THE ANALYSIS OF INTERFERENCE.

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For more than fifteen years geneticists and cytologists have been using a quantity known as "coincidence" as a measure of interference. Although there is a verbal similarity between the various definitions, a brief survey of the literature has shown that at least three different quantities are being used to measure interference, two under the name of "coincidence" and one under the suggested name of "fraction realised". The purpose of this paper is not merely to urge the consistent use of one quantity, but to show also that those at present in use suffer from serious defects:

(1) None of them are true "isolates", *i.e.* they are all functions, not only of the two segments between which the interference is to be measured, but also of the location of other genes which are followed in the experiment.

(2) Two of the quantities have an expectation differing from unity in the absence of interference, in spite of the fact that equality to unity is supposed to be a criterion of non-interference.

The quantity which we shall propose as a measure of interference has an expected value which

(1) depends on the four genes defining the two segments between which interference is measured, but on no other genes,

(2) equals unity when there is no interference.

The methods of measuring coincidence.

Coincidence is defined as the ratio of the frequency of double recombinations to the frequency expected in the absence of interference.

In an experiment where only three genes are followed, defining the consecutive segments 1 and 2, we have

Total number of individuals $= n$

Number showing recombination in segment 1 $= n_1$

Number showing recombination in segment 2 $= n_2$

Number showing simultaneous recombination in segments 1 and 2 $= n_{12}$

And the measure of coincidence is

$$\frac{\frac{n_{12}}{n}}{\frac{n_1}{n} \times \frac{n_2}{n}} = \frac{n_{12} n}{n_1 n_2}$$

The objections which we have noted above do not arise until experiments are performed in which more than three genes are followed. We shall suppose that the data of a multiple-factor experiment have been classified under subtotals with the following notation:

[0] = number of individuals showing no recombination.
[r] = number of individuals showing recombination in segment r *and nowhere else.*
[r, s] = number of individuals showing recombination in segments r and s *and nowhere else.*
[r, s, ..., t] = number of individuals showing recombination in segments r, s, ..., t *and nowhere else.*

Then suppose, for example, it is desired to measure the interference between segments 3 and 6. The number showing recombination in segment 3 is obviously

$$n_3 = [3] + [1, 3] + [2, 3] + \ldots + [1, 2, 3] + [1, 3, 4] + \ldots,$$

i.e. the sum of all brackets containing a 3.

n_6 is similarly calculated. But when it comes to calculating n_{36}, the number of double recombinations in 3 and 6, shall we include, in addition to [3, 6], all, some, or none of the multiple recombinations which involve 3 and 6?

(**A**) The most common practice, which seems to be due to Weinstein(1), is to include all multiples in which recombination is observed in 3 and 6, and in no intermediate segment. For example, [1, 3, 6], [2, 3, 6, 7] are included, and [3, 4, 6], [3, 5, 6, 7] are rejected.

(**B**) From the coincidence values obtained, it appears that Graubard(3), while calculating n_3 and n_6 in the usual way, rejects all triple and higher multiple recombinations in the calculation of n_{36}, *i.e.* he takes $n_{36} = [3, 6]$.

(**C**) Schweitzer(4), in 1934, criticised Weinstein's method and suggested the use of a quantity which he termed "fraction realised". This is defined in such a way that for our example its value would be

$$\frac{[3, 6] \times \{[0] + [3] + [6] + [3, 6]\}}{\{[3] + [3, 6]\} \times \{[6] + [3, 6]\}},$$

i.e. all individuals showing recombination in any segment other than 3 and 6 are rejected from the start, and the coincidence is calculated on the residual data.

Schweitzer's justification for this procedure is that it gives results approximately = unity for segments lying in different arms of the

Drosophila melanogaster II-chromosome, between which it is believed there is no interference.[1]

THE OBJECTIVE MEASUREMENT OF INTERFERENCE.

However many genes are followed in an experiment, we can, with reference to any two segments p and q (not necessarily adjacent), classify the data in the four cells of a 2×2 table (Table I).

TABLE I.

	Recombination in the pth segment	No recombination in the pth segment	Totals
Recombination in the qth segment	w	x	$w+x$
No recombination in the qth segment	y	z	$y+z$
Totals	$w+y$	$x+z$	n

w = number of individuals showing recombination in the segments p and q, *and nowhere or anywhere else.*
x = number of individuals showing recombination in the segment q, no recombination in segment p, *and recombination nowhere or anywhere else.*
y = etc.
z = number of individuals showing no recombination or showing recombination anywhere except in segments p and q.

If there is no interference between segments p and q, the probabilities of an individual falling into the various cells of the table are clearly as shown in Table II.

TABLE II.

ab	$b\,(1-a)$	b
$a\,(1-b)$	$(1-a)\,(1-b)$	$1-b$
a	$1-a$	1

If, however, there is interference between the segments, then the probability of an individual falling in the double recombination class is diminished. With the marginal probabilities fixed, the table has only one degree of freedom, and consequently the completely general case can be represented by Table III.

TABLE III.

cab	$b\,(1-ca)$	b
$a\,(1-cb)$	$1-a-b+cab$	$1-b$
a	$1-a$	1

[1] See Addendum, p. 63.

We recognise the parameters a and b as the recombination percentages for the segments p and q respectively, and c as a measure of interference between segments p and q. Moreover, c is independent of the other genes which have been followed in the experiment, and is equal to unity when there is no interference.

The problem is now reduced to this:

(1) Given the observations recorded in Table I, what are the best estimates of the parameters a, b and c?

(2) What are the variances of these estimates?

We shall find efficient estimates by means of the method of maximum likelihood(5). The likelihood function is

$$L = w \log (cab) + x \log \{b (1-ca)\} + y \log \{a (1-cb)\} + z \log (1-a-b+cab).$$

Equations of maximum likelihood are

$$0 = \frac{\partial L}{\partial a} = \frac{w}{a} - \frac{xc}{1-ca} + \frac{y}{a} - \frac{z(1-cb)}{1-a-b+cab},$$

$$0 = \frac{\partial L}{\partial b} = \frac{w}{b} + \frac{x}{b} - \frac{yc}{1-cb} - \frac{z(1-ca)}{1-a-b+cab},$$

$$0 = \frac{\partial L}{\partial c} = \frac{w}{c} - \frac{xa}{1-ca} - \frac{yb}{1-cb} + \frac{zab}{1-a-b+cab}.$$

The solution of these equations is

$$\begin{cases} \hat{a} = \dfrac{w+y}{n}, \\ \hat{b} = \dfrac{w+x}{n}, \\ \hat{c} = \dfrac{wn}{(w+x)(w+y)}. \end{cases}$$

This result is not unexpected, since it gives an exact fit.

We may now evaluate the variances of these statistics by means of the formula

$$\frac{1}{n} V(T) = S\left\{p \left(\frac{\partial T}{\partial w}\right)^2\right\} - \left(\frac{\partial T}{\partial n}\right)^2,$$

where the summation proceeds over the different classes, p is the probability of an individual falling into a particular class, and w, x, y, z are put equal to their expected values after differentiation.

The variances are

$$V(\hat{a}) = \frac{a(1-a)}{n},$$

$$V(\hat{b}) = \frac{b(1-b)}{n},$$

$$V(\hat{c}) = \frac{c}{n}\left\{\frac{1-ca-cb-cab+2c^2ab}{ab}\right\}.$$

The first two are the well-known formula for the variance of an estimate of recombination percentage. The third, giving the variance of an estimate of coincidence, was found in a different way by Muller and Jacobs-Muller(6), who appeared, however, to have had some doubt about its accuracy.

Our conclusion, then, is that we may consistently and efficiently estimate coincidence by the quantity $\frac{n \cdot n_{pq}}{n_p \cdot n_q}$, where

n = total number of individuals.

n_p = number of individuals showing recombination in segment p, *and nowhere or anywhere else.*

n_q = etc.

n_{pq} = number of individuals showing recombination in segments p *and* q, *and nowhere or anywhere else.*

AN EXAMPLE OF THE CALCULATION OF COINCIDENCE.

To illustrate the differences between the various measures of interference, and to make our argument concrete, we will calculate the coincidences for segments 1 and 4 in the *X*-chromosome of *Drosophila*, where the genes are

sc (1) *ec* (2) *cv* (3) *ct* (4) *v* (5) *g* (6) *f*.

The data are from Bridges and Olbrycht, requoted from Schweitzer(4).

TABLE IV.

[0]	9554	[1, 2]	3	[2, 5]	191	[5, 6]	46	[2, 3, 4]	1	[1, 2, 3, 4]	1
[1]	994	[1, 3]	10	[2, 6]	230	[1, 2, 6]	1	[2, 4, 5]	1	[1, 2, 3, 6]	1
[2]	1465	[1, 4]	87	[3, 4]	26	[1, 3, 5]	2	[2, 4, 6]	4		
[3]	1425	[1, 5]	140	[3, 5]	110	[1, 3, 6]	3	[2, 5, 6]	1	Total number	
[4]	2512	[1, 6]	147	[3, 6]	161	[1, 4, 5]	7	[3, 4, 6]	4	of flies	
[5]	1717	[2, 3]	8	[4, 5]	76	[1, 4, 6]	9	[3, 5, 6]	2	$n = 20{,}786$	
[6]	1525	[2, 4]	95	[4, 6]	225	[1, 5, 6]	1	[4, 5, 6]	1		

The total numbers of flies showing recombination in segments 1 and 4 respectively are

$$n_1 = 1406,$$

$$n_4 = 3049.$$

(**A**) Weinstein's coincidence is

$$w=\frac{n\times\{[1,4]+[1,4,5]+[1,4,6]\}}{n_1\times n_4}$$
$$=\frac{20786\times 103}{1406\times 3049}=0{\cdot}4994.$$

(**B**) Graubard's coincidence is

$$g=\frac{n\times[1,4]}{n_1\times n_4}$$
$$=\frac{20786\times 87}{1406\times 3049}=0{\cdot}4218.$$

(**C**) Schweitzer's fraction realised is

$$f=\frac{\{[0]+[1]+[4]+[1,4]\}\times[1,4]}{\{[1]+[1,4]\}\times\{[4]+[1,4]\}}$$
$$=\frac{13147\times 87}{1081\times 2599}=0{\cdot}4071.$$

(**D**) The coincidence we are proposing is

$$c=\frac{n\times\{[1,4]+[1,4,5]+[1,4,6]+[1,2,3,4]\}}{n_1\times n_4}$$
$$=\frac{20786\times 104}{1406\times 3049}=0{\cdot}5043.$$

Now suppose that an experiment is performed in which the gene dividing segments 2 and 3 is not followed, and that the material behaves in exactly the same way. Then a recombination in either 2 or 3 alone appears as a recombination in the combined segment 2+3, and double recombinations in 2 and 3 are undetected. Hence

[2, 3]	is included	in	[0]
[2, 3, 4]	,,	,,	[4]
[1, 2, 3, 4]	,,	,,	[1, 4]
[1, 2, 3, 6]	,,	,,	[1, 6]

Under these circumstances it is obvious that the calculation of Weinstein's coincidence, Graubard's coincidence, and Schweitzer's fraction realised will all lead to results differing from those previously obtained. The new values, which are given in Table V for comparison, are indeed only slightly different, but that is because only a slight change has been made in the experiment. It is clear that the differences are sometimes very considerable. The equality of w and c on the new data is accidental; generally all four quantities are different.

It should be noted that these discrepancies are in no sense errors arising from the use of a finite sample. We might substitute for the numbers in the data the true (*i.e.* expected) numbers and see that, in

TABLE V.

	Old	New
Weinstein	0·4994	0·5043
Graubard	0·4218	0·4267
Fraction realised	0·4071	0·4114
c	0·5043	

general, the first three measures of interference have limiting values which are dependent on the locations of all genes in the experiment, while c has a limiting value depending only on the locations of segments 1 and 4.[1]

COINCIDENCE VALUES FOR A CHROMOSOME WITH NO INTERFERENCE.

It is of interest to see what values are expected in a chromosome in which there is no interference. If such a chromosome is divided into segments 1, 2, ..., k and the probability of recombination in segment r is a_r, then the probability of recombination in segments p, q, ... and no recombination in segments u, v, ... (no conditions being made on recombination in the remaining segments) is

$$a_p a_q \ldots (1-a_u)(1-a_v) \ldots .$$

(**A**) The expected value of Weinstein's coincidence for the segments p and q is

$$\exp(w) = \frac{a_p a_q \prod_{r=p+1}^{q-1}(1-a_r)}{a_p a_q} = \prod_{r=p+1}^{q-1}(1-a_r),$$

where $\prod_{r=p+1}^{q-1}(1-a_r)$ denotes the product of all terms $(1-a_r)$ for values of r from $p+1$ to $q-1$.

The expected value of w is therefore less than unity and *decreases as the distance between the segments p and q increases.* If sufficient genes are followed to detect nearly all the cross-overs between p and q, the expected value approximates to $e^{-L_{pq}}$, where $100.L_{pq}$ is the map distance between the nearer ends of the segments.

[1] Schweitzer uses a similar argument in his criticism of Weinstein's method, but does not realise that it applies equally to his own "fraction realised".

This conclusion should be compared with Weinstein's results and his deduction: "The evidence presented in this paper(1) indicates that for the sex chromosome of *Drosophila melanogaster*, when the intermediate region reaches a value of about 46, coincidence is approximately 1·00; and as the intermediate distance increases still further, coincidence decreases again....For regions more than 46 units apart interference reappears again." But we have seen that Weinstein's coincidence falls off, even in the absence of interference, and consequently his final conclusion is not legitimate.

(**B**) The expected value of Graubard's coincidence is similarly

$$\exp(g) = \frac{a_p a_q \prod_{r \neq p, q} (1 - a_r)}{a_p a_q} = \prod_{r \neq p, q} (1 - a_r),$$

where $\prod_{r \neq p, q} (1 - a_r)$ denotes the product of terms $(1 - a_r)$ for all values of r from 1 to k, except p and q. This quantity is consistently less than unity, and when a sufficient number of genes are followed approximates to

$$\frac{e^{-L}}{(1 - l_p)(1 - l_q)},$$

where $100.L$ is the map length of the chromosome, and $100.l_p$, $100.l_q$ are the map lengths of segments p and q.

Graubard did, in fact, obtain coincidences less than unity, and averaging 0·7, for segments lying in different arms of the *Drosophila* II-chromosome, and was led wrongly to the conclusion: "From the data on coincidence of sections located in both arms of the chromosome it is apparent that crossing over in the two arms is not entirely independent. If crossing over in one arm were entirely independent of that of the other, then, theoretically, coincidence should be approximately one, which was not the case. We must therefore assume that although crossing over in one arm is largely independent of the other, some mechanism exists, connected perhaps with the spindle fibre, which interferes with simultaneous crossing over in both."[1]

(**C**) Schweitzer's fraction realised has an expected value

$$\exp(f) = \frac{\{\prod_{r \neq p, q} (1 - a_r)\} \{a_p a_q \prod_{r \neq p, q} (1 - a_r)\}}{\{a_p \prod_{r \neq p, q} (1 - a_r)\} \{a_q \prod_{r \neq p, q} (1 - a_r)\}} = 1.$$

It appears then that "fraction realised" has an expectation unity when

[1] In a later paper, Graubard comes to the conclusion that there is no interference between crossing-over in the two arms, and uses Schweitzer's fraction realised to obtain values approximating to unity.

there is a complete absence of interference throughout the chromosome. It is also possible to prove that, whatever the nature of interference in either arm of a chromosome, if there is no interference across the spindle-fibre attachment, then the expected value of fraction realised is unity when the segments lie in different arms. To this extent, "fraction realised" is indeed an improvement on Weinstein's coincidence, but our first objection remains when there is interference.

Even when there is no interference, fraction realised is at a disadvantage compared with c, because it has a greater standard error. If the probability of an individual showing recombination in no segments other than p and q is P, then it can be shown that

$$\frac{\text{Variance of fraction realised}}{\text{Variance of } c} = \frac{1}{P}.$$

P is estimated from the proportion of individuals which remain after the rejection of those showing recombination in segments other than p and q. In our example we have

$$\frac{\text{Variance of fraction realised}}{\text{Variance of } c} = \frac{20786}{13147} = 1{\cdot}58.$$

In other words the proportion of information lost (on Fisher's definition) is simply equal to the proportion of flies rejected.

INTERFERENCE IN THE *X*-CHROMOSOME OF *DROSOPHILA MELANOGASTER*.

From data combined by Anderson and Rhoades(2) we have recalculated the coincidences between six segments in the *X*-chromosome of *Drosophila*. These are set out in a symmetrical table (Table VI), with

TABLE VI.

Coincidences in the X-chromosome of Drosophila melanogaster.

sc (1) *ec* (2) *cv* (3) *ct* (4) *v* (5) *g* (6) *f*

	1	2	3	4	5	6
1		0·034 *0·011*	0·125 *0·026*	0·547 *0·043*	1·002* *0·064*	1·010* *0·064*
2	0·034		0·059 *0·016*	0·365 *0·029*	0·874 *0·049*	1·059* *0·053*
3	0·125	0·059		0·124 *0·019*	0·635 *0·047*	0·823 *0·052*
4	0·547	0·365	0·124		0·241 *0·023*	0·707 *0·036*
5	1·002*	0·874	0·635	0·241		0·188 *0·023*
6	1·010*	1·059*	0·823	0·707	0·188	

Standard errors are given in italic figures. Coincidences marked with an asterisk do not differ significantly from unity.

standard errors attached. It will be noticed that coincidence is in no case significantly greater than unity; *i.e.* there is no suggestion of "negative" interference. The only pairs of segments, between which the data do not prove interference, are 1–5, 1–6 and 2–6.

The absence of interference between different arms of the II-chromosome of *Drosophila melanogaster*.

Using Graubard's data(3), we have calculated c between segments 1, 2, 3 in one arm and segments 5, 6, 7 in the other, where the genes are

$$a_l\ (1)\ t_w\ (2)\ b\ (3)\ p_r\ (4)\ c_n\ (5)\ v_g\ (6)\ L^c\ (7)\ s_p.$$

The standard errors attached have been calculated by using the estimates of a and b for each experiment, but with c taken equal to unity. If the estimated values of c had been used, the results would have been only slightly different, and in any case those given are the best estimates for testing the hypothesis that there is no interference. It will be noticed that the thirty-six values are nicely distributed about unity, eighteen being above and eighteen below.

TABLE VII.

Coincidences in the II-chromosome of Drosophila melanogaster.

Segments	Temperature of the experiment			
	14°	16·5°	25°	30°
1–5	1·00 ± 0·11	0·96 ± 0·09	0·97 ± 0·11	1·01 ± 0·11
1–6	1·40 ± 0·21	1·20 ± 0·15	1·11 ± 0·18	1·21 ± 0·17
1–7	1·19 ± 0·08	0·93 ± 0·06	0·89 ± 0·06	1·06 ± 0·05
2–5	1·08 ± 0·06	0·97 ± 0·05	1·05 ± 0·06	1·06 ± 0·06
2–6	0·89 ± 0·10	1·04 ± 0·08	0·97 ± 0·10	0·96 ± 0·10
2–7	0·88 ± 0·04	1·03 ± 0·03	0·97 ± 0·03	0·99 ± 0·03
3–5	0·87 ± 0·10	0·96 ± 0·10	1·01 ± 0·16	1·19 ± 0·12
3–6	0·93 ± 0·17	0·94 ± 0·15	1·00 ± 0·25	1·15 ± 0·19
3–7	1·33 ± 0·07	0·99 ± 0·06	0·98 ± 0·08	0·89 ± 0·06

In making a general test of non-interference across the spindle-fibre attachment, one may not average the nine coincidences for each temperature, because these estimates are correlated. The method we employ is to classify the data in 4×4 tables, according to the number of recombinations observed in the two arms. X is the number of recombinations in the right arm, and Y the number in the left arm, both running from 0 to 3. The variance of Y may then be analysed into the three degrees of freedom for differences between the X classes, and a remainder for variation within the X classes. The three degrees of freedom may be further divided into one for the linear regression of Y on X, and two for deviation from the linear regression.

TABLE VIII.

Temperature 14° C.

Number of flies = 3501

X \ Y	Left arm 0	1	2	3
Right arm 0	913	853	62	0
1	769	685	71	0
2	76	64	8	0
3	0	0	0	0

Analysis of variance.

	Degrees of freedom	Sum of squares	Mean square
Linear regression	1	0·043	0·043
Deviations from linearity	2	0·009	0·005
Total for differences between X classes	3	0·052	
Remainder	3497	1152·107	0·329
Total	3500	1152·159	

There is no suggestion whatever of interference at 14° C.

TABLE IX.

Temperature 16·5° C.

Number of flies = 5739

X \ Y	Left arm 0	1	2	3
Right arm 0	1482	1367	107	1
1	1288	1228	75	2
2	102	78	8	0
3	1	0	0	0

Analysis of variance.

	Degrees of freedom	Sum of squares	Mean square
Linear regression	1	0·103	0·103
Deviations from linearity	2	0·406	0·203
Total for differences between X classes	3	0·509	
Remainder	5735	1825·684	0·318
Total	5738	1826·193	

There is no suggestion whatever of interference at 16·5° C.

TABLE X.

Temperature 25° C.

Number of flies = 5284

X \ Y		Left arm 0	1	2	3
Right arm	0	1677	1222	43	2
	1	1298	899	25	0
	2	71	43	3	0
	3	0	1	0	0

Analysis of variance.

	Degrees of freedom	Sum of squares	Mean square = s	$\frac{1}{2}\log_e s$
Linear regression	1	0·448	0·448	0·750
Deviations from linearity	2	0·377	0·189	
Total for differences between X classes	3	0·825		
Remainder	5280	1453·690	0·275	0·506
Total	5283	1454·515		$z = 0·244$

The z test shows that the linear regression is not significant, and consequently that there is no evidence of interference at 25° C.

TABLE XI.

Temperature 30° C.

Number of flies = 4514

X \ Y		Left arm 0	1	2	3
Right arm	0	1304	1027	83	6
	1	1009	817	76	3
	2	97	84	5	0
	3	1	1	0	1

Analysis of variance.

	Degrees of freedom	Sum of squares	Mean square = s	$\frac{1}{2}\log_e s$
Linear regression	1	0·258	0·258	
Deviations from linearity	2	1·973	0·987	1·145
Total for differences between X classes	3	2·231		
Remainder	4510	1514·070	0·336	0·606
Total	4513	1516·301		$z = 0·539$

The z is below the 5 per cent. level of significance, and hence the data do not show interference at 30° C.

Finally we have pooled the data for all temperatures and analysed the variation into three degrees of freedom for differences between temperatures, three for differences between X classes, nine for interaction, and a remainder. Each analysis is followed by a brief statement of the conclusions drawn from it.

TABLE XII.

The analysis of the pooled data.

Total number of flies = 19,038

	Degrees of freedom	Sum of squares	Mean square
Differences between temperature classes	3	32·078	10·693
Differences between X classes	3	1·148	0·383
Interaction	9	2·471	0·273
Total for differences in temperature and X	15	35·697	
Remainder	19,022	5945·649	0·313
Total	19,037	5981·346	

From this analysis it is obvious that the temperature affects the number of recombinations in the left arm of the II-chromosome. There is still, however, no evidence that the number of recombinations in the left arm is affected by the number of recombinations in the right arm.

In conclusion, we may say that the data, separately and together, show that there is no interference across the spindle fibre attachment in the II-chromosome of *Drosophila*.

ADDENDUM.

In a paper just published(7), Schweitzer again uses fraction realised, and claims that it is a direct expression of the interference relations between two segments, since "only those classes having direct reference to the events in the particular regions being studied are included" in the calculation. But it is not yet known that the behaviour of chromosomes can be expressed as a synthesis of the effects of interference "forces" between pairs of segments.

Without assuming anything about the way in which chromosome behaviour will eventually be analysed, one must devise a parameter which is a function of only two segments, and which is therefore calculable from *any* experiment in which these two segments are marked. It is the coincidence described in the present paper, and not fraction realised, which fulfils these requirements.

It is interesting to note that in spite of his theoretical arguments, Schweitzer uses (figs. 10 *et seq.*) a quantity called "double cross-overs 'corrected' in per cent." which for any one set of data is proportional to the coincidence of the present paper.

SUMMARY.

Various methods are in use for calculating a quantity to measure the interference between recombination in non-adjacent segments. Three are investigated in this paper and are shown to be unsatisfactory, because they lead to results which depend not only on the two segments in question, but also on the location of other genes followed in the experiment. Two of them, including the most popular, have expectations less than unity in the absence of interference. Since equality to unity is taken as a criterion of non-interference, this has led to erroneous conclusions.

The exact method, which is given in this paper, while being free from the above objections, is just as simple in calculation. A formula is derived for the standard error of this estimate.

Coincidences have been recalculated for the *X*- and II-chromosomes of *Drosophila*. In the *X*-chromosome, the coincidence rises steadily to unity for extreme segments. Between segments in different arms of the II-chromosome coincidences approximate to unity, showing absence of interference. Finally a statistical analysis of the II-chromosome data has been made to prove that there is no interference across the spindle fibre attachment.

ACKNOWLEDGMENT.

I am indebted to Dr K. Mather of the Galton Laboratory for assistance in preparing this paper.

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