Sex-Related Differences in Crossing Over in *Caenorhabditis elegans*

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ABSTRACT

In the nematode *Caenorhabditis elegans*, hermaphrodite recombination has been characterized and is the basis of the genetic map used in this organism. In this study we have examined male recombination on linkage group I and have found it to be approximately one-third less than that observed in the hermaphrodite. This decrease was interval-dependent and nonuniform. We observed less recombination in the male in 5 out of 6 intervals examined, and no observable difference in one interval on the right end of LG I. Hermaphrodite recombination frequencies are the result of recombination in two germlines; oocyte and hermaphrodite spermatocytes. We have measured recombination in the oocyte and have found it to be approximately twofold lower than that calculated for hermaphrodite spermatocytes and not significantly different from the male spermatocyte frequency. Thus, recombination frequencies appear to be a function of gonad physiology rather than the sex of the germline. Evidence from experiments examining the effect of karyotype on recombination in males sexually transformed by the *her-1* mutation into XO hermaphrodites (normally *XX*), suggests the sexual phenotype rather than genotype determines the recombination frequency characteristic of a particular sex. Hermaphrodite recombination is known to be affected by temperature, maternal age, and the *rec-1* mutation. We have examined the effect of these parameters on recombination in the male and have found male recombination frequency increased with elevated temperatures and in the presence of Rec-1, and decreased with paternal age.

SEXUAL differences in crossing over are known to occur in a number of organisms. There may exist two qualitatively different situations when examining the relationship between sex and recombination frequency. The first is the absence of recombination in one sex, a characteristic of *Drosophila melanogaster* males (MORGAN 1912) and *Bombyx mori* females (TANAKA 1913). The more common situation is one where recombination exists in both sexes, but with a reduced frequency in one (for review, see DUNN and BENNETT 1967). Recombination frequency in the female is generally higher in *Drosophila ananassae* (MORIWAKI 1937), in mice (SLIZYNSKI 1960), and in humans (WHITE *et al.* 1985; DONIS-KELLER *et al.* 1987). Alternatively, male recombination frequency is generally higher in maize (RHOADES 1941; ROBERTSON 1984), and in *Tribolium castaneum* (SOKOLOFF 1964). However, sex-related differences in recombination frequency are not uniform for all regions of the genome. In maize, some intervals have been reported to be longer in the female meiosis (ROBERTSON 1984). In mice, significant sex differences in recombination frequency went in opposite directions on different chromosomes (DAVISSON and RODERICK 1981) and in humans, some regions were the same genetic size in both sexes (DONIS-KELLER *et al.* 1987). This suggests local differences in recombination between the sexes are not representative of the chromosome, nor of the genome as a whole. In this study, we have investigated the effect of sex on recombination in the nematode *Caenorhabditis elegans*. Each of the autosomes in *C. elegans* are marked by a region where genes cluster on the meiotic map as a result of less recombination per base pair than the genome average (BRENNER 1974; GREENWALD *et al.* 1987; KIM and ROSE 1987; PRASAD and BAILLIE 1989; STARR *et al.* 1989). By examining intervals spanning linkage group (LG) I, we have investigated the effect of sex on recombination in intervals inside and outside such a region.

The biology of *C. elegans* provides a unique opportunity to examine the effect of sex on recombination. Laboratory populations consist largely of self-fertilizing hermaphrodites (5AA;*XX*). Males (5AA;XO), arise spontaneously as a result of *X* chromosome nondisjunction (HODGKIN, HORVITZ and BRENNER 1979) and are maintained by cross-fertilization with hermaphrodites. The standard genetic map of *C. elegans* (EDGLEY and RIDDLE 1987) is based on hermaphrodite recombination frequencies that are the product of crossover events in two germlines; oocyte and hermaphrodite spermatocyte. The frequency of recombination in these two germlines has been shown to be different (ROSE and BAILLIE 1979a). We have measured recombination frequencies in the male and hermaphrodite germlines and have found differences in crossover frequencies between oocytes and the two

types of spermatocytes (male and hermaphrodite).

One approach in studying the relationship between sex and recombination frequency is measuring recombination in sexually transformed individuals. Hormone treatments have been used in the Medaka, *Oryzias latipes*, to transform *XY* fish, normally male, into functional females. Crossing over in these transformed males was found to occur at a higher frequency than in normal males (YAMAMOTO 1961). This suggests that differences in recombination between the sexes are not completely the result of the sex chromosome constitution, but also depend on the physiological differences associated with sex. In *C. elegans*, mutations exist which result in the complete transformation of the sexual phenotype. One such mutation, *her-1*, transforms fertile *XO* males into self-fertile hermaphrodites (HODGKIN 1980). We have used this mutation to examine the effect of karyotype on recombination frequency.

Meiotic recombination frequency in higher eukaryotes is affected by several known parameters. Recombination frequency increases at temperature extremes in *D. melanogaster* (PLOUGH 1917, 1921), *Neurospora crassa* (MCNELLY-INGLES, LAMB and FROST 1966) and *Coprinus lagopus* (LU 1969, 1974). A decrease in meiotic recombination frequency with maternal age has been observed in *D. melanogaster* (BRIDGES 1927; NEEL 1941), in *C. elegans* (ROSE and BAILLIE 1979a), and on some chromosomes in the mouse, *Mus musculus* (FISHER 1949; BODMER 1961; REID and PARSONS 1963). Existing human data is not conclusive about maternal age effects although some evidence suggests a paternal age effect may exist (LANGE, PAGE and ELSTON 1975; ELSTON, LANGE and NAMBOODIRI 1976). In *C. elegans*, hermaphrodite recombination frequency increases with temperature and decreases with maternal age (ROSE and BAILLIE 1979a). The presence of the *rec-1* mutation was also found to increase hermaphrodite recombination (ROSE and BAILLIE 1979b; RATTRAY and ROSE 1988). We have now examined the effect of temperature, age, and Rec-1 on recombination in *C. elegans* males.

MATERIALS AND METHODS

General methods: Wild-type and mutant strains were maintained and mated on Petri plates containing nematode growth medium (NGM) and streaked with *Escherichia coli* (BRENNER 1974). All experiments were carried out at 20° unless otherwise noted. The wild-type strain N2 and mutant strains of *C. elegans* var. Bristol used in this study were obtained from D. L. BAILLIE at Simon Fraser University, British Columbia, or from the Caenorhabditis Genetics Center at the University of Missouri, Columbia. The following genetic markers were used:

LG I: *bli-3(e579)*; *unc-11(e47)*; *dpy-5(e61)*; *unc-13(e450)*; *unc-29(e403)*; *unc-75(e950)*; *unc-101(m1)*; *unc-54(e190)*.

LG V: *her-1(e1520)*.

The following translocations were used in this study: *szT1(I;X)* (FODOR and DEAK 1985; MCKIM, HOWELL and ROSE 1988), *hT1(I;V)* (MCKIM, HOWELL and ROSE 1988), *hT2(I;III)* (isolated by K. PETERS), and *hT3(I;X)* (isolated by K. MCKIM).

Recombination mapping: Recombination frequency in the hermaphrodite was measured by scoring the number of recombinant progeny of a *cis*-heterozygote, under the conditions described by ROSE and BAILLIE (1979a). The recombination frequency (p) between two markers was calculated using the formula $p = 1 - (1 - 2R)^{1/2}$ where R is the number of visible recombinant individuals divided by the number of total progeny (BRENNER 1974). The total progeny number of the hermaphrodite is 4/3 × (number of wild types + one recombinant class). Map distances in the male were determined by scoring the progeny resulting from mass mating seven males heterozygous for a pair of *cis*-linked markers to five homozygous hermaphrodites (new hermaphrodites each day) every 24 hr for 4 days. On the 4th day the males were left on plates with the same hermaphrodites for a 5th day, after which the hermaphrodites were transferred. Since mapping in the male involves recombination in only one germline, the recombination frequency (p) is equal to R. The total progeny number of the male is 2 × (number of wild types + one recombinant class). This differs from the total progeny number of the hermaphrodite for the following reasons. In both male and hermaphrodite recombination experiments, the double homozygote class is not scored because of its reduced viability, and the total progeny number is calculated from the wild-type class. Mapping in the hermaphrodite involves crossing two heterozygous germlines, whereas mapping in the male involves crossing one germline heterozygous for a pair of markers to one which is homozygous. For this reason, the ratio of wild-type progeny to progeny homozygous for the markers differs in hermaphrodite and male recombination experiments. Thus, the number of wild-type progeny must be multiplied by 4/3 and 2, respectively, to correct for the inviable class. Both classes of recombinants were used in the calculations unless otherwise noted. In cases where only one class of recombinants was used, $R = 2 \times$ (one recombinant class) divided by the total progeny number. All hermaphrodite recombinants were progeny tested. The progeny of putative recombinants that had mated before being picked were screened for the presence of both male and hermaphrodite individuals of the recombinant phenotype. In the case of the *bli-3 unc-11* interval, *bli-3* penetrance is low and Bli-3 recombinants were scored as wild-type and later subtracted. The *unc-75 unc-101* and *unc-101 unc-54* map distances were based on the Unc-75 and Unc-101 recombinant classes, respectively. 95% confidence intervals were calculated using the statistics of CROW and GARDNER (1959). In the event the number of recombinants exceeded 300, confidence intervals were approximated using the equation $1.96(nxy)^{1/2}$ where x is the number of recombinants (n), divided by the number of wild types plus recombinants, and y is equal to $1 - x$.

Recombination in hermaphrodite germlines: Recombination frequency in oocytes was measured by scoring the male progeny of *dpy-5 unc-75/+ +* or *unc-11 dpy-5/+ +* hermaphrodites mated to a male carrying an appropriate cross-over suppressor. The translocation *hT2* was chosen because it suppresses crossing-over in both these regions (K. PETERS and K. MCKIM, unpublished results). Males of the genotype *dpy-5 unc-75; +/hT2(I;III)[+ +;dpy-18]* or *unc-11 dpy-5; +/hT2(I;III)[+ +;dpy-18]* were mated to heterozygous hermaphrodites every 24 hr and the male progeny were scored. The oocyte recombination frequency (a), is 2 × the number of recombinant individuals divided by the total progeny. The total number of progeny is 4/3 × (number of

wild types + one recombinant class). Knowing the value of R for the hermaphrodite and a, the recombination frequency in the oocytes, the following equation was solved for b, the recombination frequency in hermaphrodite spermatocytes.

$$R = 1/2b(1 - a) + 1/2a(1 - b) + 1/2ab.$$

Recombination in Her-1 hermaphrodites: To examine recombination in Her-1(*XO*) individuals, *hT1(I;V)[unc-29; + ; +]/szT1(I;X)[+ ; + ; lon-2]* males were crossed to *her-1* homozygous hermaphrodites. Because of the segregational properties of *szT1* (McKim, Howell and Rose 1988), all wild-type males resulting from this cross were of the genotype + ; *her-1/hT1(I;V)[unc-29; +]*. These males were then crossed to *hT3(I;X)[dpy-5 unc-29; +];szT1* homozygotes to produce + + ;*O/hT3(I;X)[dpy-5 unc-29; +]*; *her-1/+* males. When the latter males were mated to *dpy-5 unc-75; her-1* hermaphrodites, the only wild-type hermaphrodites that resulted were of the genotype + +/*dpy-5 unc-75; her-1/her-1; +/O*. Recombination was measured in these individuals by scoring Dpy-5 and Unc-75 recombinants.

Variation with age: The variation of recombination with parental age was examined in two intervals: *dpy-5 unc-75* and *dpy-5 unc-13*. Young heterozygous males were individually mated to 5 new homozygous hermaphrodites every 12 hr for 4 days. Heterozygous L4 hermaphrodite controls were brooded every 12 hr for 3 days under the same conditions. The recombination frequency in every 12-hr period was calculated as described above.

Variation with temperature: The effect of temperature on male recombination was examined in the *dpy-5 unc-75* and *dpy-5 unc-13* intervals. Seven heterozygous males were mass mated to five homozygous hermaphrodites and transferred to new hermaphrodites every 24 hr at temperatures of 15° or 25°. Hermaphrodite controls were picked from the same plates as experimental males and were transferred every day. All progeny were permitted to develop at 20° to avoid any inviability produced by such temperature extremes.

RESULTS

Male recombination frequency is lower than hermaphrodite: Differences in recombination frequencies between the sexes were initially studied in two intervals: *dpy-5 unc-75* and *dpy-5 unc-13*. The latter interval is located within the chromosome *I* genetic cluster and the former includes the cluster and a large region to the right. In both intervals, the frequency of recombination was approximately twofold lower in the male (data shown in Tables 1 and 2). To determine if the reduced recombination frequency in the male was general across the length of chromosome *I*, other intervals inside and outside the cluster were investigated. The results for six intervals spanning LG I is shown in Figure 1 (data shown in Table 3). In the *dpy-5 unc-29 unc-75* interval, only hermaphrodites were scored because the phenotypes of male recombinants were subtle and progeny testing was not possible. Male recombination frequency was lower in five of the intervals tested when compared to hermaphrodite controls. The differences in recombination frequencies between the hermaphrodite and the male in these intervals were not uniform; they varied from 1.3-fold in *unc-11 dpy-5* to 2-fold in *dpy-5 unc-13* and *unc-75 unc-101*. In the *unc-101 unc-54* region, the male meiotic distance was not different from that observed in the hermaphrodite. The difference for a comparably sized interval, *bli-3 unc-11* was 1.6, suggesting sex-related differences are interval-dependent and not

TABLE 1.

Male brood analysis

Genotype	Wild types ♀	Wild types ♂	Dpy ♀	Dpy ♂	Unc ♀	Unc ♂	pX100 (C.I.)[a]
dpy-5 unc-13/++							
0–12 hr	594	535	10	8	6	14	1.7 (1.2–2.2)
13–24 hr	789	761	11	5	9	10	1.1 (0.8–1.5)
25–36 hr	751	703	2	2	4	5	0.4 (0.2–0.7)
37–48 hr	849	890	6	8	7	3	0.7 (0.4–1.0)
49–60 hr	453	503	5	3	2	3	0.7 (0.3–1.1)
61–72 hr	442	382	2	1	0	3	0.4 (0.2–0.8)
73–84 hr	233	238	0	1	5	1	0.7 (0.3–1.4)
85–96 hr	109	113	0	0	1	1	0.4 (0.1–1.5)
Totals	4241	4140	36	28	34	40	0.8 (0.7–1.0)
dpy-5 unc-75/++							
0–12 hr	667	693	46	49	58	58	7.2 (6.3–8.1)
13–24 hr	556	568	28	41	29	41	5.8 (4.9–6.8)
25–36 hr	712	782	48	61	44	52	6.4 (5.6–7.3)
37–48 hr	879	794	45	42	34	34	4.4 (3.8–5.1)
49–60 hr	378	389	21	15	18	7	3.8 (3.0–4.8)
61–72 hr	611	655	27	31	27	19	3.9 (3.2–4.7)
73–84 hr	352	346	16	17	16	12	4.2 (3.3–5.2)
85–96 hr	76	81	3	2	0	6	3.4 (1.7–5.7)
Totals	4231	4308	234	258	226	229	5.3 (5.2–5.4)

[a] C.I. = 95% confidence interval.

TABLE 2

Hermaphrodite brood analysis

Genotype	Wild types	Recombinants Dpy	Recombinants Unc	pX100 (C.I.)[a]
dpy-5 unc-13/++				
0–12 hr	334	6	7	2.8 (1.5–4.6)
13–24 hr	647	11	9	2.3 (1.5–3.5)
25–36 hr	786	5	7	1.1 (0.6–1.9)
37–48 hr	718	5	6	1.1 (0.5–2.0)
49–60 hr	383	5	1	1.2 (0.5–2.5)
61–72 hr	251	2	2	1.1 (0.4–2.9)
Totals	3,119	34	32	1.6 (1.2–2.0)
dpy-5 unc-75/++				
0–12 hr	1,120	73	88	10.6 (9.1–12.3)
13–24 hr	2,583	171	179	10.0 (9.7–10.4)
25–36 hr	2,893	175	197	9.5 (9.2–9.8)
37–48 hr	2,560	114	154	7.8 (6.8–8.7)
49–60 hr	1,051	51	64	8.1 (6.7–9.7)
61–72 hr	596	39	25	8.0 (6.1–9.9)
Totals	10,803	623	707	9.1 (8.9–9.2)

[a] C.I. = 95% confidence interval.

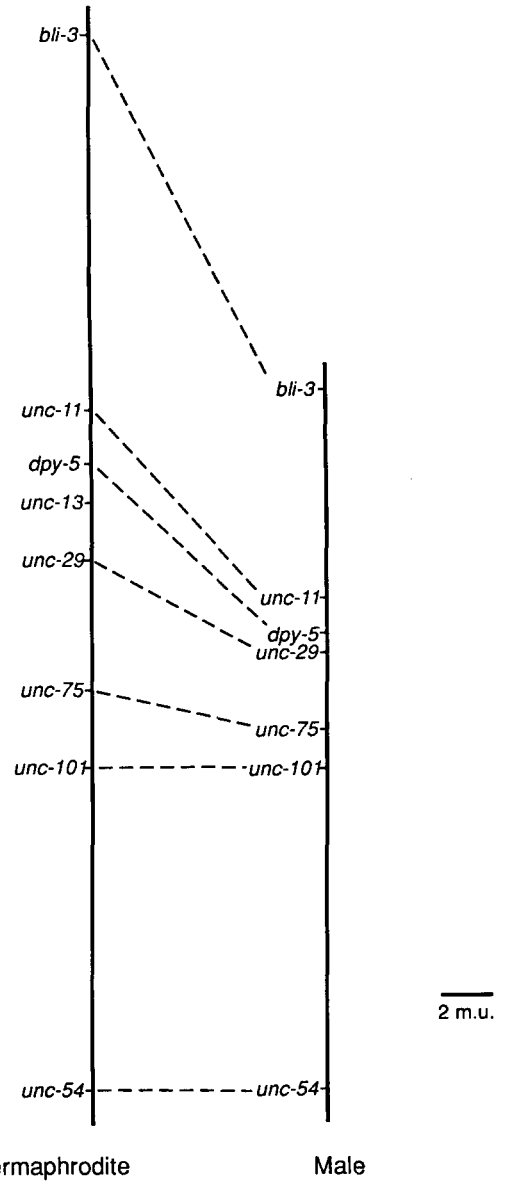

FIGURE 1.—Male and hermaphrodite meiotic maps of LG I. Three-factor experiments positioned *unc-75* between *dpy-5* and *unc-101*. The LG I cluster extends from *unc-11* to *unc-29*.

size-dependent. Thus, the greatest differences in crossover frequency were observed near the gene cluster and no difference was observed at the right end of the chromosome. The total size of the meiotic map of LG I is 31.7 m.u. in the male, compared to 44.1 m.u. in the hermaphrodite (data from Table 3). As is the case in the hermaphrodite meiotic map, the male map is also marked by a centrally located cluster.

Recombination in hermaphrodite spermatocytes is higher than in oocytes: The recombination formula normally used in measuring map distances in the hermaphrodite is based on the assumption that the frequency of recombination is equal in both germlines although a previous study has shown this not to be true (ROSE and BAILLIE 1979a). To measure the difference in recombination frequency between the germlines, *dpy-5 unc-x;:+/hT2(I;III)*[+ +; *dpy-18*] males were crossed to hermaphrodites *cis*-heterozygous for a pair of LG I markers, and the male progeny scored (see MATERIALS AND METHODS). The results are shown in Table 4. In measuring the *unc-11 dpy-5* interval, an unusually small number of Dpy-5 recombinants were recovered. The most conservative approach was to use only the Unc-11 recombinants in the calculations since this would give the minimum estimate of differences in recombination between the two germlines. In both intervals studied, the frequency of recombination in hermaphrodite spermatocytes was higher than that observed in oocytes; 2-fold in *dpy-5 unc-75* and 1.5-fold in *unc-11 dpy-5*. To further examine the effect of sexual phenotype on recombination frequency, crossing over was measured in males transformed into fertile hermaphrodites by the *her-1* mutation. The results of experiments measuring recombination in the *dpy-5 unc-75* interval in Her-1 (*XO*) hermaphrodites is shown in Table 5. Most of these hermaphrodites were sterile and those that were fertile produced few progeny. For this reason, recombinants that proved to be sterile upon progeny testing were also included in the calculations. The crossover frequency in these transformed males was significantly higher than that observed in normal males. An attempt was made to examine recombination in transformed hermaphrodites using the *tra-1(e1099)* mutation but these males mated poorly and rarely produced progeny.

Male recombination varies with age: ROSE and BAILLIE (1979a) found hermaphrodite recombination frequency to decrease with age. The effect of parental age on recombination in the *dpy-5 unc-75* and *dpy-5 unc-13* intervals is shown in Figure 2 (data shown in Tables 1 and 2, respectively). In both intervals, male recombination frequency shows a general decrease with age. Consistent with the previous results, the recombination frequencies of hermaphrodite controls also decreased with age. The variation in male recombination with age shows some periodicity in both intervals tested. The statistical significance of this fluctuation is difficult to assess due to the low recovery of recombinants in later broods. In the male, the most reproducible results were obtained in the first 36 hr. The greatest number of cross progeny were also produced in this period although the variation between individual males was high. In one experiment examining the *dpy-5 unc-75* interval in the male, a small number of progeny were recovered in the 49–60-hr period and this was likely the result of the poor physical condition of the hermaphrodites used in the matings since it was not reproduced in later experiments.

Male recombination frequency increases with temperature: Crossing over in the hermaphrodite has

TABLE 3

Male recombination on linkage group I

Genotype	Wild types ♀	Wild types ♂	Recombinants ♀	Recombinants ♂	pX100 (C.I.)[a]
bli-3 unc-11/++					
Male[b]	1392	1206	135 Unc	109 Unc	9.4[c] (8.2–10.6)
Hermaphrodite	1686		170 Unc		14.8[c] (12.4–17.4)
unc-11 dpy-5/++					
Male	983	962	19 Dpy 15 Unc	12 Dpy 25 Unc	1.8 (1.4–2.2)
Hermaphrodite	3786		58 Dpy 61 Unc		2.3 (2.0–2.8)
dpy-5 unc-29/+++					
Male	2536	2451	29 Dpy 44 Unc	35 Dpy 61 Unc	1.2 (1.0–1.5)
Hermaphrodite	1822		30 Dpy 39 Unc		2.8 (2.2–3.5)
dpy-5 unc-29 unc-75/+++					
Male	581		11 Dpy-5[d]		
			6 Unc-29 Unc-75[d]		1.4 (0.8–2.2)
			17 Unc-75[e]		2.9 (1.6–4.3)
Hermaphrodite	1598		34 Dpy-5[d]		
			36 Unc-29 Unc-75[d]		3.4 (2.6–4.2)
			2 Unc-29[d,e]		
			63 Unc-75[e]		6.0 (4.7–7.6)
unc-29 unc-75/++					
Male	3374	3568	95 Unc-75 126 Unc-29	80 Unc-75 90 Unc-29	2.7 (2.6–2.8)
unc-75 unc-101/++					
Male	2634	2553	45 Unc	42 Unc	1.6[c] (1.3–2.0)
Hermaphrodite	3192		68 Unc		3.2[c] (2.7–3.8)
unc-101 unc-54/++					
Male	392	362	71 Unc	62 Unc	15.0[c] (12.7–17.2)
Hermaphrodite	1187		116 Unc		14.4[c] (11.8–17.1)

[a] C.I. = 95% confidence interval.
[b] Recombination measured in individuals of indicates sex.
[c] Calculated from one recombinant class. See MATERIALS AND METHODS.
[d] *dpy-5 unc-29.*
[e] *unc-29 unc-75.*

TABLE 4

Recombination in hermaphrodite germlines

Genotype	Wild types	Recombinants Dpy	Recombinants Unc	pX100 (C.I.)[a]
dpy-5 unc-75/++				
Oocyte[b]	4290	83	92	6.0 (5.2–6.9)
Spermatocyte[c]				12.4
unc-11 dpy-5/++				
Oocyte[b]	3707	7	24	1.9 (1.2–2.8)
Spermatocyte[c]				2.7

[a] C.I. = 95% confidence interval.
[b] Only male progeny scored.
[c] Recombination frequency in hermaphrodite spermatocytes. See MATERIALS AND METHODS.

been found to vary with temperature (ROSE and BAILLIE 1979a). To determine if temperature has a similar effect in the male, recombination was measured in *cis*-heterozygous males at experimental temperatures of 15° and 25°. The results are shown in Table 6 with 20° controls for comparison. Recombination frequency in the male and in the hermaphrodite decreased at 15° and increased at 25° in both intervals tested. In the *dpy-5 unc-13* interval, the magnitude of the temperature effects was the same in both sexes; at 25° recombination frequency increased approximately 40% and at 15°, it decreased 40%. In the *dpy-5 unc-75* interval, however, the magnitude of the temperature effect was at least twofold greater in the male when compared to that of hermaphrodite controls. Male crossover frequency remained lower than that observed in the hermaphrodite at all temperatures and in both intervals tested.

Male recombination frequency increases with Rec-1: The *rec-1* mutation increased meiotic recombination threefold in the hermaphrodite (ROSE and BAILLIE 1979b). This increase retained the meiotic distribution of crossover events. To determine if this mutation had the same effect in the male, recombination was measured in *unc-11 dpy-5 rec-1/+ + rec-1*

TABLE 5

Recombination in Her-1 (XO) hermaphrodites

Genotype	Wild types ♀	Wild types ♂	Recombinants Dpy ♀	Recombinants Dpy ♂	Recombinants Unc ♀	Recombinants Unc ♂	pX100 (C.I.)[a]
dpy-5 unc-75/++; her-1/her-1 (XO)	53		4		5		12.5 (6.2–23.1)
dpy-5 unc-75/++ Male	2503	2457	148	132	122	135	5.1 (5.0–5.3)

[a] C.I. = 95% confidence interval.

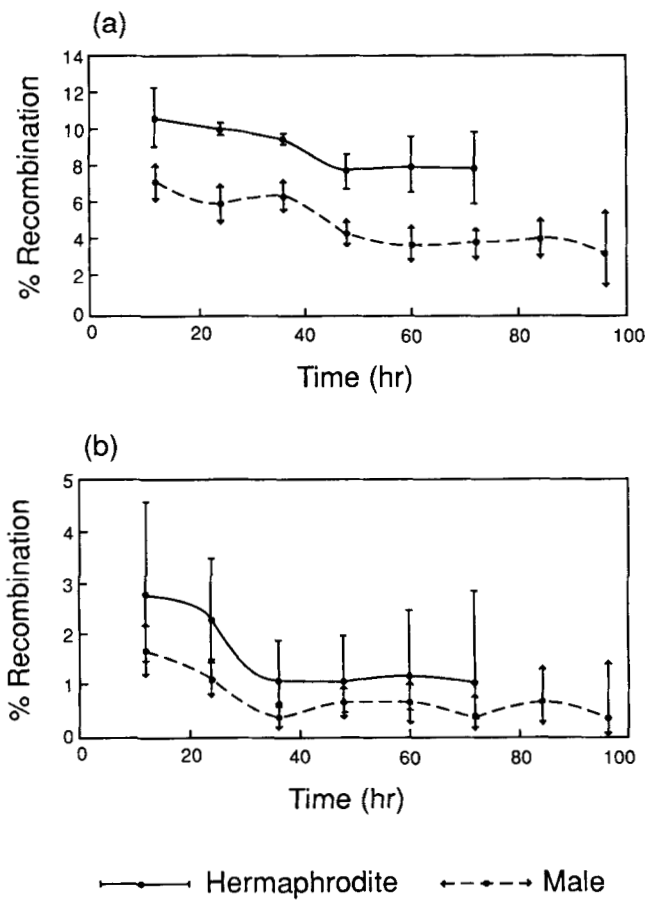

FIGURE 2.—The variation of recombination frequency with parental age in the (a) *dpy-5 unc-75* interval and (b) *dpy-5 unc-13* interval. Brood analysis for male heterozygotes is represented by dashed bold line. Hermaphrodite controls represented by solid thin line. Vertical bars represent 95% confidence intervals.

and *dpy-5 unc-13 rec-1/+ + rec-1* individuals. The results of these experiments are shown in Table 7. Recombination frequency in the male increased threefold in the *unc-11 dpy-5* interval (from 1.8 to 5.0, data in Tables 3 and 7, respectively) and fivefold in the *dpy-5 unc-13* interval (from 0.8 to 4.3, data in Tables 6 and 7, respectively). Rec-1 hermaphrodite crossover frequencies remained higher than those observed in the male.

DISCUSSION

Our results show that recombination frequency is generally higher in the *C. elegans* hermaphrodite than in the male, although the increases are not uniform along the length of the chromosome and one interval showed no sex-related difference. One possible explanation of these differences is they are the result of high interference values in the hermaphrodite. HODGKIN, HORVITZ and BRENNER (1979) found complete interference on the *X* chromosome of the hermaphrodite but measured a moderate *C* value (coefficient of coincidence) on an autosome in the male. This may be explained if high interference is limited either to the hermaphrodite or to the *X* chromosome but neither possibility has been confirmed. It is unlikely that low interference in the male is the basis of sex-related differences in recombination frequency for several reasons. First, large decreases in the male meiotic map were observed in small intervals in the cluster, a region in which double-crossing over would be extremely rare. Second, in a large interval like *bli-3 unc-11*, the male meiotic map showed a 36% decrease in recombination when compared to the hermaphrodite. The number of double-crossovers one would expect in this interval (approximately 2), cannot possibly account for the magnitude of this decrease. Thus, while it is possible that interference values differ between the hermaphrodite and the male, it is unlikely to be the sole explanation of differential rates of crossing over between the sexes.

BRENNER (1974) measured recombination frequency in oocytes on the *X* chromosome and found this frequency to be the same as the hermaphrodite frequency. We have measured oocyte recombination frequency in two intervals on LG I and have found them to be lower than both the total hermaphrodite frequency and the crossover frequency in hermaphrodite spermatocytes. These results may be explained if differences in recombination frequency between the hermaphrodite germlines are genetic interval-dependent or limited to the autosomes. Although we have found recombination to vary with age in male spermatocytes, it is unlikely hermaphrodite spermatocytes contributes to the variation of recombination frequency with age in the hermaphrodite since spermatogenesis in hermaphrodites is restricted to the fourth larval stage, at which time about 300 sperm are produced (HIRSH, OPPENHEIM and KLASS 1976;

TABLE 6

Effect of temperature on male recombination

Genotype	Wild types		Recombinants				pX100 (C.I.)[a]
			Dpy		Unc		
	♀	♂	♀	♂	♀	♂	
15°							
dpy-5 unc-13/++							
Male[b]	1,870	1,992	9	14	6	12	0.5 (0.4–0.7)
Hermaphrodite	1,218		9		8		1.0 (0.6–1.6)
dpy-5 unc-75/++							
Male	2,345	2,528	93	103	111	89	3.9 (3.8–4.0)
Hermaphrodite	2,206		121		130		8.4 (7.4–9.5)
20°							
dpy-5 unc-13/++[c]							
Male	4,242	4,140	36	28	34	40	0.8 (0.7–1.0)
Hermaphrodite	3,119		34		32		1.6 (1.2–2.0)
dpy-5 unc-75/++[c]							
Male	4,231	4,308	234	258	226	229	5.3 (5.2–5.4)
Hermaphrodite	10,803		623		707		9.1 (8.9–9.2)
25°							
dpy-5 unc-13/++							
Male	968	1,077	15	10	10	11	1.1 (0.8–1.5)
Hermaphrodite	3,024		52		42		2.3 (1.9–2.8)
dpy-5 unc-75/++							
Male	1,105	1,142	139	122	114	107	9.7 (9.4–10.0)
Hermaphrodite	1,574		125		140		12.4 (11.0–13.9)

[a] C.I. = 95% confidence interval.
[b] Recombination measured in individuals of indicated sex.
[c] Data from brooding experiments.

TABLE 7

Effect of Rec-1 on male recombination

Genotype	Wild types		Recombinants				pX100 (C.I.)[a]
			Dpy		Unc		
	♀	♂	♀	♂	♀	♂	
unc-11 dpy-5 rec-1/++ rec-1							
Male[b]	866	755	40	43	57	30	5.0 (4.3–5.7)
Hermaphrodite	2,033		91		91		6.7 (5.7–7.6)
dpy-5 unc-13 rec-1/++ rec-1							
Male	922	908	46	41	36	43	4.3 (3.7–5.0)
Hermaphrodite	2,111		103		86		6.6 (5.7–7.7)

[a] C.I. = 95% confidence interval.
[b] Recombination measured in individuals of indicated sex.

WARD and CARREL 1979). This has previously been pointed out in studies examining the variation of recombination with hermaphrodite age (ROSE and BAILLIE 1979a). If the recombination frequency in hermaphrodite spermatocytes (b) is constant, it follows that as the oocyte recombination frequency approaches zero with increasing age, the value of R in the hermaphrodite should never fall below $1/2b$. For example, in the *dpy-5 unc-75* interval the value of R in the final brood (0.08) is still higher than $1/2b$ (0.06). Of further interest is the possibility that the variation of recombination frequency with age is a continuum of the two germlines. Since the first brood measures the earliest oocyte recombination frequency (those events occurring right after the switch from spermatogenesis), one would expect the two germlines to have similar frequencies in this brood. In the *dpy-5 unc-75* interval for example, knowing the value of R in the first brood (0.10) and the value of b (0.12), the value of a (0.09), the frequency of recombination in the oocyte, can be calculated. As predicted, the oocyte recombination frequency in this brood is close to, but not higher, than the sperm frequency.

YAMAMOTO (1961) measured recombination in hormonally transformed *XY* males of the Medaka and found the recombination frequency to be much higher than that observed in normal males. We have measured recombination in males sexually trans-

formed by the *her-1* mutation. Similar to the previous results, the recombination frequency was significantly higher in the transformed males when compared to normal males although the small sample size must be taken into consideration. This result can be interpreted as evidence that it is the sexual phenotype and not genotype that determines the frequency of recombination during gametogenesis.

Meiotic recombination frequency in both sexes of *C. elegans* is affected by age and temperature. Recombination frequency decreases with maternal age in Drosophila (BRIDGES 1927; NEEL 1941), in mice (FISHER 1949), and in *C. elegans* (ROSE and BAILLIE 1979a). We have observed a fall in crossover frequency with paternal age in two intervals. This variation of recombination frequency with parental age does not affect the results of other experiments. As described in MATERIALS AND METHODS, only L4 hermaphrodites, which are easily identifiable at that stage, and young males were used in later experiments further characterizing recombination. The population of males used in these experiments were considered to be synchronous since all male recombination experiments were replicated and reproducible results were obtained. For example, the curves derived from four separate experiments examining the variation of recombination frequency with paternal age in the *dpy-5 unc-13* interval could be superimposed.

Elevated temperatures produce increases in recombination values in a number of organisms including Drosophila (PLOUGH 1917), Coprinus (LU 1969, 1974), and Neurospora (MCNELLY-INGLES, LAMB and FROST 1966). In Drosophila, the greatest temperature related changes in crossover frequency occur in centromeric regions, where recombination is normally suppressed (PLOUGH 1917; BRIDGES 1915, 1927; STERN 1926; MATHER 1939). ROSE and BAILLIE (1979a) examined two intervals in the LG I cluster of the hermaphrodite and found 2–3-fold increases in recombination frequency at elevated temperatures. We have observed similar increases of recombination values in the male in an interval within this cluster. However, in an interval that included a large region outside the cluster, the hermaphrodite recombination frequency was less sensitive to the effects of temperature than was the male frequency. This may be explained if male recombination in the *dpy-5 unc-75* interval is suppressed relative to the hermaphrodite and as a result, is more sensitive to the effect of temperature.

The results of experiments using the *rec-1* mutation, a general recombination enhancer, can also be interpreted in light of sex-related differences in cluster size. This mutation increased the frequency of male recombination in both intervals tested. In the male, a greater enhancement effect (5-fold increase) was observed in the *dpy-5 unc-13* interval, located within the cluster, when compared to the *unc-11 dpy-5* interval (3-fold increase), a larger region at the left end of the cluster. A possible explanation is the *dpy-5 unc-13* region is more recombinationally suppressed in the male and may for this reason be more sensitive to the effects of Rec-1.

In conclusion, we have found male recombination across the length of LG I to be approximately one-third less than that observed in the hermaphrodite. This decrease, however, was not uniform and one interval showed no sex-related difference in crossover frequency. By measuring recombination in the two germlines of the hermaphrodite and in transformed males, we have concluded it is the physiology of the gonad, rather than the sexual karyotype of the germline that determines the recombination frequency characteristic of specific sex. We have also found that male recombination in *C. elegans* varies with age, temperature and the *rec-1* mutation, suggesting recombination is quantitatively rather than qualitatively different between the sexes. For this reason, we recommend that the standard practices recommended by ROSE and BAILLIE (1979a) for hermaphrodite recombination experiments be also applied to male recombination studies (*i.e.*, that studies be carried out at 20° and all progeny from the male should be counted).

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