keep in mind that the 22 families were selected on the basis of a red haired member of each, the member having been selected without prior knowledge of the hair color of other members of his or her immediate family. Thirteen of the families were those of the first 13 pupils listed by the teachers at the school as having red hair, and the other nine were those of red haired individuals encountered at random over a 6 year period. Selection was against families with no red haired members.

Tab. 2*b* reveals close agreement between the observed and calculated frequencies of red and blond haired offspring among families in which both parents have red hair. There are five of these families, and it is of interest to note that there are also dark haired offspring, all of which occur in two of the families. Various shades of brown and black doubtless involve several genes with cumulative effects, somewhat like skin pigmentation. In such situations it is not uncommon for some of the offspring to be darker or lighter than either parent.

Tab. 2*c* shows close agreement between the calculated and observed frequencies of hair colors among offspring of parents of whom one is blond and the other is non-blond. Four families are included in this group. Among these one parent is red haired, and among the others one is dark haired. In each of the latter at least one of the offspring is red haired, so we may assume that each dark haired parent possesses red hair pigment. Thus these four families belong to the category in which one parent is of recessive phenotype and the other possesses the gene for red hair.

Tab. 2*d* gives the comparison between observed and calculated numbers of offspring for red or blond hair, among families in which one parent is red or dark haired, and the other is dark haired. In some of these families it is impossible to determine from phenotype alone as to whether both parents or only one of them possesses the dominant gene for red pigment. But as each family has at least one red haired member, we can rule out matings of blonds × blonds. The expected proportion of genotypic blonds to red haired in the general population is q^2. Among these q^4 gives the proportion expected from two genotypically blond parents. Therefore the expected

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Tab. 2. Tests for statistical significance of differences

a.

On the assumption that red is recessive to blond hair, deviation of observed ratio from expected on the basis of maximum possible proportion of recessives within families. The maximum is 0.500

Phenotype	Observed	Calculated	χ^2	df
Red Hair	37	26	9·344	1
Blond Hair	15	26		

b.

On the assumption that red hair is dominant to blond and hypostatic to brown and black. Offspring of red haired × red haired

Expected proportion of recessives $= \dfrac{q^2}{(1 + q)^2}$

Phenotype	Observed	Calculated	χ^2	df
Red Hair	12	11.256	0.250	1
Blond Hair	2	2.744		

c.

Same assumption as in *b*. Offspring of blond × non-blond parents

Expected proportion of recessives $= \dfrac{q}{1 + q}$

Phenotype	Observed	Calculated	χ^2	df
Red Hair	7	6.696	0.102	1
Blond Hair	5	5·378		

d.

Same assumption as in *b* and *c*. Offspring of red or dark haired × dark haired parents

Expected proportion of recessives $= \dfrac{(q^2 - q^4)}{1 - (q^2 - q^4)}$

Phenotype	Observed	Calculated	χ^4	df
Red Hair	30	27.840	0.550	1
Blond Hair	10	12.160		

e.

Same assumption as in *b*, *c* and *e*. Offspring of all parents

Expected proportion of recessives $= \dfrac{(q^2 - q^4)}{1 - (q^2 - q^4)}$

Phenotype	Observed	Calculated	χ^2	df
Red Hair	43	45·936	0.671	1
Blond Hair	17	20.064		

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Fig. 1. Photographs of family No. 16. *a*: mother with children, note blond son; *b*: father; *c*: mother and one dark-haired daughter. At younger age mother's hair was completely red

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ratio of blond to red haired offspring among the families in 2*d* $= \frac{(q^2 - q^4)}{1 - (q^2 - q^4)}$.
The agreement between the observed and calculated frequencies is close.

Tab. 2*e* includes all 22 families and the same formula as that employed in 2*d* applies for testing the significance of deviations from the expected ratio. Here again there is only a small deviation from the expected ratio. Each of the four gene frequency tests are in good accord with the hypothesis that red hair pigment is dominant to blond and hypostatic to dark.

Discussion

Although the statistical analysis includes data from only two generations, many of the red haired parents volunteered information pertaining to the occurrence of red hair in one or both of their parents, their siblings, and in some instances their grandparents and even great grandparents. However, it was felt that our data would have greater validity if restricted to individuals who were seen by the investigator. Decision as to classification of hair color is sometimes difficult and more or less arbitrary. Occasionally one encounters an adolescent or an adult, especially the latter, possessing dark auburn hair. These we have classed as red, as they obviously do possess red pigment. Inquiries have revealed that such persons frequently had bright red hair when they were quite young. The school survey included several very young children many of whom while now blond or red haired will doubtless change to brown or possibly to auburn as they become older. It is not clear as to why in some instances red haired children become brown or sandy haired adults, whereas in others their hair changes to auburn. Possibly there may be two or more alleles at the red hair locus, each of which results in a slightly different shade of red, some of which are more easily masked than others by brown. In spite of the difficulties in classification of hair as to shade of color, the hypothesis that red hair is dominant to blond and is hypostatic to brown and black is strongly supported by family data and gene frequency analysis.

Summary

1. The proportions of red haired offspring within families in which one or both parents are red haired are too high to support the hypothesis that red hair is inherited as a simple recessive trait.

2. Family data and gene frequency analysis give strong support to the hypothesis that red pigment in human hair is dominant to its absence, and is hypostatic to brown and black.

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References

Birbeck N. A., Barnicot N. A. (1959). Pigment Cell Biology. Academic Press, New York, 549-61.
Davenport C. B. (1910). Heredity of skin color in Negro-White crosses. *Carnegie Inst. Washington Publ.*, 188.
Neel J. V. (1943). Concerning the inheritance of red hair, *J. Hered.*, **34:** 93-96.
Reed T. E. (1952-53). Red hair color as a genetical character. *Ann. Eug.*, **17:** 115-39.

RIASSUNTO

1. La proporzione di figli con capelli rossi in famiglie in cui tale carattere è presentato da uno o da ambedue i genitori, è troppo elevata per sostenere l'ipotesi di un meccanismo recessivo semplice.
2. L'analisi dei dati familiari e delle frequenze geniche sostiene nettamente l'ipotesi che il pigmento rosso del pelo nell'uomo sia dominante rispetto all'assenza del carattere ed ipostatico nei riguardi del bruno e del nero.

RÉSUMÉ

1. La proportion de fils roux dans les familles où l'un des parents ou tous les deux présentent ce caractère est bien trop élevée pour soutenir l'hypothèse d'une récessivité simple.
2. L'analyse des données familiales et des fréquences géniques est nettement en faveur de l'hypothèse que le pigment rouge dans le poil chez l'homme est dominant vis-à-vis de l'absence du caractère et hypostatique vis-à-vis du brun et du noir.

ZUSAMMENFASSUNG

1. Die Verhältnisse von rothaarigen Abkömmligen innerhalb Familien, in denen einer oder beide Eltern rothaarig sind, sind zu hoch, um die Voraussetzung zu unterstützen, dass rotes Haar als einfaches rezessives Merkmal erblich sei.
2. Analyse von Angaben über Familienverhältnisse und Genhäufigkeit leistet starke Unterstützung zur Voraussetzung, dass roter Farbstoff in menschlichem Haar dominant ist und braunem und schwarzem gegenüber hypostatisch.

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