

CENTROMERIC EFFECT ON THE DEGREE OF NONRANDOM DISJUNCTION IN THE FEMALE *DROSOPHILA MELANOGASTER*¹

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ABSTRACT

From crosses of females possessing a heteromorphic X-chromosome bivalent, *FR1/+*, the shorter crossover products were recovered on the average more frequently than the longer reciprocals as predicted by NOVITSKI's (1951) hypothesis of nonrandom disjunction (NRD). The present study stemmed from an unexpected result of these crosses. Evidence for a centromeric effect on NRD was obtained, suggested by a negative correlation between the degree of NRD, *c*, and the distance between the region of exchange and the centromere as inferred from SET's (single exchange tetrads). Studies on sex chromosome systems other than *FR1* confirmed these results. An analogous centromeric effect on preferential segregation had been clearly demonstrated in maize (KIKUDOME 1958, 1959; RHOADES and DEMPSEY 1966). However, prior to the present investigation, no such effect of the centromere on NRD in *Drosophila* had been described, although reanalysis of part of the data of NOVITSKI (1951) and NOVITSKI and SANDLER (1956) suggests some evidence of a seriation of increasing *c* values extending from the most distal region of the chromosome toward the centromere. A suggestion that the effect in *Drosophila* may be related in some way to the time required for chiasma terminalization, *i.e.*, those terminalizing earlier (distally located crossovers) permitting more random disjunction of the chromatids from the asymmetric dyad and those terminalizing later, progressively less random, is considered and rejected since in general the expected pattern of *c* values for the various double exchange tetrads (DET's) is inconsistent with that prediction and provides evidence suggesting the possibility of reversals, in part, of *c* values obtained for SET's.

NOVITSKI (1951) demonstrated that, from *Drosophila* females carrying nonhomologous X chromosomes differing in length, the shorter of the two is recovered about twice as frequently as the longer. This phenomenon, termed nonrandom disjunction (to be referred to as NRD), is postulated to depend upon the occurrence of an exchange between the homologues resulting in the formation of asymmetric dyads composed of two structurally dissimilar chromatids, and the nonrandom inclusion of the shorter chromatid into the functional egg. Thus, given that the conditions necessary for NRD are fulfilled, (1) a greater relative recovery of the shorter crossover product *versus* the longer is expected and (2) for different crossover regions of the same homologous pair of chromo-

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somes the same or very similar degrees of nonrandomness will be found since all exchange dyads possess the same degree of asymmetry. In the present paper, results are reported from experiments in *Drosophila* which are consistent with prediction (1) but at variance with prediction (2), resembling an effect found in corn (KIKUDOME 1958, 1959; RHOADES and DEMPSEY 1966).

Genetic analysis of meiotic crossovers

In the present paper, the term c is defined as the probability of recovering the shorter element of an asymmetric dyad (or the shorter chromosome of a heteromorphic bivalent) in the functional egg at Division II of meiosis, given a particular kind of exchange tetrad at Division I. The value of c of a symmetric dyad is expected to be 0.50, whereas that of an asymmetric dyad is expected to be greater than 0.50. If CO = crossovers, ET = exchange tetrads, S = shorter element and L = longer element, then c is estimated from raw data for any given kind (for example, x) of exchange tetrad (*i.e.* x ET) from the following formulation:

$$c = \frac{\text{Net } x\text{CO-S coming from } x\text{ET}}{(\text{Net } x\text{CO-S} + \text{Net } x\text{CO-L}) \text{ coming from } x\text{ET}}$$

where x ET can represent either no exchange tetrads (NET), single exchange tetrads (SET), or double exchange tetrads (DET).

It is assumed that the c values of both dyads from a heteromorphic bivalent are equal, *i.e.*, $c_1 = c_2$. In addition, it is assumed that the two kinds of three-strand double exchanges occur with equal frequency. With these assumptions, it can be seen that from single exchange tetrads (SET's), the absolute and relative recoveries of NCO-S:NCO-L and of SCO-S:SCO-L are equal (Figure 1). Thus, given

Types of single exchange	Dyads present before SE	Dyads produced after SE and expected c and $1-c$ values for each dyad	Consequences of SE on the recovery of chromatids under assumption that $c_1 = c_2$
SE-I		c_{I1} $\frac{\text{NCO-S}}{\text{SCO-IL}}$ $1-c_{I1}$	NCO-S: NCO-L = SCO-IS: SCO-IL = c_I : $1-c_I$
		c_{I2} $\frac{\text{SCO-IS}}{\text{NCO-L}}$ $1-c_{I2}$	
SE-II		c_{II1} $\frac{\text{NCO-S}}{\text{SCO-IIL}}$ $1-c_{II1}$	NCO-S: NCO-L = SCO-IIS: SCO-IIL = c_{II} : $1-c_{II}$
		c_{II2} $\frac{\text{SCO-IIS}}{\text{NCO-L}}$ $1-c_{II2}$	

FIGURE 1.—Consequences of single exchanges on the recovery of different kinds of crossover products under the assumption of $c_1 = c_2$ for each region.

that the number of SCO-S recovered from SET's of a particular region is known (e.g., n), it can be inferred that n number of NCO-S have also been produced. Similarly, the absolute and relative recoveries of NCO-S:NCO-L, of SCO-IS:SCO-IL, and of SCO-IIS:SCO-IIL coming from double-exchange tetrads (DET's) are all equal to those of DCO-S:DCO-L (Figure 2). Thus, given that the number of DCO-S recovered is known (e.g., n), we can infer (under the conventional assumptions for a tetrad analysis) that n number of NCO-S, n number of SCO-IS, and n number of SCO-IIS have also been produced. From this, it is possible to calculate any net crossovers in any region (x CO's) coming from any exchange tetrads in that region (x ET's). The reasoning behind the method of calculation of NCO's, SCO's, and DCO's coming from triple-exchange tetrads (TET's) is

Types of double exchange & expected frequency of occurrence	Dyads present before DE	Dyads produced after DE and expected c and $1-c$ values for each dyad	Consequences of DE on the recovery of chromatids under assumption that $c_1 = c_2$ ($c_1' = c_2'$)
Region: I II DE _{I, II} -2S (.25)		0.5 NCO-S	NCO-S: NCO-L = DCO-L: DCO-S = DCO-S: DCO-L = .5 : .5
		0.5 DCO-S	
		0.5 DCO-L	
		0.5 NCO-L	
Region: I II a. DE _{I, II} -3S (.50)		c_1 DCO-S	DCO-S: DCO-L = NCO-S: NCO-L = SCO-IS: SCO-IL = SCO-IIS: SCO-IIL = c : $1-c$
		$1-c_1$ SCO-IL	
		c_2 SCO-IIS	
		$1-c_2$ NCO-L	
		c_1' NCO-S	
		$1-c_1'$ SCO-IIL	
		c_2' SCO-IS	
		$1-c_2'$ DCO-L	
Region: I II b. DE _{I, II} -3S (.50)		c_1' NCO-S	SCO-IS: SCO-IL = SCO-IIL: SCO-IIS = SCO-IIS: SCO-IIL = .5 : .5
		$1-c_1'$ SCO-IIL	
		c_2' SCO-IS	
		$1-c_2'$ DCO-L	
Region: I II DE _{I, II} -4S (.25)		.5 SCO-IIL	SCO-IS: SCO-IL = SCO-IIL: SCO-IIS = SCO-IIS: SCO-IIL = .5 : .5
		.5 SCO-IL	
		.5 SCO-IS	
		.5 SCO-IIS	
Summary of consequences of DE's of all kinds under assumption:		1. DCO-S: DCO-L = $[(.25)(.5) + (.5)(c)] : [(.25)(.5) + (.5)(1-c)]$. 2. SCO-IS: SCO-IL = $[(.5)(c) + (.25)(.5)] : [(.5)(1-c) + (.25)(.5)]$. 3. SCO-IIS: SCO-IIL = $[(.5)(c) + (.25)(.5)] : [(.5)(1-c) + (.25)(.5)]$. 4. NCO-S: NCO-L = $[(.25)(.5) + (.5)(c)] : [(.25)(.5) + (.5)(1-c)]$.	

FIGURE 2.—Consequences of double exchanges on the recovery of different kinds of crossover products under the assumption that $c_1 = c_2$ for each region.

similar to that for single and double exchanges, but are not presented here because of the relative rarity of triple exchange events.

MATERIALS AND METHODS

The following types of *X* chromosomes were employed in the present study: (1) Fragment 1 (*FR1*), *Y^SX*, consisting of a normally arranged *X* chromosome having the short arm of the *Y* chromosome appended distally. In combination with a normal *X* chromosome, single exchanges and certain types of double exchanges generate asymmetric dyads. (2) *X* chromosomes carrying *Dp(1;1)sc^{V1}*, a γ^+ -bearing duplication marking the right arm of the *X* chromosome and permitting detection of crossovers between proximal euchromatic markers and the centromere; (3) *Y^SX:Y^L*, a normally arranged *X* chromosome to which the short arm of the *Y* chromosome is appended distally and the long arm proximally; (4) *In(1)sc^{S1Lsc^{SR}} + dl-49, sc^{S1} sc^S (Insc)* and *In(1)dl-49 + B^{M1}*, both of which are *X*-chromosome balancers; (5) *In(1)sc^S*, a long inversion transposing distally some 80% or so of the proximal heterochromatin including *bb⁺*; and (6) *In(1)sc^{Lsc^{SR}}*, an *X* chromosome which carries the distal end of *In(1)sc^L* and the proximal end of *In(1)sc^S* and is deficient for *bb⁺* and a considerable portion of basal heterochromatin. In females heterozygous for *In(1)sc^S* and *In(1)sc^{Lsc^{SR}}*, single exchanges and certain types of double exchanges produce asymmetric dyads. Detailed descriptions of all chromosomes employed as well as mutant markers used may be found in LINDSLEY and GRELL (1968).

RESULTS AND ANALYSIS

Experiment 1. Heterozygous *Y^S y cv v f / + + + +* females were crossed to OR-R males. From Table 1 it may be seen that, as expected, *c* values for the crossover regions are greater than 0.5. However, a surprising finding is that for different regions of the chromosome, different *c* values were obtained. Based on 16,160 males scored, SET *c* values for Regions 1, 2, and 3 (distal to proximal) were 0.5685, 0.6365, and 0.6894, respectively. A variance test of the null hypothesis

TABLE 1

Recovery of progeny from matings of Y^S y cv v f / + + + + females with Oregon-R males

Crossover classes	Male phenotypes	No. of male progeny	Net rCO's from rET's	<i>c</i> values
NCO	+ + + +	7286	4310	0.6203
	γ cv v f	4194	2638	
SCO-1	+ cv v f	296	274	0.5685
	γ + + +	223	208	
SCO-2	+ + v f	1076	1049	0.6365
	γ cv + +	611	599	
SCO-3	+ + + f	1652	1605	0.6894
	γ cv v +	748	723	
DCO-1,2	+ cv + +	1	1	
	γ + v f	1	1	
DCO-1, 3	+ cv v +	21	21	
	γ + + f	14	14	
DCO-2, 3	+ + v +	26	26	
	γ cv + f	11	11	

Crossover regions are 1 (γ -cv), 2 (cv-v), 3 (v-f). (The number of DCO's is too small for meaningful analysis).

of homogeneity between different crossover classes gave a chi-square value of 36.32 with three degrees of freedom, the probability of which is less than 0.001 (SNEDECOR and COCHRAN 1967). A linear regression of c on D gives a sample regression equation of $Y = -0.0031X + 0.7604$, where D is arbitrarily defined as the distance between the midpoint of the region of exchange and the centromere, measured in map units. A correlation coefficient of -0.9891 with one degree of freedom gives a P values of between 0.5 and 0.10. The higher than expected value of 0.5 for c for NCO's is likely attributable, in large measure, to a

TABLE 2

Genetic analysis of data from a cross of $Y^S y cv car y^+ / y^2 sc v f$ females to $y^2 sc f$ males

Crossover classes	Male phenotypes	No. of male progeny	Net xCO's coming from xET's	c values
NCO	scute	2957	862	0.8796
	non-scute	1402	118	
SCO-1	scute	338	198	0.5577
	non-scute	239	157	
SCO-2	scute	934	684	0.6042
	non-scute	560	448	
SCO-3	scute	914	633	0.6299
	non-scute	526	372	
SCO-4	scute	171	100	0.6452
	non-scute	113	55	
SCO-5	scute	138	92	0.7132
	non-scute	71	37	
DCO-1, 2	scute	15	13	0.8667
	non-scute	8	2	
DCO-1, 3	scute	87	86	0.6418
	non-scute	51	48	
DCO-1, 4	scute	30	29	0.6304
	non-scute	18	17	
DCO-1, 5	scute	11	9	0.6000
	non-scute	14	6	
DCO-2, 3	scute	181*	174	0.7016
	non-scute	75	74	
DCO-2, 4	scute	37	32	0.5818
	non-scute	23	23	
DCO-2, 5	scute	28	20	0.7692
	non-scute	13	6	
DCO-3, 4	scute	8	4	0.2000
	non-scute	17	16	
DCO-3, 5	scute	13	9	.04286
	non-scute	15	12	
DCO-4, 5	scute	0	0	0.0000
	non-scute	1	1	

Regions are: 1 ($y-cv$), 2 ($cv-v$), 3 ($v-f$), 4 ($f-car$), 5 ($car-y^+$). Triple crossovers, although included in the analysis, are not listed.

* Includes at least some exceptional males which result from the fertilization of nullo-X eggs (due to primary nondisjunction in the parental female) by $y^2 sc f$ sperm.

combination of undetected crossovers in the *f*-centromere region, and to a higher *c* value in the *f*-centromere region, evidence for which is presented below.

Experiment 2. In order to analyze the region to the right of *f*, *car* and *Dp(1)sc^{v1}*, γ^+ were used. Females of the composition $\gamma cv car \cdot \gamma^+ / \gamma^2 sc v f$ were mated with $\gamma^2 sc f$ males. The data and analysis of this mating are shown in Table 2. Based on 9030 males scored, SET *c* values for Regions 1, 2, 3, 4, and 5 were 0.5577, 0.6042, 0.6299, 0.6452, and 0.7132, respectively. A variance test of the null hypothesis of homogeneity between different crossover classes gave a chi-square value of 34.06, which is significant at the 0.001 level with five degrees of freedom. A linear regression of the net *c* on *D* yielded a sample regression equation of $Y = -0.0022X + 0.6869$. The correlation coefficient is -0.9243 , which with three degrees of freedom, is significant at the 0.05 level. Lastly, *c* values of the present experiment correlate with those of Experiment 1 with an *r* value of 0.9957, which has a *P* value of slightly greater than 0.05. In this experiment, the *c* value of 0.67 for NCO's is probably the result of reduced viability of the *Dp*-bearing *FR1* chromosome, since a shift of the duplication to the non-*FR1* homologue generates a *c* value of 0.35 as observed in Experiment 4.

Experiment 3. In order to determine the effect of the presence of an arm of the *Y* chromosome proximal to the centromere, in addition to the one attached distally, females of the composition $Y^S \gamma w^a cv v f Y^L / + + + + +$ were mated with OR-R males. Results of this experiment are shown in Table 3. Based on

TABLE 3

Genetic analysis of data from a cross of $Y^S \gamma w^a cv v f Y^L / + + + + +$ females to OR-R males

Crossover classes	Male phenotypes	No. of male progeny	Net xCO's coming from xET's	<i>c</i> values
NCO	non- γ	2499	725	>1.0000
	γ	1087	-43	
SCO-0	non- γ	18	6	0.5000
	γ	16	6	
SCO-1	non- γ	382	275	0.5218
	γ	324	252	
SCO-2	non- γ	857	738	0.6150
	γ	545	462	
SCO-3	non- γ	733	542	0.6758
	γ	395	260	
DCO-0, 2	non- γ	7	7	0.7000
	γ	3	3	
DCO-0, 3	non- γ	4	3	0.3000
	γ	7	7	
DCO-1, 2	non- γ	16	16	0.5714
	γ	12	12	
DCO-1, 3	non- γ	90	89	0.5973
	γ	60	60	
DCO-2, 3	non- γ	96	96	0.5854
	γ	68	68	

Regions are: 0 (γw^a), 1 ($w^a cv$), 2 ($cv v$), 3 ($v f$). A triple crossover, 0,1,3 has been included in the analysis.

7220 males scored, SET c values for Regions 0, 1, 2, and 3 were 0.5000, 0.5218, 0.6150, and 0.6758, respectively. A variance test of the null hypothesis of homogeneity between different crossover classes gave a chi-square value of 82.54, which is significant at the 0.001 level with four degrees of freedom. A linear regression of c on D gave a sample regression equation of $Y = -0.0041X + 0.7723$. The r value of -0.9870 is significant at the 0.02 level. It is of interest to note that the extreme value of c for NCO's found in this experiment is similar to that reported by NOVITSKI and SANDLER (1956, Table 7 of that paper; also see Table 6a of the present article). However, based on our findings from experiments determining relative fitness values (W) of the $Y^S X \cdot Y^L$ chromosome compared with its homologue, that the two stand in the ratio of 0.758:1.000, and

TABLE 4

Genetic analysis of data from a cross of $Y^S y \vee f \cdot Y^L / y^2 sc cv car \cdot y^+$ females to OR-R males

Crossover classes	Male phenotypes	No. of male progeny	Net xCO's coming from xET's	c values
NCO	scute	478	68	0.3579
	non-scute	348	122	
SCO-1	scute	85	39	0.5735
	non-scute	52	29	
SCO-2	scute	186	134	0.6979
	non-scute	123	58	
SCO-3	scute	167	98	0.7153
	non-scute	98	39	
SCO-4	scute	41	22	0.7333
	non-scute	31	8	
SCO-5	scute	35	16	1.0000
	non-scute	18	0	
DCO-1, 2	scute	4	2	1.0000
	non-scute	1	0	
DCO-1, 3	scute	33	32	0.6809
	non-scute	16	15	
DCO-1, 4	scute	3	3	0.6000
	non-scute	3	2	
DCO-1, 5	scute	8	7	0.7000
	non-scute	5	3	
DCO-2, 3	scute	30	28	0.4375
	non-scute	37	36	
DCO-2, 4	scute	10	10	0.4348
	non-scute	15	13	
DCO-2, 5	scute	11	9	0.4286
	non-scute	15	12	
DCO-3, 4	scute	6	6	0.5455
	non-scute	6	5	
DCO-3, 5	scute	2	1	1.0000
	non-scute	3	0	
DCO-4, 5	scute	0	0	—
	non-scute	1	0	

Regions are: 1 ($y-cv$), 2 ($cv-v$), 3 ($v-f$), 4 ($f-car$), 5 ($car-y^+$). TCO's, although included in the analysis, are not listed here.

further, on the assumption of a frequency of 9% crossing over in the *f*-centromere region (entirely reasonable), the deviation from a *c* value of 0.5 for NCO's is not significant.

Experiment 4. A small-scale experiment to determine *c* values to the right of *f* was carried out by mating females of the composition $Y^s \gamma v f \cdot Y^L/\gamma^2 sc cv car \cdot \gamma^+$ with OR-R males. The results are shown in Table 4. A total of 1880 males were scored which yielded SET *c* values of 0.5735, 0.6979, 0.7333, and 1.000 for Regions 1, 2, 3, 4, and 5, respectively. The trend is consistent with a proximal increase in *c* values, including the *f*-centromere region, although the data (likely due to the relatively small sample size) do not statistically rule out the null hypothesis of homogeneity between different crossover classes (chi-square = 3.83, df = 5, *P* is greater than 0.50). From a linear regression of *c* on *D*, an *r* value of -0.8068 is obtained; the corresponding probability is between 0.05 and 0.10.

Experiment 5. In his original paper on nonrandom disjunction, NOVITSKI (1959) employed heterozygous sc^4sc^8/sc^8 females to test for NRD in free rod-X females. That experiment was repeated by the present authors using females of the composition $\gamma sc^4sc^8/sc^8, f m cv w^a$. The raw data from this experiment and analysis thereof are shown in Table 5. Males scored totalled 6324, and gave SET *c* values of 0.5889, 0.6322, 0.6731 and 0.8405 for Regions 1, 2, 3 and 4, respectively.

TABLE 5

Genetic analysis of data from a cross of $\gamma sc^4-sc^8/w^a cv m f sc^8$ females to γ males

Crossover classes	Male phenotypes	No. of male progeny	Net xCO's coming from xET's	<i>c</i> values
NCO	γ	1998	419	0.6486
	non- γ	1113	227	
SCO-1	γ	325	202	0.5889
	non- γ	226	141	
SCO-2	γ	617	507	0.6322
	non- γ	383	295	
SCO-3	γ	652	527	0.6731
	non- γ	351	256	
SCO-4	γ	191	137	0.8405
	non- γ	94	26	
DCO-1, 2	γ	27	27	0.8438
	non- γ	5	5	
DCO-1, 3	γ	71	71	0.5820
	non- γ	51	51	
DCO-1, 4	γ	25	25	0.4630
	non- γ	29	29	
DCO-2, 3	γ	54	54	0.5510
	non- γ	44	44	
DCO-2, 4	γ	29	29	0.4265
	non- γ	39	39	
DCO-3, 4	γ	0	0	—
	non- γ	0	0	

Regions are: 1 (γ -*f*), 2 (*f*-*m*), 3 (*m*-*cv*), 4 (*cv*-*w*^a).

The variance test of the null hypothesis of homogeneity between crossover classes gave a chi-square value of 9.72, which is significant at the 0.05 level with four degrees of freedom. A linear regression of c on D yielded an r value of -0.9320 with corresponding probability between 0.05 and 0.10. The greater than 0.5 value of c of NCO's would not differ significantly from 0.5 if each mutant marker depresses the viability of the male progeny an average of some 2%.

Briefly, then: (1) c values are not uniform over the entire length of the X chromosome; variance tests of the null hypothesis of homogeneity of c values for different regions of the X chromosome gave P values of <0.001 , <0.001 , <0.001 , >0.50 , and <0.05 in Experiments 1, 2, 3, 4, and 5, respectively (the high probability in Experiment 4 being likely due to the relatively small sample size) and (2) probability values obtained from linear regressions of c on D were quite similar in the five experiments: 0.05–0.10, slightly greater than 0.05, <0.02 , 0.05–0.10, and 0.05–0.10. These probabilities all suggest a negative correlation between the degree of NRD and the distance between the region of exchange and the centromere, although additional experiments will be necessary to determine if the relationship between c and D is indeed linear.

TABLE 6a

Genetic analysis of male progeny recovered from a cross of FR1 y cv v f-YL/car females to y v car males

Crossover class:	No. of male progeny recovered	c values
NCO	1622	0.9627
SCO-1'	859	
	308	0.5947
SCO-1''	201	
	478	0.5619
	350	
SCO-2'	531	0.6055
	328	
SCO-2''	120	0.4902
	97	
DCO-1, 1''	11	0.6111
	7	
DCO-1, 2'	69	0.6635
	35	
DCO-1, 2''	27	0.5510
	22	
DCO-1', 2'	78	0.6290
	46	
DCO-1', 2''	35	0.6250
	21	
DCO-2', 2''	8	0.8000
	2	

Crossover regions are: 1' (γ -cv), 1'' (cv-v), 1 (γ -v), 2' (v-f), 2'' f-car), 2 (v-car). Data are taken from NOVITSKI and SANDLER (1956), Table 7. In all cases, the shorter of the two crossover classes is given before the longer.

DISCUSSION

As suggested above, the phenomenon described in the present paper is well established in corn; however, its occurrence prior to the present work had not been noted in *Drosophila*. To determine if any evidence exists in the literature for an effect of this kind, data in the papers of NOVITSKI and SANDLER (1956) and NOVITSKI (1951) were reanalyzed. Table 6a presents the results of a tetrad analysis of the male progeny data from $Y^s \gamma cv v f Y^L / car$ females (NOVITSKI and SANDLER 1956). Contrary to the findings of the present authors, for the regions $\gamma-cv$, $cv-v$, and $v-f$, no evidence of a seriation is apparent. Table 6b presents results of a tetrad analysis of the female progeny data where crossing over was detectable only in longer regions, *i.e.*, $\gamma-v$ and $v-car$, as well as an analysis of male progeny data where appropriate regions are combined to permit more direct comparison with female progeny data. Under these circumstances a seriation is suggested in both male and female progeny data. Analysis of the data of NOVITSKI (1951) from sc^+sc^s/sc^s females is presented in Table 7. A clear seriation is seen for regions 1-3 in male and female progeny data; only region 4, which also represents the smallest number (22), appears to be out of line. We have no ready explanation for the discrepancies between our results and those of these authors. It is of course possible that "physiological conditions" in the oocyte in some way define the seriation pattern and that conditions in the different experiments were not the same.

The mechanism responsible for this centrometric effect in *Drosophila* is unknown, and although serious speculation concerning its nature is premature, it may be of interest to show the consequences of one line of thought on this problem. Since distally located crossovers coming from SET's gave lower c values than proximal crossovers, the possibility suggested itself that the time required for chiasma to terminalize could be in some way related to this effect, those terminalizing first (or within some given time interval) permitting more random orientation and ultimate disjunction of the chromatids of the asymmetric dyad,

TABLE 6b

Genetic analysis of male and female as well as combined male-female data from the experiment described in Table 6a

Crossover classes	No. of male progeny	c values	No. of female progeny	c values	Combined male-female	Combined c values
NCO	1622	0.9825	1887	0.8769	3509	0.9158
	859		959		1818	
SCO-1	786	0.5747	853	0.5685	1639	0.5716
	551		605		1156	
SCO-2	651	0.5949	735	0.6314	1386	0.6132
	425		433		858	
DCO-1, 2	209	0.6276	264	0.6256	473	0.6265
	124		158		282	

In this case, some regions in the male data presented in Table 6a have been combined so that data from male and female progeny can be directly compared.

TABLE 7

Genetic analysis of male progeny data of NOVITSKI (1951) from females of the composition $y\ sc^4\ car\ m\ w^a\ sc^8/f\ v\ cv\ sc^8$

Crossover classes	Male phenotypes	No. of male progeny	Net xCO's coming from xET's	<i>c</i> values
NCO	<i>y</i>	648	25	0.2747*
	non- <i>y</i>	345	66	
SCO-1	<i>y</i>	156	104	0.6710
	non- <i>y</i>	82	51	
SCO-2'	<i>y</i>	274	231	0.7108
	non- <i>y</i>	118	94	
SCO-[2''+3]	<i>y</i>	235	192	0.7442
	non- <i>y</i>	103	66	
SCO-4	<i>y</i>	44	10	0.4545
	non- <i>y</i>	32	12	
DCO-1, 2'	<i>y</i>	9	9	0.6923
	non- <i>y</i>	4	4	
[DCO-1, 2'']	<i>y</i>	27	27	0.5745
[DCO-1, 3]	non- <i>y</i>	20	20	
DCO-1, 4	<i>y</i>	16	16	0.6957
	non- <i>y</i>	7	7	
[DCO-2', 2'']	<i>y</i>	16	16	0.5714
[DCO-2', 3]	non- <i>y</i>	12	12	
DCO-2', 4	<i>y</i>	18	18	0.6923
	non- <i>y</i>	8	8	
[DCO-2'', 4]	<i>y</i>	0	0	0.0000
[DCO-3, 4]	non- <i>y</i>	5	5	

Some regions are regrouped to be more directly comparable to regions in Experiment 5. The regions are: 1' (*y-car*), 1'' (*car-f*), 1 (*y-f*), 2' (*f-m*), 2'' (*m-v*), 2 (*f-v*), 3 (*v-cv*), 4 (*cv-w^a*). In all cases the shorter of the two crossover classes is given before the longer.

* Net *c* would not be significantly different from expected value of 0.50 if $W (y\ sc^4\ w^a\ m\ car\ sc^8) = 0.96$ and $W (cv\ v\ f\ sc^8) = 1$ are assumed, in which case the corrected numbers of net NCO-S and net NCO-L are 52 and 66, respectively. (*W* stands for relative fitness.)

and those terminalizing later, becoming progressively less random, the shorter chromatid being oriented more often closer to the anaphase pole. If this were the case, it would be anticipated that examination of *c* values of DET's would show that those involving regions 1 and 2 would be lower than those involving 4 and 5. From a total of 89 DET 1,2's in the five experiments carried out by us, the value of *c* turned out to be surprisingly high, 0.7416, resembling the value of *c* of SET's for regions 4 and 5. Conversely, the one DET 4,5 recovered was a crossover-long, and on the basis of 22 DET 3,5's, *c* was 0.4545. Consequently, average *c* values for SET's and DET's for all regions from the five experiments were computed and are presented in Table 8.

Whereas no firm conclusion can be reached on the basis of the DET analysis presented above, the following observations may be useful: (1) *c* values for DET'S involving region 1 in combination with other regions appear to decline, up to a point, the more proximal the second crossover; *c* values for DET's involving regions 1 and 2, 1 and 3, and 1 and 4 are respectively 0.7416, 0.6076, and

TABLE 8

Average c values for SET's and DET's for all regions of the X chromosome from the present five experiments

Regions	SET's <i>c</i>	<i>N</i>	Regions	DET's <i>c</i>	<i>N</i>
1	0.5562	1787	1,2	0.7416	89
2	0.6256	4974	1,3	0.6076	497
3	0.6736	5055	1,4	0.5428	105
4	0.7442	348	1,5	0.6400	25
5	0.7448	145	2,3	0.6168	611
			2,4	0.4765	149
			2,5	0.6170	47
			3,4	0.3225	31
			3,5	0.4545	22
			4,5	0.0000	1

0.5428; this pattern is interrupted for DET 1,5's in that *c* rises to 0.6400, although the numbers in this class are relatively low (25); (2) the *c* value for DET 2,3's, 0.6168,, appears to be firm, involving as it does some 600 cases; (3) with the exception of DET 2,5's where *c* is 0.6170, when one crossover is proximal to region 1 and the other proximal to region 3, *c* values are at or under 0.5000; the average *c* value of these DET's including DET 2,5's is 0.4800 (120/250) and 0.4483 (91/203) excluding DET 4,5's. It would appear, therefore, that DET's do not behave as predicted, suggesting the possibility of reversals, in part, of *c* values inferred from SET's. Whereas the pattern obviously requires further definition, the analysis carried out provides no support for the suggestion regarding chiasma terminalization as the mechanism underlying the centromeric effect. A formal alternative explanation is that chromatid interference occurs, with 3-strand DET's in excess at the distal end and 2-strand DET's at the proximal end.

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