

INHERITANCE OF THE P.T.C. TASTE CHARACTER IN MAN: AN ANALYSIS OF 126 RĀRHI BRĀHMIN FAMILIES OF WEST BENGAL

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INTRODUCTION

Harris & Kalmus (1951), and Das (1956*a*) have recently studied the problem of inheritance of phenylthiocarbamide (and allied substances) taste sensitivity on the basis of taste threshold distributions of 384 and 845 sib-pairs, respectively. Their results failed to confirm the existing hypothesis of simple unifactorial recessive inheritance of taste deficiency. But whereas Harris & Kalmus (1951) surprisingly found their data closer to a non-genetic chance hypothesis than the genetic, Das noticed his data more inclined toward the genetic than to the chance hypothesis. Even a satisfactory agreement ($\chi^2 = 4.34$, 3 D.F., $P > 0.2$) with the simple genetic hypothesis was obtained by Das on excluding the border line phenotypes having the thresholds 5, 6, or 7. These results and the historical context briefly stated below demanded an efficient scrutiny of the problem of inheritance, using reliable family data (Harris & Kalmus, 1951).

The genetic hypothesis in question, was propounded by Blakeslee (1932), and Snyder (1932) on the basis of family studies conducted by the now obsolete dry crystal method and the simple serial dilution method of taste testing, respectively. The results of these two methods as also those of the 'paper strip' method devised later did not always agree with one another (Blakeslee, 1932; Boyd & Boyd, 1937; Hartmann, 1939; Harris & Kalmus, 1949; and Mohr, 1951) in individual cases, although they might betray no appreciable difference in the mass data in respect of the taster/non-taster ratio.

Attention was drawn to the procedural flaws in the dry crystal method of taste testing almost right after the discovery of the phenomenon of dimorphism in P.T.C. taste perception. Thus, Blakeslee (1932) wrote—'The fact that a few could taste bitterness in the solutions even in high (*D*) dilution, but were unable to taste the crystals suggested trying saturated solution of the compound on negative subjects'. Blakeslee's dilution (*D*) was 1 in 320,000, which could be tasted bitter only by the 'tasters'. It comes in between the solutions numbered 9 and 10 in the scale employed by Harris & Kalmus (1949) and the followers of their method. Obviously, such individuals as could taste a dilution of 1 in 320,000, but not the crystals would be entered as non-tasters, if the dry crystal method of testing were adopted; while on the contrary, the serial dilution method would have counted them among the tasters. Again, Hartmann (1939) after a critical study 'concluded that employment of the dry substance for the test will not give so many diagnosed non-tasters, according to the threshold value definition, as there are actually'. The two sources of error just stated above affected the number of non-tasters in the dry crystal method in opposite ways—the former would enhance and the latter would reduce it. Perhaps they nearly balanced each other in mass data and thereby justified the statement that 'for anthropological purposes there is little difference between these methods' (Boyd & Boyd, 1937). To the geneticists the situation was not at all satisfactory. The conscientious anthropologists also could hardly remain complacent. The simple serial dilution method was no

doubt an improvement upon the dry crystal method, but it had the drawback of its results being highly subjective. The experimenter had to depend solely upon the comments of the individual whose taste threshold was measured, which could never be free from biases, or even fraud.

With the introduction of the 'sorting technique' by Harris & Kalmus (1949), which has since superseded all the older methods by virtue of its being free from the errors inherent in the crystal method and due to its considerable degree of objectivity, there arose very naturally a question of a fresh assessment of the position of the genetic hypothesis.

Snyder's analytical procedure known as the single autosomal gene substitution method (Snyder, 1932; Hogben, 1946) was also not very rigorous. Referring to this very method of analysis 'which has almost become the standard way of verifying unifactorial inheritance', Race & Sanger (1954) have written—'that the method does in fact usually give a very good fit is probably due to the shortage of large families in the data'. In fact, there were about 2.55 and 2.20 sibs per sibship, respectively, in the families studied by Snyder (1932) and Blakeslee (1932). These figures indeed indicated a shortage of large families, which favourably influenced the results of those investigations. It was desirable that a set of P.T.C. family data should be subjected to analyses by rigorous methods which were fortunately there already.

METHOD

In the present investigation the sorting technique (Harris & Kalmus, 1949) has been used in testing the families. The family data have been analysed by the methods stated below, all of which are rigorous.

(i) *Test for randomness of the matings.* As suggested by Smith (1956), the randomness of the four possible matings (phenotypical) has been tested by arranging the matings in a '2 × 2' contingency table and applying the χ^2 test of 'independence'.

(ii) *Fisher's method.* It has been used by Taylor & Prior (1939), Race, Ikin, Taylor & Prior (1942), and Race & Sanger (1952, 1954) in blood groups genetics. The expected and the observed numbers of (a) families containing exclusively dominant children, and (b) families containing at least one recessive child are compared, calculating $\chi^2 = (\text{observed} - \text{expected})^2 / \text{expected}$. Smith (1956) has recently suggested a modification of this test, calculating $\chi^2 = (\text{observed} - \text{expected})^2 / \text{variance}$ (with 1 D.F.) for the families which contain at least one recessive child. Smith's suggestion has also been followed as a check-up. Fisher's method, it may be mentioned, does not take any account of the actual numbers of the recessives in the families. A test which does so would be most desirable and that is realized in the next analysis.

(iii) *Analysis based on a priori expectation of the number of recessives in sibships of different sizes.* This method has been developed by Bernstein (1929), Hogben (1932), Haldane (1932) and Fisher (1934), and explained by Hogben (1946), Stern (1950) and, more usefully, by Smith (1956). The procedure outlined by the last author has been followed here.

MATERIAL

Members of 129 Rárhí Bráhmín families living for generations in the south suburban municipality near Calcutta could be persuaded to taste testing. Only the families containing two or more children suitable for the test were included for reasons of their obvious usefulness in the sib-pair study already reported (Das, 1956a). Both of the parents could be tested in

127 families; the father of one and the mother of another were not available for the tests. The average sibship size was 3.8 nearly. The mean age in years of 128 fathers tested was 47.6 and that of 128 mothers was 36.3 approximately.

BASIC DATA

The taste threshold distributions for the parents are given in Table 1. Those for the children were presented before (Das, 1956*a*). The boundary line separating the two phenotypes comes in between the thresholds 5 and 6, exactly as in the case of the children. The test of 'homogeneity' by ' 2×12 ' table (Fisher, 1946) applied to the distributions in Table 1 after merging the classes 11 and 12 has yielded $\chi^2 = 13.78$, 11 D.F., with $P > 0.2$.

Table 1. *Taste threshold distributions of the parents*

Threshold no. ...	0	1	2	3	4	5	6	7	8	9	10	11	12	13-14
Fathers (128)	4	8	6	11	5	1	4	6	9	41	29	3	1	—
Mothers (128)	5	14	6	3	6	6	1	3	10	32	32	10	—	—
Total (256)	9	22	12	14	11	7	5	9	19	73	61	13	1	—

The test of 'independence' by the ' 2×2 ' table (Fisher, 1946) applied to the taster and the non-taster type frequencies in 128 fathers and 128 mothers has given $\chi^2 = 0.4714$ with $P > 0.3$. The results indicate that statistically significant sex difference exists between the paternal and the maternal groups neither in respect of the taste threshold distributions, nor in respect of the relative proportion of the taster and the non-taster phenotypes. The entire parental data have, therefore, been added together in estimating the taste gene frequencies. The proportion of the non-tasters, the homozygous recessives, in the total parental population is found to be 0.2930 with a standard error of 0.0284. Now assuming the validity of the hypothesis of the simple single factor inheritance with complete dominance of the taster gene (T) over its non-taster allele (t), the frequencies of the taster and the non-taster genes in the population represented by 256 parents are found to be respectively,

$$p = 0.4587 \quad \text{and} \quad q = 0.5413. \quad (1)$$

These gene frequencies have been used in the genetic analyses that follow. It may, however, be mentioned that the ratio of 181 tasters to 75 non-tasters in the parental population agrees very closely (' 2×2 ' table; $\chi^2 = 0.3806$, $P > 0.5$) with that of 335 tasters to 154 non-tasters in the filial population (Das, 1956).

The phenotypic composition of the 127 families grouped in accordance with the mating types are presented in Table 2 in the form demonstrated by Race & Sanger (1954) in the course of their analysis of the P blood groups data. It is found in Table 2 that among the sibships produced by non-taster to non-taster matings, there are two instances, in which the sibs are not all non-tasters. The taste thresholds of the members of these two families have been presented below Table 2, with age and sex. Before taking up the analyses of the family data, it was necessary to scrutinize the two exceptional families which had the serial numbers 3 and 66. The only taster child in the family, no. 66 with the taste threshold at solution no. 6, could perhaps be explained as a true non-taster which was misclassified as a taster due to its taste

threshold having fallen in the border-line region, where the threshold distributions of the taster and the non-taster groups overlap (Hartmann, 1939; Penrose, 1951, 1954, and Das, 1956a). The taster children of the other family, no. 3, could not be easily reconciled in this way. It was either a real exception to the hypothesis, indicating a variation of the genic action, or some extragenic influence was certainly there. All the members of this interesting family were

Table 2. *Data of 127 families with 487 children tested with P.T.C.*

Mating		Children tested		Mating		Children tested	
Type	No.	Taster	Non-taster	Type	No.	Taster	Non-taster
Taster × taster	12	2	—	Taster × non-taster	4	1	1
	13	3	—		2	2	1
	6	4	—		1	1	2
	2	5	—		1	—	3
	1	6	—		5	3	1
	3	7	—		4	2	2
Taster × taster				Non-taster × taster	1	4	1
	1	—	2		1	2	3
	1	1	1		2	1	4
	2	2	1		1	5	1
	2	—	3		1	3	3
	7	3	1		1	4	3
	3	2	2				
	1	1	3		2	1	1
	1	4	1		1	—	2
	1	3	2		5	2	1
	1	2	3		1	1	2
	1	5	1		2	3	1
	1	3	3		1	2	2
	1	6	2		1	—	4
Taster × non-taster				Non-taster × non-taster	1	2	3
	1	4	4		1	4	2
	1	7	4		1	2	4
Taster × non-taster	1	2	—		1	—	2
	2	3	—		1	—	4
	1	4	—		1	3	1
	1	5	—		4	—	5
	1	6	—		1	1	4
Non-taster × taster					1	—	6
	4	2	—				
	2	3	—				
	2	4	—				
	1	5	—				
	1	6	—				

Family no.		Father	Mother	Children				
				I	II	III	IV	V
3	Threshold	0	2	9	2	7	10	—
	Age (years)	44	33	16	13	9	7	—
	Sex	M.	F.	F.	M.	F.	M.	—
66	Threshold	1	1	3	2	6	3	2
	Age (years)	55	38	18	14	12	8	6
	Sex	M.	F.	M.	F.	M.	M.	F.

put to serological tests. No genetic discrepancy was noticed in the family bloods in respect of the A_1A_2BO and the MN blood groups, nor in the ABH secretion in their saliva. But the Rh types of the family revealed a parent-child discrepancy. While the father and the mother were respectively $ccddee$ and $CcDee$, their children were in order of birth $CcDee$, $ccddee$, $CCDee$ and $CcDee$ (the phenotype notations are those used in Mourant, 1954). The third child was certainly a misfit and the obvious conclusion was that an extra-marital influence must have been responsible for the discrepancies in the Rh blood types and probably as well in the P.T.C. taste phenotypes. This family has, therefore, been excluded from the data used in the genetic analyses.

ANALYSES

(i) *Test for randomness of the matings*

In Table 3, the four phenotypical matings, $\bar{T} \times \bar{T}$, $\bar{T} \times \bar{t}$, $\bar{t} \times \bar{T}$ and $\bar{t} \times \bar{t}$ have been arranged in a '2 x 2' contingency table in order to apply the test of 'independence'. The χ^2 value of 0.972 with 1 D.F. indicates a really good fit ($P > 0.3$). A divergence from the expectation as large, or a larger one would be found nearly once in every three such investigations. With this confirmation at the outset about the randomness of the matings, we may proceed with the tests that follow, which are valid only when this condition is satisfied. ($\bar{T}$ and $\bar{t}$ have been used throughout to represent the taster and the non-taster phenotypes, respectively; whereas the dominant and the recessive taste genes have been represented by T and t , respectively.)

Table 3. *Test for randomness of matings*

	Father		Total
	$\bar{T}$	$\bar{t}$	
Mother $\bar{T}$	62	26	88
$\bar{t}$	30	8	38
Total	92	34	126

$$\chi^2 = 0.972; 1 \text{ D.F.}; P > 0.3.$$

(ii) *Fisher's method of analysis*

First, the procedure given by Taylor & Prior (1939), and Race & Sanger (1954) will be followed. The mathematical expressions to be used here can be obtained neatly from Table 4, following the process outlined in (a) and (b) below.

(a) *Matings of the type $\bar{T} \times \bar{T}$*

Adding up the products of the corresponding figures in columns 3 and 6, and then dividing this sum by the total probability, $p^2(1+q)^2$, for the mating type $\bar{T} \times \bar{T}$, we obtain,

$$\text{probability of all the } c \text{ sibs of a sibship being tasters} = 1 - [4q^2/(1+q)^2] [1 - (\frac{3}{4})^c]. \quad (2)$$

(b) *Matings of the types $\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$*

Adding up the products of the corresponding figures in columns 3 and 6, and then dividing this sum by the total probability, $2pq^2(1+q)$, for these matings, we obtain,

$$\text{probability of all the } c \text{ sibs of a sibship being tasters} = p/(1+q) + [2q/(1+q)] (\frac{1}{2})^c. \quad (3)$$

Table 4. *Probability of all the sibs of a sibship being tasters**(p = frequency of the T gene and q = frequency of the t gene)*

Mating			Sibs		
Phenotype 1	Genotype 2	Probability 3	Probability of a sib being		Probability of all the c sibs being tasters 6
			Taster 4	Non-taster 5	
$\bar{T} \times \bar{T}$	$TT \times TT$ $TT \times Tt$ $Tt \times Tt$ Total	p^4 $4p^3q$ $4p^2q^2$ $p^2(1+q)^2$	1 1 $\frac{3}{4}$	0 0 $\frac{1}{4}$	1 1 $(\frac{3}{4})^c$
$\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$	$TT \times tt$ $Tt \times tt$ Total	$2p^2q^2$ $4pq^3$ $2pq^2(1+q)$	1 $\frac{1}{2}$	0 $\frac{1}{2}$	1 $(\frac{1}{2})^c$
$\bar{t} \times \bar{t}$	$tt \times tt$	q	0	1	0

Table 5. *Analysis of $\bar{T} \times \bar{T}$ families*

Sibship size c 1	Total no. sibships 2	No. of sibships (all sibs tasters)		No. of sibships (at least 1 sib non-taster)		
		Expected 3	Observed 4	Expected 5	Observed 6	Variance 7
2	14	10.97	12	3.03	2	2.372
3	17	12.15	13	4.85	4	3.466
4	17	11.27	6	5.73	11	3.804
5	5	3.12	2	1.88	3	1.174
6	3	1.78	1	1.22	2	0.723
7	3	1.72	3	1.28	0	0.734
8	2	1.11	0	0.89	2	0.494
11	1	0.53	0	0.47	1	0.249
Total	62	42.65	37	19.35	25	13.016

Table 6. *Analysis of $\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$ families*

Sibship size c 1	Total no. sibships 2	No. of sibships (all sibs tasters)		No. of sibships (at least 1 sib non-taster)		
		Expected 3	Observed 4	Expected 5	Observed 6	Variance 7
2	12	5.68	5	6.32	7	2.990
3	14	5.40	4	8.60	10	3.313
4	16	5.46	3	10.54	13	3.595
5	7	2.24	2	4.76	5	1.520
6	6	1.85	2	4.15	4	1.281
7	1	0.30	0	0.70	1	0.211
Total	56	20.93	16	35.07	40	12.910

The analysis is conveniently set out as in Tables 5 and 6. It may be clarified here that throughout this paper, *c* represents the number of children who were actually tested in a family, which could therefore be sometimes less than the number of children existing.

A few words may be necessary as to how the columns of Tables 5 and 6 have been derived. From (1), (2) and (3) the probabilities of all the sibs being taster in sibships of various sizes have been evaluated for the respective mating types, assigning successively the values 2, 3, 4, etc., to *c*. On multiplying each value of the probability by the corresponding total number of sibships, the column 3 has been obtained. Column 5 = (column 2) - (column 3), and column 6 = (column 2) - (column 4). The variances of the expected numbers (column 5) have been obtained in the way explained by Smith (1956). These variances are included in column 7.

Table 7. Summary of analysis by Fisher's method

Mating phenotype	Sibship composition	No. of sibships		χ^2	D.F.
		Expected	Observed		
$\bar{T} \times \bar{T}$	All sibs tasters	42.65	37	2.40	1
	All sibs not taster	19.35	25	($P > 0.1$)	—
$\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$	All sibs taster	20.93	16	1.85	1
	All sibs not taster	35.07	40	($P > 0.1$)	—
			Total	4.25 ($P > 0.1$)	2

In Table 7 has been summarized the test for 'goodness of fit' calculating $\chi^2 = (\text{observed} - \text{expected})^2 / \text{expected}$ (Taylor & Prior, 1939, and Race & Sanger, 1954). The results, ($\chi^2 = 2.40$, 1 D.F.; $\chi^2 = 1.85$, 1 D.F.; and $\chi^2 = 4.25$, 2 D.F.), indicate a fairly good fit with $P > 0.1$ for both the mating types separately as well as jointly. This result was published earlier in a brief abstract (Das, 1956*b*).

The results of the analysis following the procedure prescribed by Smith (1956) are now briefly given below.

For the $\bar{T} \times \bar{T}$ matings we have from Table 5

Total expected number of families with at least one non-taster child = 19.35.
 Total observed number of families with at least one non-taster child = 25, and
 Total variance of the expected number of families with at least one non-taster child = 13.016.
 Therefore, deviation = observed - expected = 5.65.
 and, s.e. = $\sqrt{\text{variance}} = \sqrt{13.016} = 3.61$.
 Hence, deviation/s.e. = 1.565, and $\chi^2 = (5.65)^2 / 13.016 = 2.45$,
 with 1 D.F. This corresponds to $P > 0.1$.

For $\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$ matings we have from Table 6

Total expected number of families with at least one non-taster child = 35.07.
 Total observed number of families with at least one non-taster child = 40, and
 Total variance of the expected number of families with at least one non-taster child = 12.910.
 Therefore, deviation = observed - expected = 4.92,
 and, s.e. = $\sqrt{\text{variance}} = \sqrt{12.910} = 3.59$.
 Hence, deviation/s.e. = 1.370 and $\chi^2 = (4.92)^2 / 12.910 = 1.88$,
 with 1 D.F. This also corresponds to $P > 0.1$.

It is then found that Smith's test also leads to the conclusion that there is good fit ($P > 0.1$) for the totals of fraternities of different sizes. Considering them separately there is noticed also a fairly satisfactory agreement in each of them, with only one exception in the sibship size, $c=4$, produced by $\bar{T} \times \bar{T}$ mating (Table 5), which gives ($\chi^2 = 7.27$, 1 D.F., $P < 0.01$). This is significant. We now pass on to the next test and reserve the final conclusion till that is completed.

(iii) *Analysis based on a priori expectation of the number of recessives in sibships of different sizes each containing at least one recessive sib*

Hogben (1946), Stern (1950) and Smith (1956) have explained this method of test for segregation ratios in family data. We have found it convenient to follow the procedure prescribed by the last author, which is, however, equivalent to that of Hogben (1932, 1946), except for certain useful additions.

For 'taster $\times$ taster' families containing at least one non-taster child, we can write (Smith, 1956),

$$A_c = \frac{\frac{1}{4}c}{1 - (\frac{3}{4})^c}, \quad (4)$$

and,
$$B_c = A_c \left[\frac{3+c}{4} - A_c \right], \quad (5)$$

where A_c = the expected number of non-tasters per sibship of c sibs, and B_c = the corresponding variance. The total expected number of non-tasters for sibships of size c is given by $M_c A_c$, and its variance by $M_c B_c$, where M_c = the number of sibships of size c containing at least one non-taster.

For 'taster $\times$ non-taster' families (including also $\bar{t} \times \bar{T}$) containing at least one non-taster child, we write (Smith, 1956),

$$a_c = \frac{\frac{1}{2}c}{1 - (\frac{1}{2})^c}, \quad (6)$$

and,
$$b_c = a_c \left[\frac{1+c}{2} - a_c \right]. \quad (7)$$

The total expected number of non-tasters and the corresponding variance for any particular sibship size c are also given by $m_c a_c$ and $m_c b_c$, respectively. Here, a_c , b_c and m_c have the same meanings as the corresponding terms A_c , B_c , and M_c , respectively, for the $\bar{T} \times \bar{T}$ families. It may be pointed out that A_c , B_c , a_c and b_c are independent of the gene frequencies, p and q , but M_c and m_c would certainly be determined by them.

The numerical values of (4), (5), (6) and (7) have been tabulated by Hogben (1946) as well as Smith (1956), which have been used in our analysis set out conveniently in Tables 8 and 9.

In Tables 8 and 9, we have calculated $\chi^2 = (\text{observed} - \text{expected})^2 / \text{variance}$ (Smith, 1956), for each individual family size and added the values up at the bottom of the tables. Family sizes have been merged together for calculation of χ^2 when they involved too small numbers (say, below 5).

The total χ^2 value of 11.95 with 4 D.F. for the $\bar{T} \times \bar{T}$ families indicates a significant divergence ($P > 0.02$), such that as great, or a greater one can occur by chance in less than one out of fifty such trials. But the total χ^2 of 9.45 with 5 D.F. for the $\bar{T} \times \bar{t}$ (including also $\bar{t} \times \bar{T}$) families reveals a fairly satisfactory agreement ($0.1 > P > 0.05$).

Although the different family sizes individually show fairly to excellently 'good fit' in most of the family sizes, there are two instances of clear divergence, namely, the family sizes, $c=2$ and 3 (merged together), of the $\bar{T} \times \bar{T}$ mating type (Table 8); and the family size, $c=4$, of the $\bar{T} \times \bar{t}$ mating type (Table 9). The latter gives $\chi^2=4.45$ which with 1 D.F. has a probability less than 5%, and the former yields $\chi^2=9.59$ which with 1 D.F. has a probability even less than 1%. However, as the numbers involved are very small, the χ^2 distribution may not fit very well and these probabilities may not be very accurate. It seems better to examine the agreement of the totals by calculating χ^2 , and by comparing the difference between the observed and the expected with its standard error. For the $\bar{T} \times \bar{T}$ families, we have from Table 8, deviation = 7.54, variance = 13.39 and S.E. = $\sqrt{13.39} = 3.66$. Therefore, $\chi^2 = (\text{deviation})^2/\text{variance} = 4.26$ with 1 D.F., and deviation/S.E. = 2.06. These results indicate a significant divergence ($0.05 > P > 0.02$).

Similarly, for the $\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$ families we have, from Table 9, deviation = -11.83, variance = 29.21, and S.E. = $\sqrt{29.21} = 5.41$. Therefore, $\chi^2 = (\text{deviation})^2/\text{variance} = 4.79$ with 1 D.F., and deviation/S.E. = 2.19. These values also point to a significant discrepancy ($0.05 > P > 0.02$).

Table 8. *Average number of non-taster children in $\bar{T} \times \bar{T}$ families each with at least one non-taster child*

Size of sibship, c	No. of such sibships, M_c	Total observed non-tasters	Total expected non-tasters $M_c A_c$	Variance $M_c B_c$	χ^2 (1 D.F.)
1	2	3	4	5	6
2	2	3	2.29	0.244	9.593
3	4	8	5.19	1.052	
4	11	16	16.09	4.620	0.002
5	3	6	4.92	1.776	0.617
6	2	4	3.65	1.552	
8	2	6	4.45	2.344	1.735
11	1	4	2.87	1.805	
Total	25	47	39.46	13.397	11.947 (4 D.F.)

Table 9. *Average number of non-taster children in $\bar{T} \times \bar{t}$ and $\bar{t} \times \bar{T}$ families each with at least one non-taster child*

Size of sibship c	No. of such sibships m_c	Total observed non-tasters	Total expected non-tasters $m_c a_c$	Variance $m_c b_c$	χ^2 (1 D.F.)
1	2	3	4	5	6
2	7	8	9.33	1.554	1.140
3	10	14	17.14	4.900	2.012
4	13	21	27.73	10.166	4.454
5	5	15	12.91	5.410	0.811
6	4	10	12.19	5.516	1.030
7	1	3	3.53	1.667	
Total	40	71	82.83	29.213	9.447 (5 D.F.)

As a further check we examined the pooled χ^2 as suggested by Smith (1956). In Table 10 we have added up the four χ^2 values based on totals, each with 1 D.F. The single χ^2 so obtained has a value 13.38 with 4 D.F., which corresponds to $P > 0.01$. It means that the present family data in their entirety indicate a significant disagreement with the Blakeslee-Snyder hypothesis. An equally large, or a still larger divergence is likely to be found even less than once in a hundred of such investigations. The trend of the data is, however, fluctuating. In some tests fairly good agreement and in others significant discrepancy have been noticed. The values of P are within about 1% and about 10%. There are reasons to believe that this order of

Table 10

Comparison	χ^2	D.F.	P
(a) Total observed and expected number of $\bar{T} \times \bar{T}$ families producing at least one non-taster child each	2.45	1	> 0.1
(b) Total observed and expected number of $\bar{T} \times t$ and $t \times \bar{T}$ families producing at least one non-taster child each	1.88	1	> 0.1
(c) Total observed and expected number of non-taster children produced by the families of the type stated in (a)	4.26	1	< 0.05
(d) Total observed and expected number of non-taster children produced by the families of the type stated in (b)	4.79	1	< 0.05
Adding up the four values of χ^2 we obtain a total	13.38	4 D.F.	< 0.1

discrepancy could be attributed to a minor variation of the genic action such as slight lack of penetrance of the taster gene. The point is discussed below with certain evidences. So far as the family data presented here are concerned it is certain that the simple single factor inheritance with complete dominance of the taster gene is not adequate for their full interpretation. But for that matter it would be injudicious to think that any chance factor can account for the situation any better than this hypothesis (Harris & Kalmus, 1951). Results in Table 7 are strong indications of the P.T.C. taste character being genetically determined and the mode of inheritance being at least grossly represented by Blakeslee-Snyder's hypothesis. The other results suggest that the hypothesis must be modified. There are certain phenomena described below, which also should be properly accommodated.

Other phenomena demanding a revision of the hypothesis

(1) Various authors have reported the age and the sex variations in P.T.C. taste threshold distributions as also in the relative proportions of the two phenotypes (Boyd & Boyd, 1937; Hartmann, 1939; Falconer, 1946; Harris & Kalmus, 1949; Lugg & Whyte, 1955; and others). Haldane (1941) and Boyd (1950) suggested an influence of age and sex upon the penetrance of the taste gene. It is necessary to point out here that before the introduction of the idea of variable penetrance, or any other suitable amendments in this connexion, the age and the sex variations themselves should first of all be more thoroughly studied. The present family material does not exhibit any significant age or sex difference in the parental or the filial data (Das, 1956*a*). (Nearly 2000 individuals have recently been tested to investigate these points more thoroughly.)

(2) Stern (1950) mentioned a few instances of lack of penetrance of the taste gene from twin studies. He noticed discordance in respect of P.T.C. taste phenotype between the members of

identical twin pairs. It is most desirable that a larger number of monozygotic twin pairs be tested by the 'sorting technique' to arrive at a reliable conclusion. Stern again did not mention exactly what method of taste testing was employed in the investigation.

(3) A probable evidence for incomplete dominance of the taster gene has been found in the present investigation. A modification of the sib-pair analysis (to be reported later) on the assumption of about 90 % penetrance of the dominant taster gene indicated a satisfactory agreement of both the sets of sib-pair data reported by Harris & Kalmus (1951), and Das (1956*a*) with the theoretical expectations. Prof. J. B. S. Haldane was gracious enough to examine the family data reported here. The mean taste thresholds of the taster children from (a) $\bar{T} \times \bar{T}$ families, and (b) $\bar{T} \times \bar{t}$ (including also $\bar{t} \times \bar{T}$) families were found to be 9.319 ± 0.074 and 8.748 ± 0.099 , respectively. They had a difference of 0.561 which was 4.52 times as large as its s.e. 0.124. Prof. Haldane pointed out that 'this is highly significant. The most obvious explanation, though not necessarily the correct one, is that (TT) homozygotes have a higher value (lower concentration) for their threshold than (Tt), in other words, that dominance is incomplete'.

(4) There is yet another kind of P.T.C. taste phenotypical variation which is worth mention here. There are individuals who describe their taste perception in a clearly different way from the usual 'bitter' taste of the substance. The variations include sour, sweet, and also saline (Boyd & Boyd, 1937; Lugg & Whyte, 1955). But together they may not exceed 1-2 % of the mass data normally in a population. At least that has been the experience so far in this laboratory. Lugg & Whyte (1955) have, however, reported a rather large percentage of sour, sweet, saline and other variants. This seems very unusual and such a large proportion of these as observed by them has not been reported previously by any author. It would be very useful if the frequencies of these variants are also recorded carefully and reported for other populations. It can be seen very easily that the standard error of the percentages of the taste phenotypes, even for a sample as big as 400 individuals, exceeds 1.5 %. Therefore, for most of the populations inclusion or exclusion of these variants in anthropological studies will not affect the results significantly. But in cases where these variations form a comparatively large sector of the population, evidently the matter cannot be treated so lightly, as for example, we may again refer to the populations studied by Lugg & Whyte (1955). Instead of going ahead with determination of the percentages of the different variants, it appears imperative first to take up the question of inheritance of these variations through family studies.

CONCLUSION

Keeping in mind the points which have been discussed as to the variations of the phenotype, and the probable irregularity of the genic action, we may conclude that: (a) The hypothesis of Blakeslee and Snyder may be accepted as a rough approximation, which needs some essential amendments for making the theory satisfactory. (b) It seems that minor amendments would be sufficient; because only minor quantitative adjustments of the data are necessary for a 'good fit'. (c) Such minor (though absolutely essential) corrections are not likely to minimize the utility of P.T.C. taste threshold data in anthropological researches. Certain reservation is, however, necessary at present in the use of the P.T.C. taste gene frequencies estimated on the basis of the existing incorrect theory, particularly where precision is desirable. (d) The geneticists should not take the situation as totally discouraging. Penrose's estimation of the value

of the statistic $D/\bar{S}$ (Penrose, 1951, 1954) for the taste threshold distribution among the English (4.7 corresponding to a misclassification of about 0.9 %) based on the data of Harris & Kalmus (1949), Ghosh's estimation of $D/\bar{S}$ for the Padmaraj (4.73) and the Bagdi (4.47) communities of West Bengal (Ghosh, 1956) and the writer's value (5.29) for the Rārhi Brāhmin (parents) have shown that in all of these populations $D/\bar{S}$ is much larger than 3, the lowest limit according to Penrose (1951, 1954) for a metric character distributed bimodally being suitable for the purpose of genetic studies. It would certainly be worth while to determine the value of $D/\bar{S}$ for other populations for further confirmation. At any rate the trait may well continue to be used by geneticists, as in the past, in some at least of their research programmes.

SUMMARY

1. P.T.C. taste threshold data for 127 families have been given, of which one family has been rejected on account of illegitimacy.
2. A χ^2 test by the '2 × 2' contingency table indicates that the matings in the families studied were random ($\chi^2 = 0.97$, $P > 0.3$).
3. Analysis of the families by Fisher's method following Race & Sanger (1954) indicated a 'good fit' ($P > 0.1$) between the observed and the expected numbers of $\bar{T} \times \bar{T}$ as well as $\bar{T} \times \bar{t}$ (including $\bar{t} \times \bar{T}$) families.
4. Fisher's test following Smith (1956) indicated a 'good fit' ($P > 0.1$) for the totals of families of each of the types $\bar{T} \times \bar{T}$ and $\bar{T} \times \bar{t}$ (also $\bar{t} \times \bar{T}$)—each family containing at least one non-taster child. But a significant discrepancy ($P < 0.01$) was found for the family size 4 of $\bar{T} \times \bar{T}$ type mating type considered singly.
5. Comparison of χ^2 calculated on the totals of the observed and the expected numbers of non-tasters in sibships produced by $\bar{T} \times \bar{T}$ as well as by $\bar{T} \times \bar{t}$ (including $\bar{t} \times \bar{T}$) matings, each of which contained at least one non-taster indicated a significant discrepancy ($0.05 > P > 0.02$).
6. Discrepancies have been noticed between the observed and the expected numbers of non-taster children in the combined family sizes 2 and 3 out of $\bar{T} \times \bar{T}$ matings, and the family size 4 out of $\bar{T} \times \bar{t}$ (and $\bar{t} \times \bar{T}$) matings—each producing at least one non-taster child ($P < 0.01$ and $P < 0.05$, respectively).
7. Totals of χ^2 values for families of all sizes (calculated separately for each size) in respect of the numbers of non-taster children indicated a significant discrepancy ($P < 0.02$) for $\bar{T} \times \bar{T}$ families, but a satisfactory agreement ($P > 0.05$) for the $\bar{T} \times \bar{t}$ (including $\bar{t} \times \bar{T}$) families—each family containing at least one non-taster child.
8. Summing up the χ^2 values calculated on totals under the four different tests following Smith (1956), a single χ^2 of 13.38 with 4 D.F. was obtained, which finally indicated a significant divergence ($P < 0.01$) between the theory and the data taken as a whole.
9. It has been suggested that an assumption of incomplete penetrance (say, about 90 %) of the dominant taste gene might interpret the entire P.T.C. data (including the sib-pair data of Harris & Kalmus, and Das referred to already) more satisfactorily than the simple hypothesis as it stands to-day.

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REFERENCES

- BERNSTEIN, F. (1929). *Variations- und Erblichkeitstatistik*. Hdbch. Vererbungswiss. Berlin: Gebrüder Bornträger.
- BLAKESLEE, A. F. (1932). Genetics of sensory thresholds—taste for phenyl-thio-carbamide. *Proc. Nat. Acad. Sci., Wash.*, **18**, 120.
- BOYD, W. C. & BOYD, L. G. (1937). Sexual and racial variations in ability to taste phenyl-thio-carbamide with some data on the inheritance. *Ann. Eugen., Lond.*, **8**, 46.
- BOYD, W. C. (1950). *Genetics and the Races of Man*. Boston: Little, Brown and Co.
- DAS, S. R. (1956a). A contribution to the heredity of the P.T.C. taste character based on a study of 845 sib pairs. *Ann. Hum. Genetics, Lond.*, **20**, 334.
- DAS, S. R. (1956b). A family study of the P.T.C. taste character, applying Fisher's method of analysis. *First Int. Congr. Hum. Genet., Copenhagen, Book of Abstracts*, Abstr., no. 129.
- FALCONER, D. S. (1947). Sensory thresholds for solutions of phenyl-thio-carbamide. Results of tests on a large sample made by R. A. Fisher. *Ann. Eugen., Lond.*, **13**, 211.
- FISHER, R. A. (1934). The effect of methods of ascertainment upon the estimation of frequencies. *Ann. Eugen., Lond.*, **6**, 13.
- FISHER, R. A. (1946). *Statistical Methods for Research Workers*, 10th ed. Edinburgh: Oliver and Boyd.
- GHOSH, L. (1956). Taste sensitivity to phenyl-thio-carbamide in the Padmaraj (Pod) and the Bagdi of West Bengal. *Anthrop. Delhi*, **3**, 56.
- HALDANE, J. B. S. (1932). A method for investigating recessive characters in man. *J. Genet.* **25**, 251.
- HALDANE, J. B. S. (1941). The relative importance of principal and modifying genes in determining some human diseases. *J. Genet.* **41**, 149.
- HALDANE, J. B. S. (1956). Private communication.
- HARRIS, H. & KALMUS, H. (1949). Measurement of taste sensitivity to phenyl-thio-urea (P.T.C.). *Ann. Eugen., Lond.* **15**, 24.
- HARRIS, H. & KALMUS, H. (1951). The distribution of taste thresholds for phenyl-thio-urea of 384 sib-pairs. *Ann. Eugen., Lond.*, **16**, 226.
- HARTMANN, G. (1939). Application of individual taste difference towards P.T.C. in genetic investigations. *Ann. Eugen., Lond.*, **9**, 123.
- HOGBEN, L. (1932). The genetic analysis of familial traits. I. Single gene substitution. *J. Genet.* **25**, 97, 112.
- HOGBEN, L. (1946). *An Introduction to Mathematical Genetics*. New York: W. W. Norton and Co. Inc.
- LUGG, J. W. H. & WHYTE, J. M. (1955). Taste thresholds for phenylthiocarbamide of some population groups. I. *Ann. Hum. Genet., Lond.*, **19**, 290.
- MOHR, J. (1951). Taste sensitivity to phenyl-thio-urea in Denmark. *Ann. Eugen., Lond.*, **16**, 282.
- MOURANT, A. E. (1954). *The Distribution of the Human Blood Groups*. Oxford: Blackwell Scientific Publications.
- PENROSE, L. S. (1951). Measurement of pleiotropic effects in phenylketonuria. *Ann. Eugen., Lond.*, **16**, 134.
- PENROSE, L. S. (1954). The distal triradius *t* on the hands of parents and sibs of Mongol imbeciles. *Ann. Eugen., Lond.*, **19**, 10.
- RACE, R. R., IKIN, E. W., TAYLOR, G. L. & PRIOR, A. M. (1942). A second series of families examined in England for the A_1A_2BO and MN blood groups factors. *Ann. Eugen., Lond.*, **11**, 385.
- RACE, R. R. & SANGER, RUTH (1952). The inheritance of the Duffy blood groups. An analysis of 110 English families. *Heredity*, **6**, 111.
- RACE, R. R. & SANGER, RUTH (1954). *Blood Groups in Man*, 2nd ed. Oxford: Blackwell Scientific Publications.
- SMITH, C. A. B. (1956). A test for segregation ratios in family data. *Ann. Hum. Genet., Lond.*, **20**, 257.
- SNYDER, L. H. (1932). Studies in human inheritance. IX. The inheritance of taste deficiency in man. *Ohio J. Sci.* **32**, 436.
- STERN, C. (1950). *Principles of Human Genetics*. San Francisco: W. H. Freeman.
- TAYLOR, G. L. & PRIOR, A. M. (1939). Blood groups in England. III. Discussion of the family material. *Ann. Eugen., Lond.*, **9**, 18.