Relative Index Finger Length as a Sex-influenced Trait in Man[1]

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ALTHOUGH a genetic basis has been determined for numerous abnormalities of the hand and foot, relatively little attention has been given to the inheritance of normal variations in shape and structure. One of the most frequently reported normal variations in the human hand is the length of the index finger as compared with the ring finger. Ecker (1875) noted that three manifestations of relative finger length may be discerned in the living model: index finger shorter than ring finger ($2 < 4$); index finger equal in length to ring finger ($2 = 4$); and index finger longer than ring finger ($2 > 4$). Many of the earlier workers failed to recognize this variability in relative index finger length. Gerdy (1829) stated that the index finger is always shorter than the ring finger, while according to Carus (1853) and Humphry (1861), the index finger exceeds the ring finger in length. Langer (1865) declared that the index finger is shorter than or nearly equal to the ring finger. Alix (1867), Grüning (1886), Baker (1888), Schultz (1926), and Wood-Jones (1920, 1941) point out that although the index finger is usually shorter than the ring finger, it may in certain instances exceed the length of the ring finger. Ecker (1875), Mantegazza (1877), Grüning (1886), Baker (1888), Volotzkoy (1924), and Huizinga (1949) each found that all three formulas occur in both sexes but that a relatively long index finger is found more frequently in females than in males. George (1930) studied a Canadian population and found that $2 < 4$ is the most frequent formula in males while a $2 > 4$ formula predominates in females. Volotzkoy (1924), Schultz (1926) and Huizinga (1949) have noted that the various formulas may also be observed in fetuses.

Although Kloepfer (1946) has suggested that the variations in relative index finger length may be hereditary, no attempt has been made to establish

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Received January 1, 1952.

[1] Based in large part on the dissertation presented to the faculty of the Graduate School of The University of Texas in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The writer wishes to express her appreciation to Dr. C. P. Oliver, under whose direction this problem was carried out, to other members of the teaching and research staff of the Biological Laboratories of The University of Texas, and to Dr. Harold Cummins of Tulane University for helpful suggestions. She also wishes to thank the Dight Institute of Human Heredity of The University of Minnesota for making possible the collection of family histories in Minneapolis.

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the genetic basis for these formulas. The present investigation was undertaken to determine the mode of inheritance for relative index finger length and, insofar as possible, how the genes act to produce such variations. Study of the inheritance of normal traits, which have a high incidence and which develop early in fetal life, makes possible a more fundamental understanding of what rôles the genes may play in normal growth and development.

Since relative index finger length is considered to be a "normal" trait in that it is not associated with any type of abnormality, and since the variations in index finger length occur with a high incidence in the population, this trait should be particularly useful in linkage studies. If the gene which determines relative index finger length can be shown to be closely linked genetically with a gene for a severe disease having late onset or low penetrance, then this information may be valuable as a diagnostic aid.

MATERIALS AND METHODS FOR GENETIC ANALYSES

The material for population analysis consisted of outline drawings of the hands, collected at random, from students and faculty members of the Biological Laboratories of The University of Texas. Data regarding age, sex, height, religion, and nationality background were obtained from each person. The series consisted of 284 persons, of whom 189 were males and 95 were females, and was comprised of individuals belonging to the White race. For familial analysis, drawings were obtained from members of 20 families, containing 26 sibships taken from families of student and faculty members of The University of Texas and residents of Minneapolis, Minnesota.

Measurements of the relative lengths of the index and ring fingers were made from outline drawings of the left hand by using the pivot-ruler method (a new method developed by the author). In this method the left hand is placed flat on a sheet of heavy paper, so that the middle finger is in line with the arm. A thin, sharply pointed pencil is used to trace around the hand, special care being taken around the tips of the fingers and at the angles between the fingers. A celluloid ruler, 5 cm. wide, with a metric scale along each edge and having a small hole on the 0 mm. line, 2 cm. to the left of the right scale, is placed on the outline drawing of the hand so that the hole is directly over the most proximal point of the angle between the index and middle fingers. The ruler is pivoted, on a pin inserted through the hole, until the right metric scale is in line with the axis of the index finger; a reading is recorded for the length of the index finger. The ruler is again pivoted, until the left scale is parallel to the axis of the ring finger; the corresponding length of the ring finger is recorded. The length of the ring finger is subtracted from that of the index finger to determine the difference in the relative lengths of the two fingers.

Measurements of the relative lengths of the index and ring fingers were also made directly from the hands by using a hand-measuring board, similar in construction to that devised by George (1930), to permit comparison of the present population with the Canadian population studied by George (1930). The relative index finger length for any one individual was found to be the same when both the pivot-ruler and hand-measuring board methods were used.

The hands were classified into three groups: index finger shorter than ring finger, 2 < 4; index finger equal in length to ring finger, 2 = 4; and index finger longer than ring finger, 2 > 4, fig. 1. At first the index and ring fingers were considered to be equal in length if the difference in the relative lengths of the two fingers was 2 mm. or less, since a difference of this magnitude was apparent by observation of either the hand or the outline drawings, and did not require the use of special measuring devices. The use of a pivot-ruler, however, made possible more accurate determination of relative index finger

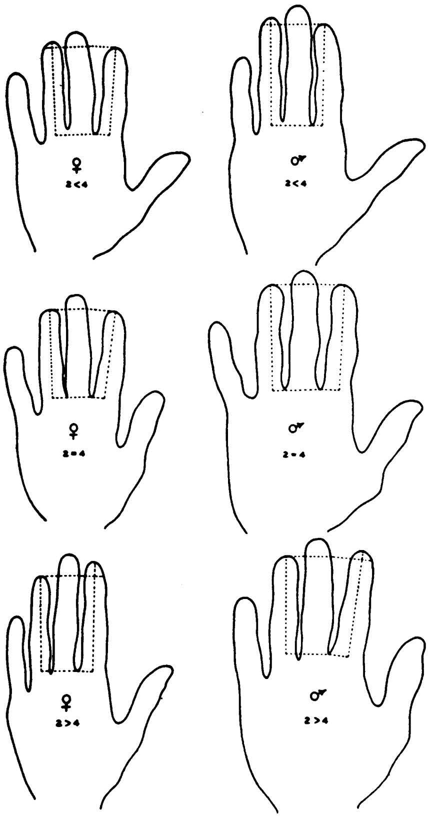

FIG. 1. Three formulas of index finger length may be discerned in the human hand: index finger shorter than ring finger; index finger equal in length to ring finger; and index finger longer than ring finger. All three formulas occur in both males and females but the short index finger formula is the most frequent one among males while the long index finger formula predominates among females. These formulas are inherited as a sex-influenced trait with the short index formula acting as a dominant in males and as a recessive in females.

length. The hands were then reclassified by using a more critical value for index finger length determination, wherein the index and ring fingers were considered equal in length *only* if the recorded difference in the relative lengths of these two fingers was less than 1 mm. The formula found on the left hand was used for classification purposes in both population and family history analyses, since the right and left hands of an individual usually showed the same formula, and since use of the left hand is standard anthropological procedure.

Two types of genetic analyses of relative index finger length were employed: (1) population analysis, and (2) familial analysis. The populations were analysed for the frequency of the various formulas in males as compared with females, and for the mode of inheritance by the mass method as developed by Snyder and Yingling (1935). The observed frequency of the formulas in the population varied with the two values (2 mm. or less than 1 mm. for $2 = 4$) used for formula determination; therefore each resulting distribution of frequencies was analysed separately by the mass method. The Canadian population reported by George (1930) was also analysed by the mass method for comparison with the present population.

Each of the family histories collected for the present study, and most of the sibships used by Kloepfer (1946) in his linkage analysis, were studied individually to see if the histories agreed with the mode of inheritance determined by the mass method gene frequency analysis. All of the histories were analysed, according to mating type, for the expected proportions of homozygous individuals among the offspring following the method devised by Phelps (1948). Only the more critical value (less than 1 mm.) was used for determining the formulas of the members of the family histories in the present study. Since in Kloepfer's data all individuals having a $2 = 4$ formula were grouped with those showing different formulas on right and left hands, not all of the histories from his data could be utilized.

POPULATION ANALYSIS

When the population used in the present study is classified according to the relative length of the index finger, all three formulas ($2 < 4$, $2 = 4$, and $2 > 4$) are found to be present in both males and females, fig. 1. The frequency distribution of the formulas differs, however, within the two sexes, and also shows some variation depending upon the value used for formula determination.

If the index and ring fingers are classified as being equal in length when their difference in relative projection is no greater than 2 mm., it may be seen in table 1 that a relatively short index finger occurs with a higher frequency in males than in females, while a longer index finger is found more commonly in females. Since a difference of 2 mm. is discernible to the unaided eye, it is probable that a value of approximately this magnitude was used by those workers who made classifications without the aid of measuring devices. The data from this population agrees with the findings of Ecker (1875) and Grüning (1886), and also, in general, with those of Volotzkoy (1924) and Huizinga (1949)

The use of the more critical value for determination of index finger length formulas, wherein the index and ring fingers are considered to be of equal length if the difference in their relative projection is *less* than 1 mm., results in an even greater diversity in the frequency distribution in the two sexes than is obtained using the 2 mm. value (table 1). A short index finger not only occurs more commonly in males than in females but actually constitutes the predominating class in males. The females show the reverse of this situation in that the long index finger class predominates over the other two classes.

These findings are in agreement with the data reported by George (1930) from a Canadian population. In his investigation, George considered the index and ring fingers to be equal in length if the difference in their relative projection was 0.5 mm. or less, as measured by a hand-measuring board. The frequencies which George found are very similar to those obtained in the present study with the use of a less than 1 mm. value (table 1). When the two sets of data are analysed with respect to the proportions of females showing a short index finger and the proportions of males with a long index finger, it is found that the deviation is 0.025 ± 0.064 in the case of females, and 0.07 ± 0.043 in the case of males. The two populations, therefore, do not differ significantly from one another, and apparently values of 0.5 mm. or less (George, 1930) and less than 1 mm. (present study) serve equally well for determining the formulas.

TABLE 1. FREQUENCY DISTRIBUTION OF FORMULAS IN PERCENTAGES

SEX	PRESENT STUDY						GEORGE, 1930		
	2.0 mm.			< 1.0 mm.			0.5 mm.		
	$2 < 4$	$2 = 4$	$2 > 4$	$2 < 4$	$2 = 4$	$2 > 4$	$2 < 4$	$2 = 4$	$2 > 4$
Males	43.4	40.7	15.9	59.2	13.8	27.0	65	15	20
Females	25.3	37.9	36.8	30.5	12.6	56.8	28	25	47

The observed associations of a short index finger with the male sex and a long index finger with the female sex in the data presented here, as well as in the data of Ecker (1875), Mantegazza (1877), Grüning (1886), Volotzkoy (1924), George (1930), and Huizinga (1949), show that the sex of the individual plays a rôle in determining the formula of relative index finger length. Such associations further suggest that the difference in distribution of formula frequencies in males as compared with females may be due to a sex-influenced mode of inheritance.

If relative index finger length is postulated to be a sex-influenced trait, inherited in the same manner as is baldness (Snyder, 1934), letting I^S represent the gene for a relatively short index finger, and I^L represent the gene for a relatively long index finger, the corresponding genotypes and phenotypes should be as follows:

Males	Females
I^SI^S = short index	I^SI^S = short index
I^SI^L = equal or short index	I^SI^L = equal or long index
I^LI^L = long index	I^LI^L = long index

An analysis for sex-influenced inheritance of a trait can be made directly from the population known for that trait. If the trait is sex-influenced, it is possible to identify individuals who are homozygous for either of the alleles concerned and thus to derive the respective gene frequencies. Using the mass method of gene frequency analysis for a sex-influenced trait, reported by Snyder and Yingling (1935), p represents the frequency of gene I^S in a given population and q represents the frequency of its allele I^L. Since the phenotypes in heterozygous males and females differ, the sex of the offspring produced by a random breeding population must be considered. For this purpose the X and Y chromosomes may be used in conjunction with the alleles for the trait as shown in table 2.

TABLE 2. DISTRIBUTION OF GENOTYPES IN A RANDOM BREEDING POPULATION

MALES FEMALES	$\frac{p}{2}$ I^SX	$\frac{p}{2}$ I^SY	$\frac{q}{2}$ I^LX	$\frac{q}{2}$ I^LY
p I^SX	$\frac{p^2}{2}$ I^SI^SXX	$\frac{p^2}{2}$ I^SI^SXY	$\frac{pq}{2}$ I^SI^LXX	$\frac{pq}{2}$ I^SI^LXY
q I^LX	$\frac{pq}{2}$ I^SI^LXX	$\frac{pq}{2}$ I^SI^LXY	$\frac{q^2}{2}$ I^LI^LXX	$\frac{q^2}{2}$ I^LI^LXY

The symbol p represents the frequency of gene I^S and q, the frequency of gene I^L. (Based on Snyder and Yingling, 1935.)

It can be seen in table 2 that the frequency of females with a short index finger, $2 < 4$, can be represented as $\frac{p^2}{2}$, which constitutes one-half of all I^SI^S individuals. Likewise the frequency of males with a long index finger, $2 > 4$, in a population can be denoted as $\frac{q^2}{2}$.

Then:

$\frac{p^2}{2}$ = proportion of $2 < 4$ females in a total population

$\frac{q^2}{2}$ = proportion of $2 > 4$ males in a total population

Then let:

$\overline{\text{♀} I^s I^s}$ = proportion of 2 < 4 females among females

$\overline{\text{♂} I^L I^L}$ = proportion of 2 > 4 males among males

Assuming that one-half of the population will be females and one-half will be males:

$$\frac{p^2}{2} = \frac{\overline{\text{♀} I^s I^s}}{2} \qquad p = \sqrt{\overline{\text{♀} I^s I^s}}$$

$$\frac{q^2}{2} = \frac{\overline{\text{♂} I^L I^L}}{2} \qquad q = \sqrt{\overline{\text{♂} I^L I^L}}$$

Since $p + q = 1$, then $\sqrt{\text{♀} I^s I^s} + \sqrt{\text{♂} I^L I^L}$ should equal unity, if relative index finger length is sex-influenced in its mode of inheritance. The two sets of formula frequencies derived from the population in this study and the frequencies obtained from the population studied by George (1930) give the values shown in table 3 for p and q, the deviations of their sums from unity, and the standard error of each deviation.

TABLE 3. GENE FREQUENCY ANALYSIS BY THE MASS METHOD OF SNYDER AND YINGLING (1935)

VALUE FOR FORMULA DETERMINATION	DERIVED p	DERIVED q	DEVIATION FROM UNITY	$\frac{\text{DEV.}}{\text{S.E.}}$
2.0 mm.	0.503	0.399	0.098 ± .055	1.78
1.0 mm.	0.550	0.520	0.070 ± .053	1.32
0.5 mm. (George, 1930)	0.529	0.447	0.024 ± .057	.425

The standard error was computed from the following formula (Snyder and Yingling, 1935):

$$\text{S.E.} = \pm \frac{1}{2} \sqrt{\frac{1 - \text{B}}{\text{N}_1} - \frac{(1 - \text{B})^2}{16\text{B}(\text{N}_1)^2} + \frac{1 - \text{D}}{\text{N}_2} - \frac{(1 - \text{D})^2}{16\text{D}(\text{N}_2)^2}}$$

where $\text{B} = \sqrt{\text{♀} I^s I^s}$, $\text{D} = \sqrt{\text{♂} I^L I^L}$, N_1 = number of individuals from which B was derived, and N_2 = number of individuals from which D was derived.

Since the deviations obtained from the summation of each set of p and q values are in each case less than two times the standard error, the theory of sex-influenced inheritance for relative index finger length is substantiated. It should be noted that the more critical the value used for formula determination, the closer the sum of p plus q approaches unity.

FAMILIAL ANALYSIS

Analysis of the sibships collected for the present study and those reported by Kloepfer (1946) shows that 41 of the 43 sibships thus far investigated exhibit phenotypic relationships between parents and offspring that are in complete agreement with the theory of sex-influenced inheritance. As may be seen in table 4, four mating types are possible with regard to the formulas found in the parents (omitting the $2 = 4$ formula), and the types of offspring possible from such matings are shown in the right hand column. For purposes of computation, the heterozygous condition, even if recognizable by the presence of a $2 = 4$ formula, is grouped with the respective dominants in each sex. Thus a $2 = 4$ male is placed with $2 < 4$ males and a $2 = 4$ female is placed with $2 > 4$ females. Investigation of sibships, wherein the parental phenotypes are known, makes possible a confirmation of the results obtained from population studies.

TABLE 4. PHENOTYPIC RELATIONSHIPS BETWEEN PARENTS AND OFFSPRING*

TYPE OF MATING	GENOTYPES OF MATINGS	OFFSPRING
$2 > 4$♂ × $2 < 4$♀	I^LI^L♂ × I^SI^S♀	♂ = all $2 < 4$ ♀ = all $2 > 4$
$2 > 4$♂ × $2 > 4$♀	I^LI^L♂ × I^LI^S♀	♂ = $\frac{1}{2}$ $2 < 4$, $\frac{1}{2}$ $2 > 4$ ♀ = all $2 > 4$
	I^LI^L♂ × I^LI^L♀	♂ = all $2 > 4$ ♀ = all $2 > 4$
$2 < 4$♂ × $2 < 4$♀	I^LI^S♂ × I^SI^S♀	♂ = all $2 < 4$ ♀ = $\frac{1}{2}$ $2 < 4$, $\frac{1}{2}$ $2 > 4$
	I^SI^S♂ × I^SI^S♀	♂ = all $2 < 4$ ♀ = all $2 < 4$
$2 < 4$♂ × $2 > 4$♀	I^LI^S♂ × I^LI^S♀	♂ = $\frac{3}{4}$ $2 < 4$, $\frac{1}{4}$ $2 > 4$ ♀ = $\frac{1}{4}$ $2 < 4$, $\frac{3}{4}$ $2 > 4$
	I^LI^S♂ × I^LI^L♀	♂ = $\frac{1}{2}$ $2 < 4$, $\frac{1}{2}$ $2 > 4$ ♀ = all $2 > 4$
	I^SI^S♂ × I^LI^S♀	♂ = all $2 < 4$ ♀ = $\frac{1}{2}$ $2 < 4$, $\frac{1}{2}$ $2 > 4$
	I^SI^S♂ × I^LI^L♀	♂ = all $2 < 4$ ♀ = all $2 > 4$

* For purposes of computation, the heterozygous condition, even if recognizable by the presence of a $2 = 4$ formula, is grouped with the respective dominants in each sex.

Of the four possible mating types, $2 > 4$♂ × $2 < 4$♀ has been observed in only three instances. Based upon the calculated gene frequencies, this mating type has the lowest probable frequency of occurrence, 0.08, which explains its rarity. Since this mating type was of necessity, according to the theory, one of I^LI^L♂ × I^SI^S♀, the resulting offspring should all have been heterozygous and there should have been no $2 > 4$ males or $2 < 4$ females produced. Two of the three histories agree with the expected types of offspring, but one history shows an only child, a daughter, with a $2 < 4$ formula which is inconsistent with the theory of sex-influenced inheritance.

Matings of $2 > 4♂ \times 2 > 4♀$ are expected to occur with a frequency of 0.21, and 8 sibships from such matings have been collected. The father with a $2 > 4$ formula must be homozygous I^LI^L and therefore, none of the daughters is expected to show a $2 < 4$ formula. The sons may show any of the three formulas depending upon the genotype of the mother. The offspring of 7 of the 8 matings exhibit phenotypes which are in agreement with the theory of inheritance; however, one sibship consisting of 2 females, both of whom show a $2 < 4$ formula, is at variance with the expected results.

Matings between $2 < 4♂$ and $2 < 4♀$ have a probable frequency of occurrence of 0.24 and 18 sibships from such matings have been recorded. The mother must be homozygous I^SI^S to appear phenotypically $2 < 4$; therefore, all of the sons from such a mating should have a $2 < 4$ or $2 = 4$ formula. The daughters may be $2 < 4$ or show either of the other two formulas depending upon whether the father is heterozygous or homozygous for the I^S gene. The absence of $2 > 4$ males among the offspring is in conformity with the theory of sex-influenced inheritance. Females showing a $2 > 4$ formula occurred in 6 of the sibships, indicating that in these sibships at least, the father must have been heterozygous.

The combination $2 < 4♂$ and $2 > 4♀$ is the only mating wherein all four (or six, if the heterozygous condition is expressed as $2 \doteq 4$) classes of offspring are expected to occur, and only then if both parents are heterozygous. Out of 14 such matings, only one showed all four classes of offspring. In 7 of the matings at least one offspring was a $2 > 4♂$ or a $2 < 4♀$ indicating that at least one of the parents was heterozygous.

Traits that are sex-influenced in their mode of inheritance differ from other autosomal traits not only with regard to the possible types of offspring which may be produced by a particular mating, but also with regard to the frequencies with which such offspring are produced. Therefore, another method of familial analysis has been used wherein the expected proportions of homozygous individuals are compared with the observed proportions resulting from a given mating type, following the method of Phelps (1948). The equations for expected proportions of homozygous individuals, i.e. $2 > 4♂$ (I^LI^L) and $2 < 4♀$ (I^SI^S), are derived by multiplying the product of the parental genotype frequencies (shown in table 5) by $\frac{1}{2}$ (the chance for producing a male or female) and multiplying this product in turn by the chances for producing the desired type of offspring.

Matings between $2 > 4♂$ and $2 < 4♀$ occurred in 3 instances producing 5 offspring (table 6). Since in this case all of the offspring are alike genetically, it is not possible to analyse for phenotypic proportions.

Matings between $2 > 4$♂ and $2 > 4$♀ occurred in 8 instances producing 12 offspring (table 6). The matings in this group may have been either I^LI^L♂ × I^LI^L♀, or I^LI^L♂ × I^SI^L♀. From such matings $2 < 4$ males can be produced only if the mother is heterozygous. The expected proportion of $2 < 4$ males can be calculated, and the expected proportion of $2 > 4$ males can be derived as the difference of the proportion of $2 < 4$ males from unity. The equation for the proportion of $2 < 4$ males is shown by the following:

$$\frac{q^2}{q^2} \times \frac{2pq}{2pq + q^2} \times \frac{1}{2} \times \frac{1}{2} = \frac{1 - p}{4 - 2q}$$

TABLE 5. GENOTYPE FREQUENCIES OF MALES AMONG MALES AND FEMALES AMONG FEMALES AS PROPORTIONS OF THE PHENOTYPES RECOGNIZABLE WITHIN THE RESPECTIVE SEX IN A RANDOM BREEDING POPULATION

GENOTYPE	FREQUENCY OF ♀ AMONG ♀	FREQUENCY OF ♂ AMONG ♂
I^SI^S	$\frac{p^2}{p^2}$	$\frac{p^2}{p^2 + 2pq}$
I^SI^L	$\frac{2pq}{2pq + q^2}$	$\frac{2pq}{p^2 + 2pq}$
I^LI^L	$\frac{q^2}{2pq + q^2}$	$\frac{q^2}{q^2}$

The proportion of $2 > 4$ males is derived as:

$$1 - \frac{1 - q}{4 - 2q} = \text{expected proportion of } 2 > 4 \text{ males}$$

The value of q which was calculated in the population analysis is substituted into the above formula. The expected proportion of $2 > 4$ males is found to be 0.838 and that of $2 < 4$ males, 0.162. Referring to table 6, it may be seen that the deviation between the expected and observed proportions is only on the borderline of significance; therefore the theory of sex-influenced inheritance is not invalidated. The occurrence of two $2 < 4$ females is, however, unexpected.

Matings between $2 < 4$♂ and $2 < 4$♀ occurred in 18 instances producing 135 offspring (table 6). The matings belonging to this group may be I^SI^S♂ × I^SI^S♀ and I^SI^L♂ × I^SI^S♀. Referring to table 4 it can be seen that $2 > 4$ female offspring are possible only from matings in which the father is heterozygous. If the expected frequency of $2 > 4$ females is calculated, then the expected frequency of $2 < 4$ females will be 1 minus the expected frequency of $2 > 4$ females. The equation for the expected frequency of $2 > 4$ females is based on the probability of a heterozygous male, I^SI^L, mated to a homozygous female, I^SI^S, and is shown by the following:

$$\frac{2pq}{p^2 + 2pq} \times \frac{p^2}{p^2} \times \frac{1}{2} \times \frac{1}{2} = \frac{1 - p}{4 - 2p}$$

The frequency of $2 < 4$ females is derived as:

$$1 - \frac{1 - p}{4 - 2p} = \text{expected proportion of } 2 < 4 \text{ females}$$

The value of p, as derived from the population analysis, when substituted into the formula gives an expected proportion of 0.155 for $2 > 4$ females and 0.845 for $2 < 4$ females. Since the deviation between the expected and observed proportions of $2 < 4$ females is not significant (table 6), the observed proportion of $2 < 4$ females fits the theory of sex-influenced inheritance. Also, the absence of $2 > 4$ males in the offspring of this mating type gives further support to the theory.

Matings between $2 < 4$ males and $2 > 4$ females occurred in 14 instances producing 50 offspring in the ratios shown in table 6. The expected frequency of $2 < 4$ females from such matings is derived as the sum of frequencies from each genetic mating type wherein it is possible to produce such offspring. In the case of an $I^SI^L♂ \times I^SI^L♀$ mating, the expected frequency of $2 < 4$ is calculated as:

$$\frac{2pq}{p^2 + 2pq} \times \frac{2pq}{2pq + q^2} \times \frac{1}{2} \times \frac{1}{4} = \frac{p - p^2}{4 + 2p - 2p^2}$$

When the value of p is substituted into the formula, a value of 0.055 is obtained as the expected frequency of $2 < 4$ females. In a like manner, the frequency of $2 < 4$ females from an $I^SI^S♂ \times I^SI^L♀$ mating can be calculated as:

$$\frac{p^2}{p^2 + 2pq} \times \frac{2pq}{2pq + q^2} \times \frac{1}{2} \times \frac{1}{2} = \frac{p^2}{4 + 2p - 2p^2}$$

resulting in a value of 0.067 as the expected frequency of $2 < 4$ females. The two frequencies are summed, showing that the total frequency for $2 < 4$ females from matings of $2 < 4♂ \times 2 > 4♀$ is expected to be 0.122, and the frequency for $2 > 4$ females is 0.878. When the expected and actual frequencies are compared, the results shown in table 6 are obtained. The deviation from the expected is not significant thereby substantiating the theory of inheritance.

The expected frequency of $2 > 4$ males is calculated as the sum of the frequencies from matings of $I^SI^L♂ \times I^SI^L♀$ and $I^SI^L♂ \times I^LI^L♀$. In the former case, the equation used is:

$$\frac{2pq}{p^2 + 2pq} \times \frac{2pq}{2pq + q^2} \times \frac{1}{2} \times \frac{1}{4} = \frac{q - q^2}{4 + 2q - 2q^2}$$

Substituting for q, the expected frequency of $2 > 4$ males from such matings is 0.055. In the latter type of mating the frequency of $2 > 4$ males is derived from the following equation:

$$\frac{2pq}{p^2 + 2pq} \times \frac{q^2}{2pq + q^2} \times \frac{1}{2} \times \frac{1}{2} = \frac{q^2}{4 + 2q - 2q^2}$$

Table 6. Analysis of family histories for expected proportions of homozygotes

MATING TYPE	OFFSPRING FORMULAS	OBSERVED NUMBER	OBSERVED PROPORTION	EXPECTED PROPORTION	DEVIATION	DEV./S.E.
$2 > 4$♂ × $2 < 4$♀	$2 < 4$♂	3	1.000	1.000	.000	
3 sibships	$2 > 4$♂	0	0.000	0.000		
5 sibs	$2 < 4$♀	1	0.500	0.000	.500	
	$2 > 4$♀	1	0.500	1.000		
$2 > 4$♂ × $2 > 4$♀	$2 < 4$♂	3	0.429	0.162	.367 ± .150	2.44
8 sibships	$2 > 4$♂	4	0.471	0.838		
12 sibs	$2 < 4$♀	2	0.400	0.000	.400	
	$2 > 4$♀	3	0.600	1.000		
$2 < 4$♂ × $2 < 4$♀	$2 < 4$♂	60	1.000	1.000	.000	
18 sibships	$2 > 4$♂	0	0.000	0.000		
135 sibs	$2 < 4$♀	67	0.893	0.845	.048 ± .042	1.14
	$2 > 4$♀	8	0.107	0.155		
$2 < 4$♂ × $2 > 4$♀	$2 < 4$♂	27	0.771	0.885	.114 ± .055	2.07
14 sibships	$2 > 4$♂	8	0.229	0.115		
50 sibs	$2 < 4$♀	4	0.286	0.122	.164 ± .091	1.81
	$2 > 4$♀	11	0.714	0.878		

which, when substituted for q, gives a value of 0.060 as the expected frequency for $2 > 4$ males. The two frequencies are summed giving an expected frequency of 0.115 for $2 > 4$ males; the frequency for $2 < 4$ males is 0.885. Comparing the observed and expected frequencies, the results shown in table 6 are obtained. Since the deviation from the expected is not a significant one, the theory of sex-influenced inheritance is given support.

From the results obtained in the familial analysis, it is seen that the observed parental and offspring phenotypes are in agreement with the expected types in all but two of the histories thus far investigated. Mutation may be considered as a possible explanation for these two exceptional histories. The observed frequencies with which the phenotypes occur in the offspring do not show significant deviations from those expected. The postulation, based on population analysis, that relative index finger length is inherited as a sex-influenced trait is therefore corroborated by the analysis of the family histories.

ANATOMICAL BASIS FOR VARIABILITY IN FORMULAS

The determination that the formulas of relative index finger length are an inherited characteristic and that this trait appears to have a sex-influenced mode of inheritance, does not in itself explain which elements in the hand are responsible for the observed variations in index finger length, nor in what manner they contribute to this variability. The question arises as to whether the observed formulas are the results of differences in the relative length of the index and ring digits (sum of the three phalanges), differences in the relative length of the index and ring metacarpals, or differences in relative ray lengths (sum of metacarpal and digit lengths). General body build must also be considered as a possible factor in the determination of index finger length formulas.

Ecker (1875) and Grüning (1886) have referred to the high degree of association which they believe exists between a long index finger and an over-average height. The present study shows, on the contrary, a lack of significant association between the various formulas of relative index finger length and the height of the individual, the probability of random assortment being 0.80–0.90 in males and 0.20–0.30 in females. Thus it appears that the formulas of index finger length are not determined by overall growth factors and must instead find their basis in factors which act directly on elements of the hand.

In a morphological study of bone length in the hand, Pfitzner (1892) found that the absolute length of the ring digit always exceeds that of the index digit to some degree. The ring ray, however, may be longer than, shorter than, or equal in length to the index ray. Therefore, he concluded that the relative length of the index and ring rays, rather than the relative length of the digits, determines the formula of index finger length. Such a theory, however, is not tenable in the light of the present study, since an analysis of his data shows that no difference exists with respect to the frequency of males or females having index rays shorter than or longer than the ring rays. Such a difference would necessarily be present if ray length is the basis for this sex-influenced trait.

Wood-Jones (1920, 1941) has postulated that a relatively long index finger may be due solely to an increase in the relative length of the index digit irrespective of the length of the metacarpal. As evidence for this theory, he cites the fact that a hand having a formula of $2 > 4$ may have an index metacarpal which is equal in projection to the ring metacarpal, while conversely, a hand showing $2 < 4$ may have an index metacarpal which projects longer than the ring metacarpal. Comparison of digit and metacarpal lengths in the data of Pfitzner (1892) supports the observation of Wood-Jones. The difference in index and ring digit lengths ($d_2 - d_4$) and the difference in index and ring metacarpal lengths ($m_2 - m_4$) assort at random in both males and females, the correlation coefficients being −.115 and −.005 respectively. Therefore, the index finger length formula is not a reflection of metacarpal length, but rather, constitutes an independent characteristic of the hand.

The basis for the variations in formula seems to lie, therefore, in the relationship between the index and ring digit lengths. It is necessary, however, to ascertain whether both the index and ring digits vary with respect to the rest of the hand, or whether, as Wood-Jones (1920, 1941) has suggested, the index digit varies independently of all other elements in the hand. Calculation of the mean ratios between index, middle, and ring digit lengths from the data of Pfitzner (1892) shows that the mean ratio of the length of the middle digit to the length of the ring digit is approximately the same in males and females. The mean ratios of the length of the ring digit to the index digit, and the length of the middle digit to the index digit are, however, greater in males than in females (table 7). These results indicate that the index digit is relatively shorter in the majority of males as compared to females, while the relative length of the ring digit is not so influenced by the sex of the individual.

TABLE 7. MEAN RATIOS OF DIGIT LENGTHS CALCULATED FROM DATA OF PFITZNER (1892)

	3/4	3/2	4/2
Males	103.85	113.17	109.01
Females	103.99	112.59	108.29

BASIS FOR THE SEX DIFFERENCE IN FORMULA FREQUENCY

The postulation of sex-influenced inheritance as the mode of transmission for relative index finger length necessarily presupposes that the sex of the individual is responsible for the differences in formula which are expressed in heterozygous males and females. Although in some cases the heterozygous individuals, either male or female, are recognizable by the presence of a $2 = 4$ formula, in the majority of heterozygotes either gene I^S or I^L is sufficiently dominant so that a $2 > 4$ formula is expressed in heterozygous females and a $2 < 4$ formula in heterozygous males.

The shift in phenotype which occurs in the heterozygous condition in sex-influenced traits has been variously explained on the basis of hormones or the activity of modifying genes on the X-chromosome. In either case, the balance between the sex factors and the genes responsible for the sex-influenced trait determines the phenotypic expression of the trait. However, the necessity of hormone for gene expression requires that the trait cannot be manifest until such time as hormone production has been initiated. The age of onset for a sex-influenced trait (pre-natal, pre-puberty, or post-puberty) may therefore suggest which type of factor might be responsible for the sex differences in the phenotypic expression in the heterozygous condition.

Two divergent views have been expressed not only with regard to the earliest appearance of the three formulas of index finger length, but also as to the stability of these formulas during growth and development. Schultz (1926) found that differences in index finger length formula could be observed in the third month of fetal life and in all age groups thereafter. He suggested that the formation of a long index finger is progressive, because he found its occurrence was *rare* in the earliest fetuses but approached the frequency found in adults towards the end of fetal life. He believed that there was little if any change in the formula of an individual after birth. Huizinga (1949), on the other hand, reported that *all* fetuses under four months of age have a long index finger formula. Furthermore, he stated that the frequency of $2 > 4$ types decreases during the later fetal period, and continues to do so until maturity, the decrease being less marked in females than in males.

In the present study, preliminary investigations disclose that all three formulas of index finger length may be discerned as early as the end of the seventh week of fetal life, at which time the terminal phalanges have just differentiated as areas of condensed tissue from the mesenchyme. A sufficient number of fetuses has not as yet been studied to determine the relative frequency of the formulas in various age groups and with respect to sex. It is definitely established, however, that at no time after seven weeks is any one of the formulas absent. The question of stability of the formula in the post-natal period needs to be further investigated by formula determinations on the same individuals over a period of years. The fact that the offspring from the family histories presented in this study agree in formula with those expected on the basis of the genetic theory (with but two exceptions), strongly suggests that the formulas are stable after birth.

At the end of the seventh week when the formulas are first observable, the fetal gonads are just in the process of sex differentiation presumably under the influence of the genic balance between the autosomes and the X-chromosomes, rather than hormones (Moore, 1948). For this reason, it is difficult to visualize hormones as the regulators of the autosomal genes for index finger length.

A seemingly more plausible explanation as to how the sex of the individual determines which formula will be expressed in the heterozygous condition, is one which postualtes genes on the X-chromosome acting in such a manner as to bring about modification of genic expression, the degree of modification being dependent upon the number of X-chromosomes present. If factors on the X-chromosome act either to accentuate the action of the autosomal gene for a long index finger, I^L, or to inhibit to a certain degree the action of the gene for a short index finger, I^S, then their presence twice in the female and once in the male would account for the difference in expression exhibited in the heterozygous condition by the two sexes. In accordance with this theory, a female with the genotype I^SI^L shows a formula of $2 = 4$ or $2 > 4$, whereas a male of the same genotype shows a phenotypic formula of $2 = 4$ or $2 < 4$. The dosage of the X-chromosome factor should also affect both of the homozygous conditions, such that two X-chromosomes in the genome have a greater effect than only one X-chromosome. Therefore, although both males and females who are homozygous I^LI^L have a $2 > 4$ formula, according to this theory the longest index finger found in females should be relatively longer than the longest index finger found in males. Conversely, although males and females both exhibit a $2 < 4$ formula when homozygous I^SI^S, the shortest index finger found in males should be relatively shorter than the shortest index finger found in females.

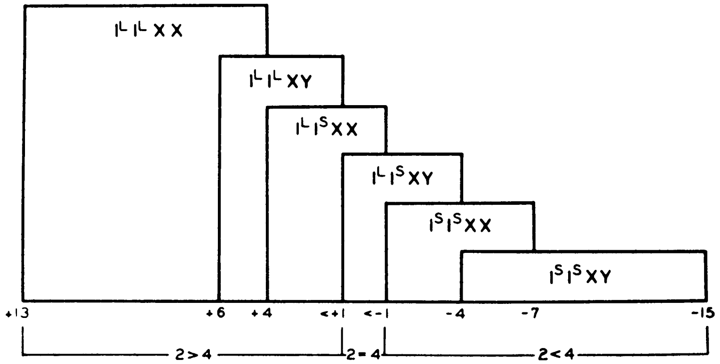

FIG. 2. Schematic diagram shows the way in which the sex of the individual is responsible for the differences in formula frequency in the two sexes. Modifying factors located on the X-chromosome act in such a way as to bring about modification of formula in both heterozygous and homozygous individuals, the degree of modification being dependent upon the number of X-chromosomes present. Thus in the heterozygous condition, females may have a long index finger formula and males, a short index finger formula; while in the homozygous condition, the longest index finger found among females is longer than any found among males, and conversely, the shortest index finger found among males is shorter than any found among females.

Corroboration for all aspects of this theory may be found in the data comprising the present study. The longest index finger found in the females projects 13 mm. beyond the end of the ring finger, while in males, the maximum projection was found to be only 6 mm. The shortest index finger found in the males is 15 mm. shorter than the ring finger, while in the females, the minimal projection is only 7 mm. When the proportion of heterozygous individuals is calculated on the basis of gene frequencies, the upper limit of difference for a heterozygous female appears to be +4 mm., whereas the lower limit for heterozygous males approximates −4mm. The relationship between the genes for the sex-influenced trait and the number of X-chromosomes is postulated to follow the pattern diagramed in figure 2.

It must be pointed out in conclusion that the scheme presented above for the inheritance of relative index finger length is only a tentative one and subject to further modification as more data are collected and the action of the genes concerned is better understood. The occurrence of two family histories which do not seem to follow the postulated mode of transmission is probably not indicative of the inaccuracy of the scheme as now proposed, but may be due to the occurrence of mutation or to over-simplification resulting from the postulation of only a single sex-linked modifying gene (or gene complex) for length. If, however, the sex-influenced modification is the result of dosage effect of one or more pairs of sex-linked alleles which differ in the degree of their modifying effect, then the theoretical discontinuity of index finger length in the population, as based on genotypic frequency, would more closely approximate the observed phenotypic continuity of index finger length variability.

SUMMARY

Three formulas of index finger length may be discerned in the human hand: index finger shorter than ring finger; index finger equal in length to ring finger; and index finger longer than ring finger. The $2 < 4$ formula is the most frequent one among males, while a $2 > 4$ formula predominates among females. Population gene frequency analysis shows that the frequency distribution of formulas in the two sexes is in conformity with that of a sex-influenced trait, wherein the gene for a short index finger behaves as a dominant in the males and as a recessive in the females. In most of the family histories investigated, the phenotypes of the parents and offspring, and the frequencies with which the phenotypes occur in the offspring, are in agreement with the theory of sex-influenced inheritance.

Differences in formula are due to variations in the length of the index digit which are independent of metacarpal or ray length and general body build. The various formulas can be observed as early as the end of the seventh week of fetal life. Hormones do not appear to be responsible for the sex difference in index finger length since the formulas are established before the period in which hormone production is initiated. It is suggested that a modifying factor located on the X-chromosome acts in such a manner as to bring about modification of index finger length in both heterozygous and homozygous individuals, the degree of modification being dependent upon the number of X-chromosomes present.

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