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NOTES AND COMMENTS

ADAPTIVE ADVANTAGE FOR CHIASMA INTERFERENCE: A NOVEL SUGGESTION

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1. Introduction

It is the purpose of this note to point out a possible simple mechanical reason for the evolution of chiasma interference. It is widely recognized that, while maintaining constant, presumably adaptively optimal, levels of recombination frequency in adjacent chromosome regions, depression of coincident recombinant frequency in the two regions below the frequency at zero interference would be expected to be accompanied by corresponding depression of coincident parental (non-recombinant) frequency in both regions. Positive interference, which implies such increase in single recombinants at the expense of double recombinants and parentals, could thus be advantageous to the extent that short chromosome pairs are prevented from becoming univalents (which are subject to irregular anaphase I distribution) in some cells. An additional, and perhaps more generally applicable, incentive for the evolutionary development of chiasma interference is suggested below. The system proposed does not assume strictly maintained, adaptively optimal recombination frequencies, but calls for limiting the proximity of adjacent crossover events. The marked increase in univalent frequency observed by Jones (1967) in an abnormal strain of rye with normal chiasma frequency but approximately random chiasma distribution, provides evidence that relaxation of interference can indeed be accompanied by the production of univalents.

2. The role of sister chromatid cohesiveness

The suggestion is based upon the following assumptions. (1) That chiasma maintenance depends upon sister chromatid cohesiveness as well as upon the occurrence of crossing over (Darlington, 1932; Maguire, 1974, 1978*a*, 1979*a*; Moens and Church, 1979). (2) That some minimum extent of sister chromatid cohesiveness is probably required for chiasma binding strength adequate for maintenance of homologue association until anaphase I. (3) That sister centromeres, although apparently present as discrete structures by metaphase I (Kezer and Macgregor, 1971; Müller, 1972), are directed toward the same pole in normal bivalents (Nicklas, 1977). Then it seems reasonable to propose, on purely mechanical grounds, that the critical region for the maintenance of association of homologues by the chiasmate mechanism is the *extent of recombined chromatid which is sister to a chromatid still joined to a centromere of the other homologue.* Thus is can be seen in fig. 1(A) and (B) that the only critical region extent of sister chromatid cohesiveness is that between the positions of the two crossovers, in the cases

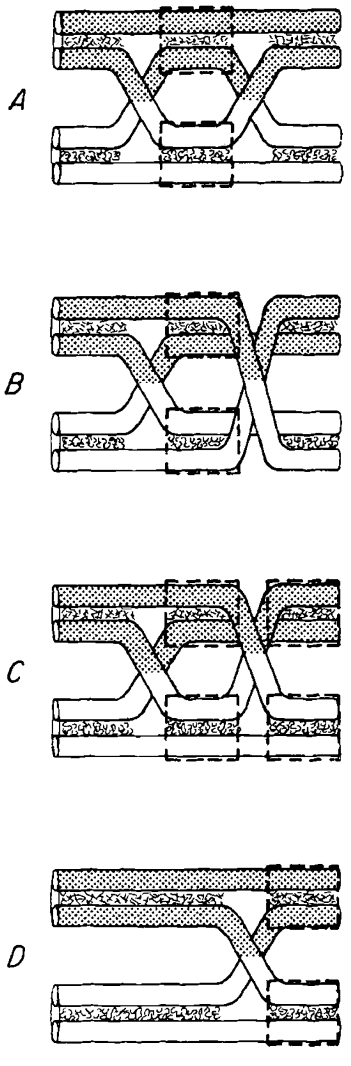

FIG. 1.—Diagrammatic representation of bivalents with 2-strand double crossovers (A), 4-strand double crossovers (B), 3-strand double crossovers (C), and a single crossover (D). In each case: one homologue is shaded, centromeres are represented by circles at the left ends, sister chromatid cohesiveness is represented by flecking between sister chromatids, and critical regions for chiasma maintenance are enclosed by dashed lines.

of 2-strand doubles and 4-strand doubles; in fact, if 4-strand doubles occurred at the same position, there would be no chiasma binding available. On the other hand, in the case of 3-strand doubles, the critical region extent of sister chromatid cohesiveness is present all the way from the more proximal crossover to the distal end of the bivalent (fig. 1(C)). Interlocking of 2-strand or 4-strand doubles could theoretically occur if the twists introduced at the break and reunion are in the same direction in the two crossovers. Such interlocking might serve to maintain chiasmata (Egel, 1979), but direct cytological observation has suggested that its frequency

may be of the order of 50 per cent (Hearne and Huskins, 1935). Numerous cytological observations point to extensive sister chromatid cohesiveness as a predominant component of chiasma anatomy.

For these reasons it seems plausible that selection pressure would tend to favour those organisms which develop either chiasma interference (such that double crossovers seldom occur so close together that bivalents will fall apart before regular metaphase I orientation, with 2- or 4-strand, non-interlocking doubles), or those which develop chromatid interference such that 3-strand doubles are strongly favoured over 2- and 4-strand doubles. The latter may be the more difficult evolutionary course and the one rarely (if ever) followed, although for most organisms data which could demonstrate chromatid interference of this sort are difficult to obtain. It is interesting that it has recently been suggested that the unexpectedly frequent occurrence of closely spaced 3-strand doubles could account for anomalous configurations observed (Tease and Jones, 1978). In contrast, early cytological observations (Hearne and Huskins, 1935; Huskins and Newcombe, 1941) strongly suggest an excess of 2-strand and/or 4-strand doubles in genetically relatively short regions. Fungal tetrad analysis has also provided evidence of a slight excess of 2-strand doubles (Perkins, 1962; Mortimer and Fogel, 1974); half tetrad analysis of attached X chromosomes of *Drosophila melanogaster*, however, has not allowed distinction between complete absence of chromatid interference and a striking excess of 2-strand doubles over short map distances (Emerson, 1969). It is conceivable that the mechanism of the crossover process itself may impose some constraints on the distribution of adjacent crossovers among the four chromatids, particularly over relatively short distances.

It can also be seen from fig. 1(D) that in the case of single crossovers, the region distal to the crossover represents the critical region of sister chromatid cohesiveness. It might therefore be expected that since crossing over in extreme distal regions would be relatively useless to normal disjunction function, it would sometimes become lost or inhibited in the course of evolution. It is interesting in this light that crossing over seems to be strongly depressed in the distal 10 per cent of euchromatin of the X chromosome of *Drosophila melanogaster*, but any crossover depression in the distal regions of the euchromatin of chromosomes 2 and 3 must be much less pronounced (Lindsley and Sandler, 1977). *D. melanogaster* is perhaps the only organism where genetic and cytological maps may be adequately correlated for such observation, and cytological observations alone are subject to the possible error of differential condensation. Short extents of condensed chromosome must often represent substantial portions of genetic map. However, the *Drosophila* data may be peculiarly irrelevant since it is also the only organism with strong evidence for distributive pairing, a special process which may provide for regular anaphase I disjunction of normal, achiasmate bivalents in *D. melanogaster* females (Grell, 1964). It is also true that, in some cases at least, there seems to be a tendency for distal chiasmata to be accompanied by proximal chiasmata, while single chiasmata tend to occur more medially within chromosome arms (Stephens, 1961). Double crossovers separated by substantial physical chromosome length, according to the scheme proposed here, would, of course, have adequate critical region extent of sister chromatid cohesiveness to provide for chiasma maintenance, regardless of their type (2-strand, 3-strand, or 4-strand). It is tempting to

speculate that the frequent centric or terminal location of heterochromatic regions, in which crossovers are rare, but sister chromatid cohesiveness appears normal, may be adaptive in the following sense. In centric regions extensive sister chromatid cohesiveness may thus persist into the second meiotic division, to function in maintenance of dyad integrity until metaphase II (Maguire, 1978*b*), while in terminal regions very distal crossovers (some of which could be single) may thus be inhibited. Additional functions of the restriction of crossovers to specific chromosome regions can, of course, also be imagined, such as a conceivable relationship of bivalent shape to spindle interaction as proposed by White (1973).

3. Terminal adhesions and achiasmate associations

It is difficult to conceive of a selective advantage for chiasma terminalization (short of a possible desirability of a particular bivalent shape at metaphase I, as just mentioned). In some cases there is strong evidence that terminalization does not occur (Peacock, 1970; Jones, 1971; Hultén, 1974; Tease and Jones, 1978). It may well be that where it occurs (Maguire, 1979*b*) it is an unavoidable result of chromosome condensation pressure, and its extent is not large. In many cases where chiasmata appear to be terminal or nearly so, this may be only apparent, and the result of differential condensation (Jones, 1977, 1978). In other cases, terminal associations of the members of bivalents, as in *D. melanogaster* males, probably result from a "stickiness' which is not of chiasmate origin (Slizynski, 1964). It may be that this, and other exotic forms of cohesiveness which serve to bind homologues together until anaphase I (Gassner, 1969; Rasmussen, 1977), and therefore provide for normal disjunction in the absence of the more usual chiasmate mechanism, have resulted from evolutionary modifications of the basic mechanism responsible for sister chromatid cohesiveness in chiasmate forms.

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