An Analysis of Interference in the Fission Yeast *Schizosaccharomyces pombe*

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ABSTRACT

The evaluation of three-point crosses at the tetrad and random spore level leads to the conclusion that both chiasma and chromatid interference are absent in the fission yeast *Schizosaccharomyces pombe.*

EXCHANGES or reciprocal recombination events at the meiotic four-strand stage do not occur independently of each other in many eukaryotes. MULLER (1916) has termed this phenomenon interference, *I*. To determine its magnitude he proposed to obtain from suitable genetic crosses the coincidence or coefficient of coincidence, *C*, by dividing the observed frequency of double recombinants (meiotic products simultaneously recombinant for two small marked segments, adjacent or not) by the frequency expected if recombination events in the two segments are independent. Then he defined $I = 1 - C$, so when observed and expected doubles match ($C = 1$) there is no interference ($I = 0$).

Subsequently MATHER (1933) made a distinction between chiasma interference and chromatid interference. Depending on the experimental context the first denotes nonrandomness of chiasmata or exchanges, respectively, concerning position. The second means nonrandomness with respect to chromatid choice. In the absence of chromatid interference 2-, 4- and 3-strand double exchanges are expected in an 1:1:2 ratio.

Positive chiasma interference, the inhibiting effect of an exchange on a second event, generally does not operate across the centromere, is absolute or pronounced for two adjacent small intervals and vanishes as the intervals are separated by an ever increasing distance. This has been found for instance in *Drosophila melanogaster* (WEINSTEIN 1918; STEVENS 1936), *Neurospora crassa* (STADLER 1956; PERKINS 1962) and *Saccharomyces cerevisiae* (MORTIMER and FOGEL 1974). Chromatid interference is absent in *D. melanogaster* (EMERSON and BEADLE 1933) and *S. cerevisiae* (MORTIMER and FOGEL 1974) while a significant but not dramatic excess of 2-strand over 4-strand double exchanges has been observed in *N. crassa* by PERKINS (1962). Positive chiasma interference seems to be the rule rather than the exception and recently two contrasting pertinent models have been presented (KING and MORTIMER 1990; FOSS *et al.* 1993). Two examples of exceptions are *Aspergillus nidulans* (STRICKLAND 1958) and fission yeast. In the latter organism two-point tetrad data have been tested for interference in the context of a model put forward by BARRATT *et al.* (1954), but none has been found (SNOW 1979; MUNZ *et al.* 1989).

The first extensive genetic map of *S. pombe* was prepared by KOHLI *et al.* (1977). This was followed by two other versions (GYGAX and THURIAUX 1984; MUNZ *et al.* 1989). In addition, physical maps of this organism have appeared (FAN *et al.* 1989, 1991) and gene lists have been compiled by KOHLI (1987) and more recently by LENNON and LEHRACH (1992).

Attempted here is an evaluation of data at the three-point level both with respect to chiasma and chromatid interference.

MATERIALS AND METHODS

Strains: All strains were from the Bernese collection.

Crosses: The crosses which have been evaluated are listed in Table 1. Materials and methods concerning JK crosses are found in KOHLI *et al.* (1977).

Media: Yeast extract agar (YEA) and malt extract agar (MEA) are described in GUTZ *et al.* (1974). Synthetic growth medium was GMA (GYGAX and THURIAUX 1984). Growth factors were added to a final concentration of 100 mg/liter.

Genetical methods and evaluation of crosses: In general the methods described by GUTZ *et al.* (1974) were adopted. Crosses have been set up as follows. One loopful of freshly grown cell material of the two parents to be crossed were placed at the center of an MEA plate supplemented with adenine, uracil, histidine, leucine and lysine. Approximately 0.2 ml of water was dropped on the cells which were then mixed with a simple glass instrument. This resulted in a round inoculated area of approximately 3 cm in diameter.

For random spore analyses a heavy loop of sporulated material was transferred to 10 ml water containing snail digestive juice 400-fold diluted compared with the purchased product in ampoules. Incubation overnight at 30° kills cells, dissolves ascus walls but does not affect spore viability (MUNZ and LEUPOLD 1979).

In tetrad analyses material from the rim of the sporulated area was transferred to fresh YEA plates. The spores of asci were then separated in the usual way with a micromanipulator.

In random spore analyses homothallic spores were included. Their frequency was always below 1%. Diploids were checked either microscopically or by their dark staining on media containing the dye Phloxine B (GUTZ *et al.* 1974). Their frequency was in no sample above 0.5%.

Some characteristics of the crosses studied by tetrad analysis are given in Table 2. In a cross $h^+ \times h^-$ involving the standard mating-type genes an exchange in the *L* segment of the

TABLE 1

Crosses evaluated

Cross	Relevant genotype of parents
JK5	*leu1-32 + h⁺* / *+ his7-366 h⁻*
JK6	*leu1-32 h⁺ +* / *+ h⁻ his5-303*
JK9[a]	*leu1-32 h⁺ his5-303 +* / *+ h⁻ + mut3-25*
JK12	*+ h⁺ + glu2-1* / *leu1-32 h⁻ his5-303 +*
X972	*ura2-10 + lys7-1 +* / *+ leu2-120 + ade2-17*
X1014	*+ leu2-120 + ade2-17* / *his1-102 + lys7-1 +*
XB1045	*lys3-37 ura1-61 +* / *+ + pro1-1*
XB1050	*leu1-32 his7-366 h⁺ +* / *+ + h⁻ his5-303*
XB1075	*ade6-704 + arg1-230* / *+ tps14-5 +*
XB1076	*ura2-10 + lys7-1* / *+ leu2-120 +*
XC1	*+ h⁺ + his5-303* / *leu1-32 h⁻ cdc18-K46 +*
XC4	*+ + + +* / *his1-102 leu2-120 lys7-1 ade2-17*
XC8	*sup3-5 + + +* / *+ ura2-10 lys7-1 ade2-17*

The markers are given in order according to the genetic map (MUNZ *et al.* 1989). A discrepancy exist with respect to *cdc18* (XC1): The correct order is *mat-cdc18-his5* in contrast to *mat-his5-cdc18* in the map. Mating-type is only given if involved in the interference study. The upper parent is always h^+ and the lower h^-. JK crosses have been analyzed by J. KOHLI. Here a reevaluation at the three-point level is undertaken since originally only two-point data have been presented (KOHLI *et al.* 1977).

[a] The mutator phenotype in JK9 has been followed on the background of *ade7-C8* (MUNZ 1975).

mating-type region will produce an h^+ h^+ h^{90} h^- tetrad (LEUPOLD 1958). Such tetrads were included. If mating-type was a member of the trio analyzed the homothallic h^{90} spore was treated as h^-. Thus the allelic difference at mating-type is taken as presence (h^+) or absence (h^{90}, h^-) of the *mat1:2-P* cassette. An overview of the mating-type situation in *S. pombe* has been presented by EGEL (1989).

Unfortunately there is an inconsistency with respect to the tetrads producing only three colonies. They were included in the JK crosses because these samples are quite small, but in the other crosses they were not recorded. Nevertheless, an examination of JK crosses with and without 3s did not reveal any obvious difference.

As can be seen from Table 2, 16 conversions were observed (nine 3+:1− and seven 1+:3−) This gives an average conversion frequency of 0.0028 based on the total number of 5694 segregations (*mat* not included). Conversion tetrads were not further considered, nor tetrads with less than three colonies and others pooled under "miscellany" in Table 2.

Statistical methods: In *G* tests of goodness of fit the correction of WILLIAMS was not applied (SOKAL and ROHLF 1981).

Chromatid interference: The 2-, 4- and 3-strand double exchanges are expected in the absence of chromatid interference in a ratio of 1:1:2. In individual crosses the numbers of double exchanges are small. Thus the probability of the observed outcome has been calculated by the multinomial distribution. As an example, the probability of obtaining the result of X1014-1 (Table 3) is

$$P = \frac{22!}{2!\,6!\,14!}\left(\frac{1}{4}\right)^2\left(\frac{1}{4}\right)^6\left(\frac{1}{2}\right)^{14} = 0.0083.$$

Next, the probability of all other possible outcomes is obtained and added if equal or smaller. This is *P* for individual trios in Table 3. The pooled data were subjected to a *G* test of goodness of fit.

Test of no interference: In the case of three-point analyses the data are advantageously presented in 2 × 2 tables (random spores) and 3 × 3 tables (tetrads) (Figure 1). The following test of no interference whatsoever has been adopted [T. P. SPEED, personal communication; BERAN and MILLAR (1987)]. (1) Based on the Poisson model (neither chromatid nor chiasma interference operating) maximum likelihood estimates of the genetic distances of the two intervals are obtained (tetrads: SNOW 1979). (2) With this the expected proportions of the two spore types or three tetrad types are calculated for each interval using the HALDANE (1919, 1931) mapping functions. (3) The expected proportions in the cells are obtained as products from the marginal values. (4) All expected relative frequencies are multiplied by sample size to obtain expected frequencies. (5) The quantity *G* is calculated (O ln (O/E), summed over all cells and multiplied by 2, with O and E observed and expected frequencies, respectively). Since in most cases some cells have very low expectations a *G* test assuming the χ^2 distribution on six degrees of freedom (tetrads) seems inadvisable. In no case were cells amalgamated. (6) Given the expected relative frequencies for all cells, a table of multinomial counts with the same sample size was simulated and the corresponding *G* value recorded; this was done 1000 times for each trio. (7) The probability of obtaining a *G* value as large or larger than the observed value for any trio was then estimated in each case by the proportion of such values found in the set of 1000 simulated values. These simulations were kindly run by T. P. SPEED and H. ZHAO and the estimated probabilities are the *P* values presented in Tables 4 and 5.

In the case of a single interval analyzed by tetrads (Table 6) testing of no interference is more straightforward, especially if none of the expectations are small. Based on the Poisson model the genetic distance is estimated by maximum likelihood, the expected frequencies are calculated and a *G* test of goodness of fit is conducted.

RESULTS

In the present analysis at most three markers have been considered at one time. Thus, in four-factor crosses involving the ordered and linked markers *ABCD* the trios *ABC* (with intervals *AB* and *BC*) and *BCD* (with intervals *BC* and *CD*) have been tested separately. In Tables 3, 4 and 5 different trios of the same cross are distinguished from each other by a dash and a number following the main cross designation. In addition, the evaluation has been restricted to intervals of small up to

TABLE 2

Characteristics of crosses studied by tetrad analysis

Cross	Mendelian segregation	Recombination in mating type region	Three colonies only	Relevant total	Conversions	Two, one, and zero colonies	Miscellany[a]
JK5	62	1	4	67	0	2	2
JK6	76	0	3	79	0	1	0
JK9	80	0	16	96	2	5	1
JK12	72	2	11	85	2	2	3
X1014	641	—	—	641	6	—	14
XB1050	217	1	—	218	1	—	5
XC1	416	8	—	424	3	—	4
XC8	102	—	—	102	2	—	0

Given are the numbers of tetrads observed. — = not determined.

[a] In this category fall tetrads with two diploid and two haploid spore clones (the result of a mating between a diploid and a haploid cell), tetrads containing mixed colonies and those with multiple nonmendelian segregations. The latter two classes are most probably due to inadequate experimentation.

TABLE 3

Test of no chromatid interference

Cross	Observed frequencies of double exchanges				P^a
	2-strand	4-strand	3-strand	Sum	
JK5	1	1	0	2	*A*
JK6	0	2	2	4	*B*
JK9-1	3	1	4	8	*B*
JK9-2	1	2	1	4	*B*
JK12-1	4	2	4	10	0.60
JK12-2	4	6	5	15	0.30
X1014-1	2	6	14	22	0.23
X1014-2	3	7	6	16	0.27
XB1050-1	1	0	0	1	*A*
XB1050-2	2	1	6	9	*B*
XC1-1	3	3	17	23	0.09
XC1-2	0	2	3	5	*B*
XC8-1	1	2	7	10	0.51
XC8-2	6	1	3	10	0.06
Sum, observed	31	36	72	139	0.76
Expected	34.75	34.75	69.5		

See also MATERIALS AND METHODS.

[a] Probability of obtaining the observed outcome or others with equal or lower probability under the hypothesis tested. For individual crosses based on the multinomial distribution, for the pooled data on the χ^2 approximation (G test with 2 degrees of freedom). *A* = The probability of any outcome is larger than 5%. *B* = The probability of the observed result alone is larger than 5%.

		BC		
		P	R	
AB	P	401 396.3	108 112.7	509
	R	77 81.7	28 23.3	105
		478	136	614

		BC			
		PD	NPD	T	
AB	PD	422 423.3	1 2.0	87 84.4	510 509.7
	NPD	4 3.1	0 0.01	0 0.6	4 3.7
	T	105 106.0	0 0.5	22 21.1	127 127.6
		531 532.4	1 2.5	109 106.1	641

FIGURE 1.—Examples of analysis of three factor crosses. (Left) Random spores (XB1045); (right) tetrads (X1014-1). P and R, parental and recombinant spores, respectively; PD, NPD and T, parental ditype, nonparental ditype and tetratype tetrads, respectively. *AB* and *BC*, two contiguous intervals. The upper number in each cell is the observed value, the lower the expectation. In the case of random spores observations in individual intervals, *i.e.*, *AB* and *BC*, respectively, always fit a Poisson model perfectly thus expectations are identical with observations. In the tetrad case, as an example, maximum likelihood estimates the genetic distance of the *AB* interval to $x = 0.1182$ Morgans or 12 cM. Inserting x in the Poissonian mapping functions gives the expected relative proportions of the three tetrad types PD = 0.7952, NPD = 0.0058 and T = 0.1991. Multiplying with 641 results in the expected absolute frequencies indicated. Expectations in the cells are equal to the products of the corresponding expectations in the margins divided by the grand total. See also MATERIALS AND METHODS.

intermediate size. Before testing the compatibility of the data with the Poisson model in general (assumption: neither of the two types of interference operating) the hypothesis of no chromatid interference is tested.

Testing absence of chromatid interference: In tetrad analyses of three-point crosses defining two small adjacent intervals double tetratypes reflect to a good approximation double exchanges, one in each interval. Depending on the tetrad constitution with respect to the outer markers they can be further subdivided into 2-, 4- and 3-strand double events. These are expected in the absence of chromatid interference in a 1:1:2 ratio. Table 3 shows that at the 5% level no significant deviations from expectation are seen, neither individually nor summed. Thus, by this test the hypothesis of no chromatid interference cannot be rejected.

Testing absence of any interference: First, the Poisson model is *assumed* to be true. Next, expected frequencies according to the model are obtained. More specifically, in the case of three-point crosses analyzed by random spores the counts of parental and recombinant progeny in individual intervals always fit a Poisson model perfectly. The expected frequencies of the four classes (P/P), (P/R), (R/P) and (R/R) are equal to the products of the corresponding row and column totals divided by the grand total (Figure 1). In the case of two-point crosses analyzed by tetrads the expected frequencies of PD, NPD and T are obtained by determining the genetic distance with the maximum likelihood procedure, inserting this value in the mapping functions for the

TABLE 4

Test of no interference: random spores

Cross	Trio *ABC*	Genomic region[a]	Observed and expected frequencies of random spore types. Constitution with respect to *AB* (top) and *BC* (bottom)						P^c	Coefficient of coincidence with standard error		Genetic distance in cM[d]	
			O/E[b]	P P	P R	R P	R R	Sum		C	SE	*AB*	*BC*
XB1076	*ura2-leu2-lys7*	*ade2*	*O*	154	19	8	1	182	0.99	1.01	0.93	5	12
			E	154.0	19.0	8.0	1.0						
X972-1	*ura2-leu2-lys7*	*ade2*	*O*	172	15	4	0	191	0.46	0.00	0.00	2	9
			E	172.3	14.7	3.7	0.3						
X972-2	*leu2-lys7-ade2*	*ade2*	*O*	153	23	13	2	191	0.97	1.02	0.64	9	15
			E	153.0	23.0	13.0	2.0						
XC4-1	*his1-leu2-lys7*	*ade2*	*O*	223	30	33	1	287	0.09	0.27	0.26	14	12
			E	225.7	27.3	30.3	3.7						
XC4-2	*leu2-lys7-ade2*	*ade2*	*O*	227	29	27	4	287	0.81	1.12	0.49	12	13
			E	226.6	29.4	27.4	3.6						
XB1045	*lys3-ura1-pro1*	*IL*	*O*	401	108	77	28	614	0.24	1.20	0.18	21	29
			E	396.3	112.7	81.7	23.3						
XB1075	*ade6-tps14-arg1*	*IIIR*	*O*	180	43	58	13	294	0.85	0.96	0.21	33	24
			E	180.5	42.5	57.5	13.5						

See also MATERIALS AND METHODS. P and R, parental and recombinant constitution, respectively.
[a] L(eft) and R(ight) arms of chromosomes *I*, *II* and *III*, respectively. *ade2* is on *IR*.
[b] *O*, observed; *E*, expected.
[c] Probability of obtaining the observed outcome or others with equal or lower probability under the hypothesis tested. Based on simulation.
[d] Based on the Poisson model (HALDANE 1919). Distance in cM $= -50 \ln(1 - 2[R/(P + R)]$.

three tetrad types and multiplying these expected relative frequencies with sample size. Here, in contrast to random spores, observations and expectations will in general be different. In a three-point situation the procedure just described applies to the two individual subintervals. The expected frequencies in the nine cells finally are based on the products of expectations, not observations, of PD, NPD and T in the two subintervals (Figure 1; see also MATERIALS AND METHODS). Both three-point data sets (random spores and tetrads) are treated in an analogous way. They are tested for compatibility with the Poisson model in general. In other words, in the case of tetrads it is not a specific test of no chiasma interference. In Tables 4, 5 and 6 observations along with expected frequencies are given. This allows a preliminary assessment of the direction and magnitude of the deviations between both.

Three-point data, random spores: The random spore results are given in Table 4 and one example, XB1045, in Figure 1. Since some of the expected frequencies are quite small the test of independence has been based on simulation. Nevertheless, other ways of testing give similar results. The G test and the χ^2 test of independence (without any corrections) have been applied to data XC4-1, XB1045 and XB1075. The corresponding probabilities are (G test stated first): XC4-1: 0.07, 0.12; XB1045: 0.23, 0.22; and XB1075: 0.86, 0.86. In no case is there reason to reject the null hypothesis. The direction of the departure from expectation is readily seen by inspection of the double-recombinant class. This direction is also expressed by the coefficient of coincidence, C, estimates of which are given in Table 4 together with the standard errors (STEVENS 1936). Reaching conclusions concerning interference based on C alone might not always be satisfactory. First, as seen in X972-1, double recombinants might not have been observed resulting in $C = 0$ and SE $= 0$. Second, XC4-1 passes the test of independence yet unity is not included within $C \pm 2$ SE. Thus C might not be normally distributed and to my knowledge a general procedure to obtain confidence limits for C has not been published. As can be seen from Table 4, $C < 1$ in three cases and $C > 1$ in four.

Three-point data, tetrads: The data are presented in Table 5 and one example, X1014-1, in Figure 1. Both observations and expectations for the individual intervals can be obtained from this table as sums of the appropriate cell frequencies. It had been decided at the outset not to amalgamate cells because this entails loss of information. Since the individual intervals involved are rather small at most few counts were made in NPD-containing cells and none in (NPD/NPD) cells. Testing by simulation was thus indispensable. The procedure tests at the same time fit to the Poisson model both within and across intervals. Of the 14 trios analyzed all pass the significance test at the 5% level except X1014-2 ($P = 0.04$). Thus there is no reason to reject the hypothesis of no interference. In keeping the policy of not aggregating cells it is simply not possible to obtain *one* coefficient as C in the random spore situation characterizing the entire pattern. By way of expedient the (T/T) class is inspected. In five trios observa-

TABLE 5

Test of no interference: tetrads, two adjacent intervals

Cross	Trio *ABC*	Genomic region[a]	*O*/E[b]	Observed and expected frequencies of tetrad types. Constitution with respect to *AB* (top) and *BC* (bottom) PD PD	PD NPD	PD T	NPD PD	NPD NPD	NPD T	T PD	T NPD	T T	Sum	P[c]	Genetic distance in cM[d] *AB*	*BC*
X1014-1	*his1-leu2-lys7*	*ade2*	*O*	422	1	87	4	0	0	105	0	22	641	0.74	12	10
			E	423.3	2.0	84.4	3.1	0.0	0.6	106.0	0.5	21.1				
X1014-2	*leu2-lys7-ade2*	*ade2*	*O*	405	4	122	1	0	0	89	4	16	641	0.04	10	14
			E	408.7	4.0	119.7	1.9	0.0	0.6	81.5	0.8	23.9				
XC8-1	*sup3-ura2-lys7*	*ade2*	*O*	55	0	17	0	0	0	20	0	10	102	0.29	18	15
			E	54.3	0.7	18.0	0.9	0.0	0.3	20.7	0.3	6.9				
XC8-2	*ura2-lys7-ade2*	*ade2*	*O*	56	1	18	0	0	0	17	0	10	102	0.56	15	17
			E	54.4	0.9	20.6	0.7	0.0	0.3	18.1	0.3	6.8				
JK5	*leu1-his7-mat*	*mat*	*O*	49	1	7	0	0	0	8	0	2	67	0.39	8	9
			E	48.0	0.2	9.0	0.2	0.0	0.0	8.1	0.0	1.5				
JK6	*leu1-mat-his5*	*mat*	*O*	41	0	20	0	0	2	12	0	4	79	0.05	14	20
			E	40.9	0.9	18.0	0.4	0.0	0.2	12.7	0.3	5.6				
JK9-1	*leu1-mat-his5*	*mat*	*O*	59	0	21	0	0	0	7	1	8	96	0.07	9	20
			E	55.5	1.1	23.7	0.2	0.0	0.1	10.6	0.2	4.5				
JK9-2	*mat-his5-mut3*	*mat*	*O*	54	0	12	1	0	0	25	0	4	96	0.90	20	9
			E	55.5	0.2	10.6	1.1	0.0	0.2	23.7	0.1	4.5				
JK12-1	*leu1-mat-his5*	*mat*	*O*	40	2	18	1	0	0	14	0	10	85	0.79	18	24
			E	38.6	1.1	20.3	0.7	0.0	0.4	15.4	0.5	8.1				
JK12-2	*mat-his5-glu2*	*mat*	*O*	32	2	21	1	0	1	12	1	15	85	0.93	24	35
			E	28.9	1.9	23.8	0.9	0.1	0.7	15.2	1.0	12.5				
XB1050-1	*leu1-his7-mat*	*mat*	*O*	166	1	17	0	0	0	33	0	1	218	0.21	8	5
			E	167.9	0.2	16.5	0.6	0.0	0.1	29.7	0.0	2.9				
XB1050-2	*his7-mat-his5*	*mat*	*O*	147	2	50	1	0	0	9	0	9	218	0.11	5	17
			E	143.1	2.2	53.0	0.2	0.0	0.1	14.1	0.2	5.2				
XC1-1	*leu1-mat-cdc18*	*mat*	*O*	272	4	73	1	0	0	51	0	23	424	0.35	10	14
			E	266.7	2.7	80.2	1.3	0.0	0.4	55.3	0.6	16.6				
XC1-2	*mat-cdc18-his5*	*mat*	*O*	305	0	19	4	0	0	91	0	5	424	0.90	14	3
			E	305.2	0.1	18.0	3.1	0.0	0.2	91.8	0.0	5.4				

See also MATERIALS AND METHODS.
[a,b,c] See Table 4. *mat* is on *IIR*.
[d] Maximum likelihood estimates assuming no interference (HALDANE 1931, SNOW 1979).

tion is smaller than expectation, in nine the departures are in the opposite direction. If anything, this trend points in the direction of negative rather than positive interference across intervals.

In addition to adjacent intervals all pairs of non-adjacent intervals in four-point crosses were tested in the same way (data not shown). In all cases was $P > 0.05$.

Two-point data, tetrads: The data analyzed in the previous sections do not all come from different parts of the *S. pombe* genome. In fact there are two "hot spots" of analysis: mating-type region on the right arm of chromosome *II* and the *ade2* region on the right arm of chromosome *I*. Partly this is because mating-type is segregating in all ordinary crosses and both regions happen to contain rather closely linked easy-to-score markers. To have a look at some other regions six two-point data sets were reevaluated. These were taken from KOHLI *et al.* (1977) and had to satisfy the following conditions: (1) location in a region not yet tested, (2) sample size intermediate to large, and (3) genetic length of the interval below 50 cM. The evaluation is given in Table 6. None of the *P* values is below 5% indicating compatibility with the Poisson model. In data KG5 the *G* test might not strictly be applicable due to low expected frequency of NPDs. Nevertheless, the small deviations of observed from expected values suggests that these deviations are indeed not significant. Concerning deviations of observations from expectations, PD and NPD go in the same direction and T in the opposite. It thus suffices to analyze the tetratypes for trend. In three cases is observation smaller than expectation and in three cases the converse holds.

In summary then, the testing of the Poisson model indicates that neither chromatid interference nor chiasma interference can be operating alone but that either both are absent or then present but "cancelling" each other in a specific way. Since chromatid interference is

TABLE 6

Test of no interference: tetrads, one interval

Cross	Gene pair *AB*	Genomic region[a]	Observed and expected frequencies of tetrad types					P^c	Genetic distance in cM[d]
			O/E[b]	PD	NPD	T	Sum		
KG1	*ura3-lys2*	*IL*	*O*	124	16	148	288	0.99	49
			E	124.0	16.1	147.9			
KG2	*his3-tps13*	*IIL*	*O*	54	6	59	119	1.00	45
			E	54.0	6.0	59.01			
KG3	*ade1-his4*	*IIR*	*O*	239	27	232	498	0.33	42
			E	235.9	22.9	239.2			
KG4	*ade8-arg4*	*IIR*	*O*	104	5	76	185	0.81	31
			E	104.4	5.5	75.1			
KG5	*ade10-fur1*	*IIIL*	*O*	101	1	40	142	0.56	18
			E	101.6	1.6	38.8			
KG6	*fur1-ade6*	*IIILR*	*O*	280	9	114	403	0.16	20
			E	277.1	5.7	120.2			

See also MATERIALS AND METHODS.
[a,b] See Table 4.
[c] See Table 4. Based on χ^2 approximation (G test with one degree of freedom).
[d] See Table 5.

absent the first alternative is very much preferred over the second.

DISCUSSION

In the present analysis five crosses have been analyzed at the random spore level and eight at the tetrad level. In crosses involving more than three linked markers overlapping groups of three were studied separately. This gives seven trios with random spores and 14 with tetrads. Needless to say that not all regions of the genome have been looked at. In fact nine trios come from the *ade2* region and ten from the mating-type region. Data of crosses of the same region could have been pooled in some cases. Since this is always possible but not the reverse the detailed presentation is preferred. In addition, six sets of two-point data from nonoverlapping regions other than *ade2* and *mat* have been evaluated.

Neither chiasma nor chromatid interference is seen when the results are analyzed by the methods indicated. Compatibility with the Poisson model was tested in 27 data sets. Twenty-six passed the test and one failed at the 5% significance level. We have agreed to share data with T. P. SPEED, Berkeley. He and his associates will evaluate unpublished *S. pombe* data and reevaluate some of the present data with recently developed statistical methods more general than the procedures applied here. More specifically, this analysis will not suffer from the limitation of using only small intervals and three markers at a time. It will be interesting to see if and in the positive case to what extent the conclusions drawn here have to be revised.

Chiasmata are an important means of ensuring proper segregation of homologous chromosomes during the first meiotic division (HAWLEY 1988). Accepting the one-to-one correspondence between exchanges and chiasmata the fraction of bivalents without chiasma and thus without exchange must be small. If an organism has genetically small chromosomes due to correspondingly small mean numbers of exchanges per bivalent the zero term of the Poisson distribution might be intolerably large. Thus, countermeasures have to come into play to reduce the zero class. *S. pombe* on the other hand seems to be a representative of the other of two extreme cases discussed by CARPENTER (1988): The mean number of exchanges per bivalent is high enough for all chromosomes to keep the proportion of bivalents without event low, even with a Poisson distribution. The genetic lengths of chromosomes *I*, *II* and *III* are 940 centimorgans (cM), 740 cM and 540 cM, respectively (graphically from MUNZ *et al.* 1989). Thus, the mean numbers of exchanges per bivalent and meiosis are 19, 15 and 11 (length in cM divided by 50). This gives corresponding Poisson null terms of 6×10^{-9}, 3×10^{-7} and 2×10^{-5}. Evidence suggesting that fission yeast is following the chiasmate mode of ensuring segregation fidelity comes from the observation that crosses homozygous for certain *rec*$^-$ mutations show high spore lethality (PONTICELLI and SMITH 1989).

In addition to the lack of interference there is no tripartite synaptonemal complex (SC) in *S. pombe* (OLSON *et al.* 1978; HIRATA and TANAKA 1982; BÄHLER *et al.* 1993). An organism showing a parallel behavior is *Aspergillus nidulans*: there is no interference (STRICKLAND 1958), no SC (EGEL-MITANI *et al.* 1982) and high mean numbers of exchanges per bivalent (CLUTTERBUCK 1992). This contrasts with other organisms which have genetically smaller chromosomes, assemble tripartite SC and show chiasma interference [*e.g.*, *S. cerevisiae*: BYERS and GOETSCH (1975) and MORTIMER *et al.* (1989); *Neurospora crassa*: PERKINS (1962) and GILLIES (1979); *Sordaria macrospora*: ZICKLER *et al.* (1992)]. Thus, the hypothesis that the SC is responsible (besides other functions) for chiasma interference can be maintained (EGEL 1978; KING and MORTIMER 1990).

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