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Epistatic interaction between unlinked inversions in Indian natural populations of *Drosophila melanogaster*

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Summary – Fourteen Indian natural populations (6 from the north and 8 from the south) of *Drosophila melanogaster* were screened for chromosome inversions and 23 paracentric inversions including 4 common cosmopolitan (In(2L)t, In(2R)NS, In(3L)P and In(3R)P), 2 rare cosmopolitan (In(3R)Mo and In(3R)C) and a recurrent endemic (In(3L)IB) found to be common in distribution were detected. Comparison of the observed and expected numbers (*via* the Hardy–Weinberg equilibrium) of different karyotypes produced by all these inversions (each treated independently) showed no significant deviation from expectation in any of the populations analysed. During the present investigation data on intra- and interchromosomal associations have been obtained to test chromosome interactions in Indian natural populations of *D. melanogaster*. The results show that different associations between linked inversions of the second and third chromosomes occur randomly, providing no evidence for epistatic interaction between linked inversions. Furthermore, the majority of pairs of unlinked inversions of major autosomes also occur in random combinations. However, highly significant non-random associations were found between In(2R)NS and In(3R)C in all the populations from south India and between In(2L)t and In(3R)P in 11 populations out of 14 analysed. There is a significant excess of individuals which are either doubly homozygous for ST (standard) at both unlinked inversion loci or doubly heterozygous, indicating epistatic interactions between unlinked inversions in these populations.

Drosophila melanogaster / inversion polymorphism / epistatic interaction / Indian populations

Résumé – Interaction épistatique entre des inversions non liées dans des populations naturelles de *Drosophila melanogaster* de l'Inde. Quatorze populations naturelles

* Correspondence and reprints

de *Drosophila melanogaster* de l'Inde (6 du Nord et 8 du Sud) ont été examinées pour des inversions chromosomiques. Vingt-trois inversions paracentriques ont été détectées, dont 4 communes et cosmopolites (*In*(2L)t, *In*(2R)NS, *In*(3L)P et *In*(3R)P), 2 rares et cosmopolites (*In*(3R)Mo et *In*(3R)C), et une inversion endémique récurrente (*In*(3I)IB) communément distribuée. La comparaison des nombres attendus et observés (sur la base de l'équilibre de Hardy-Weinberg) des différents caryotypes résultant de toutes ces inversions (chacune traitée indépendamment) ne montre aucun écart significatif dans aucune des populations analysées. Dans cette étude, des données sur des associations entre chromosomes et intra-chromosome ont été obtenues pour tester les interactions chromosomiques dans les populations naturelles de *D. melanogaster* de l'Inde. Les résultats montrent que différentes combinaisons entre des inversions liées des deuxième et troisième chromosomes apparaissent d'une manière aléatoire, ce qui n'apporte aucune preuve d'interaction épistatique entre des inversions liées. De plus, la majorité des couples d'inversions non liées impliquant les autosomes importants sont aussi des combinaisons aléatoires. Cependant, des associations non aléatoires hautement significatives ont été trouvées entre *In*(2R)NS et *In*(3R)C dans toutes les populations du Sud de l'Inde et entre *In*(2L)t et *In*(3R)P dans 11 des 14 populations analysées. Il y a un excès significatif d'individus doubles homozygotes pour ST (standard) aux 2 locus d'inversion non liés ou doubles hétérozygotes pour les 2 inversions, ce qui indique des interactions épistatiques entre des inversions non liées dans ces populations.

Drosophila melanogaster / polymorphisme d'inversion / interaction épistatique / population de l'Inde

INTRODUCTION

Genes do not act independently. Rather they tend to organize themselves in functional gene complexes which confer an adaptive advantage to the recipient genotype (Darlington and Mather, 1949). In general, relative selective values can properly be assigned to the genetic system as a whole and thus evolution depends upon the fitting together of a harmonious system of gene effects (Wright, 1964). Epistatic selection and balanced polymorphism constitute a major feature of evolution. The 1 locus-2 alleles system has been extensively used in population genetic work which established the modern understanding of evolution. But it has been realised that assumption of independent genes is unrealistic since most significant adaptation involves interaction of many polymorphic loci.

Chromosomal polymorphism mainly due to paracentric inversions is very common in different species of *Drosophila* and constitutes an adaptive trait (da Cunha, 1960; Dobzhansky, 1970; Parsons, 1973; Sperlich and Pfriem, 1986). It offers very good material to test epistatic gene interaction. Epistatic interaction between linked inversions is well documented in various species of *Drosophila*. However, less attention has been paid to the study of interaction between unlinked inversions. Prakash (1967) demonstrated the existence of interchromosomal interactions on the basis of non-random association between unlinked inversions in *D. robusta*. In contrast to this, no evidence for interchromosomal interaction has been found in *D. subobscura* (Sperlich and Feuerbach-Mravlag, 1974) and *D. ananassae* (Singh, 1982, 1983;

Singh and Singh, 1989) as various interchromosomal associations occur randomly in these species.

Drosophila melanogaster, a cosmopolitan and domestic species, presents a high degree of inversion polymorphism in its natural populations and populations show geographic differentiation of inversion polymorphism (for references see Lemeunier *et al*, 1986). Data on intra- and interchromosomal associations in natural populations have been reported by numerous investigators from several parts of the world. In certain populations interactions between linked inversions as well as between unlinked inversions is evident (Alahiotis *et al*, 1976; Stalker, 1976; Choi, 1977; Langley *et al*, 1977; Inoue and Watanabe, 1979; Yamaguchi *et al*, 1980; Knibb *et al*, 1981; Yamazaki *et al*, 1984; Aulard and Lemeunier, 1985; Afonso *et al*, 1985). However, previous study by the present authors of 6 Indian natural populations indicates no evidence for intra- and interchromosomal interactions between commonly occurring chromosome inversions in *D melanogaster* (Das and Singh, 1990). The present paper reports data on interchromosomal associations in Indian natural populations of *D melanogaster* which provide evidence for epistatic interaction between unlinked inversions.

MATERIALS AND METHODS

To study inversion polymorphism in Indian populations of *D melanogaster*, flies were collected from 14 localities. The geographic location of the collection sites, state in which situated and the month of collection have been shown in figure 1. In all the places flies were collected by exposing fermented banana traps in vegetable and fruit stalls and also near human habitations. Each naturally inseminated female was kept individually in a fresh food vial. The F₁ larvae were squashed to detect chromosome inversions by the lacto-acetic orcein method. The quantitative data are based on the identification of the karyotype of only one F₁ larva from each wild female. In total 23 paracentric inversions including 4 common cosmopolitan (In(2L)t, In(2R)NS, In(3L)P and In(3R)P), 2 rare cosmopolitan (In(3R)Mo and In(3R)C) and a recurrent endemic (In(3L)IB) found to be common in distribution were detected. The description of inversions and their frequencies have been reported elsewhere (Das and Singh, 1991). The frequency of 4 inversions showing non-random association is shown in table I. During the present study, these data have been analysed to obtain the frequency of various intra- and interchromosomal associations in India natural populations of *D melanogaster*. To test whether there is positive correlation between different karyotypes produced by unlinked inversions in natural populations, the correlation coefficient (*r*) was calculated.

RESULTS

The chromosomal analysis revealed the presence of 23 paracentric inversions. However, only 7 inversions are found to be common in distribution and maintained at considerable frequency. These inversions are: 4 common cosmopolitan (In(2L)t, In(2R)NS, In(3L)P and In(3R)P), 2 rare cosmopolitan (In(3R)Mo and In(3R)C) and one recurrent endemic (In(3L)IB). The 4 common cosmopolitan inversions

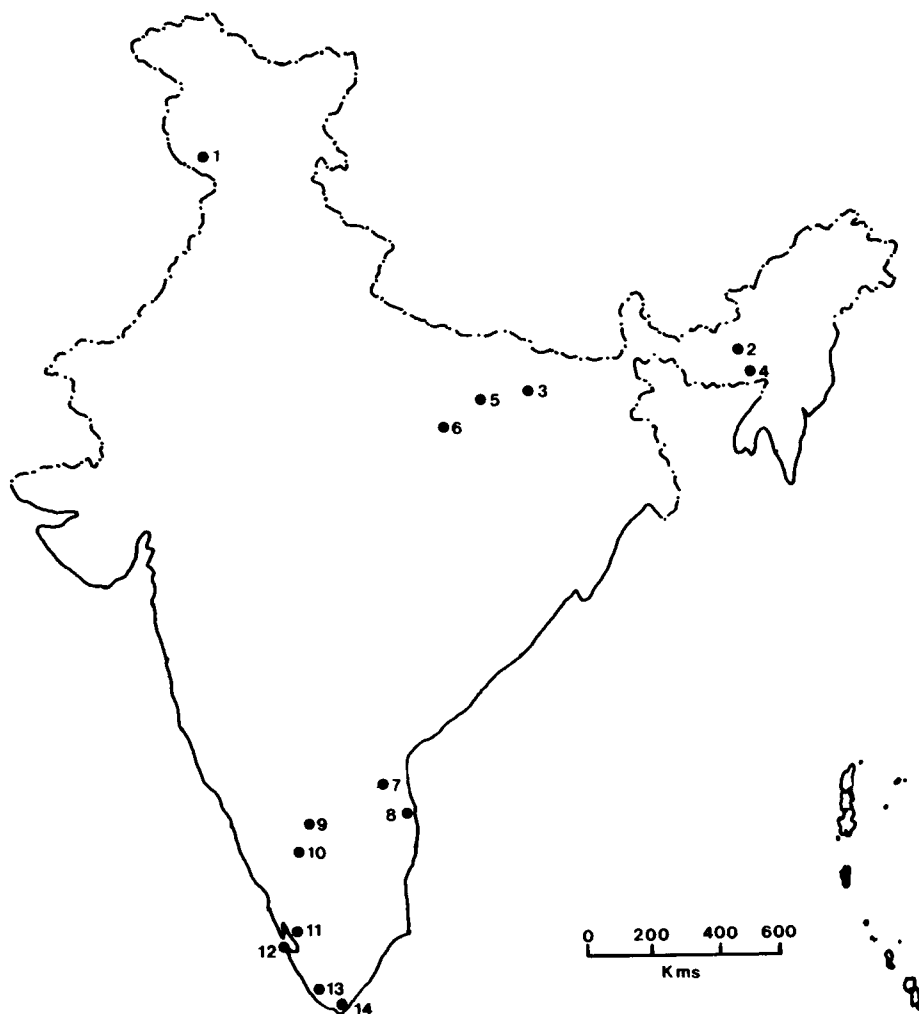


Fig 1. Map showing the localities from which *D. melanogaster* flies were collected.

1, Jammu (Jammu and Kashmir, December 1989); 2, Guwahati (Assam, November 1989); 3, Patna (Bihar, March 1990); 4, Shillong (Meghalaya, November 1989); 5, Ghaziपुर (Uttar Pradesh, March 1990); 6, Mirzapur (Uttar Pradesh, March 1990); 7, Tirupati (Andhra Pradesh, February 1990); 8, Madras (Tamil Nadu, February 1990); 9, Bangalore (Karnataka, February 1990); 10, Mysore (Karnataka, February 1990); 11, Ernakulam (Kerala, January 1990); 12, Fort Cochin (Kerala, January 1990); 13, Trivandrum (Kerala, January 1990); 14, Kanniya Kumari (Tamil Nadu, January 1990).

Table I. Frequencies (%) of 4 inversions showing non-random associations in 14 natural populations of *D. melanogaster*.

Population	Total No of chromosomes examined	Inversions			
		<i>In(2L)t</i>	<i>In(2R)NS</i>	<i>In(3R)P</i>	<i>In(3R)C</i>
Jammu	122	18.85	12.30	22.95	0
Guwahati	200	10.00	9.50	16.00	0
Patna	118	9.32	10.17	11.86	0
Shillong	132	12.12	9.85	16.67	0
Ghazipur	156	7.69	8.33	12.82	0
Mirzapur	146	5.48	10.96	14.38	0
Tirupati	108	18.52	18.52	26.85	16.67
Madras	82	18.29	19.51	26.83	10.98
Bangalore	124	16.94	15.32	29.03	12.90
Mysore	208	18.75	19.32	17.31	15.38
Ernakulam	112	9.82	23.21	16.96	14.29
Fort Cochin	124	17.74	18.55	23.39	12.10
Trivandrum	114	16.67	22.81	24.56	12.28
Kanniya Kumari	110	18.18	20.91	24.54	13.64

occur in all the populations analysed except *In(3L)P* in Patna and the populations in the south maintain these inversions at higher frequencies than those in the north. The *In(3R)Mo* is present in all the populations but at low frequency. Interestingly, *In(3R)C* could be detected only in populations from the south. The recurrent endemic inversion *In(3L)IB* occurs in all populations except Shillong at substantial frequency. Comparison of the observed and expected numbers (*ie*, the Hardy-Weinberg equilibrium) of different karyotypes produced by all these 7 inversions, treating each inversion as an independent locus, showed no significant deviation from Hardy-Weinberg equilibrium in any of the populations analysed (data not shown). To determine chromosome interactions, all these inversions have been used. At each inversion locus, 3 karyotypes – *ST/ST*, *ST/In* and *In/In* are expected. If all the 3 karyotypes are ascertained at each locus, 9 types of karyotypic combinations will be expected between 2 inversion loci. However, in some populations only 6 types could be found due to the absence of inversion homozygote (*In/In*) for certain inversions. The expected numbers of various association types have been calculated from marginal totals of $R \times C$ contingency tables. Any significant deviation from expectation would indicate non-random association resulting from interaction causing differential viability of different associations between inversions.

Intrachromosomal associations

The observed and expected numbers of various intrachromosomal associations considering different pairs of linked inversions (*In(2L)t*–*In(2R)NS*, *In(3L)P*–*In(3R)P*, *In(3L)P*–*In(3R)Mo*, *In(3L)P*–*In(3R)C*, *In(3L)IB*–*In(3L)P*, *In(3L)IB*–*In(3R)P*, *In(3L)IB*–*In(3R)Mo*, *In(3L)IB*–*In(3R)C*, *In(3R)P*–*In(3R)C*, *In(3R)P*–*In(3R)Mo* and *In(3R)C*–*In(3R)Mo*) in all the populations were calculated (data not shown).

There is a good agreement between observation and expectation in all the populations for different pairs of linked inversions which indicates that there is no evidence for linkage disequilibrium between these inversions.

Interchromosomal associations

To study interchromosomal interactions, the observed and expected numbers of different genotypes were calculated. In the majority of cases, for example, $\text{In}(2\text{L})\text{t}-\text{In}(3\text{L})\text{P}$, $\text{In}(2\text{L})\text{t}-\text{In}(3\text{L})\text{IB}$, $\text{In}(2\text{L})\text{t}-\text{In}(3\text{R})\text{C}$, $\text{In}(2\text{L})\text{t}-\text{In}(3\text{R})\text{Mo}$, $\text{In}(2\text{R})\text{NS}-\text{In}(3\text{L})\text{P}$, $\text{In}(2\text{R})\text{NS}-\text{In}(3\text{L})\text{IB}$, $\text{In}(2\text{R})\text{NS}-\text{In}(3\text{R})\text{P}$ and $\text{In}(2\text{R})\text{NS}-\text{In}(3\text{R})\text{Mo}$, the differences between observed and expected numbers of various interchromosomal combinations are non-significant (data not shown). However, in the 2 comparisons, *ie* $\text{In}(2\text{L})\text{t}$ and $\text{In}(3\text{R})\text{P}$; $\text{In}(2\text{R})\text{NS}$ and $\text{In}(3\text{R})\text{C}$, (all the 4 inversions showing significant associations are located in autosomes (figure 2), the differences are significant. The observed and expected numbers of various interchromosomal associations involving $\text{In}(2\text{L})\text{t}$ and $\text{In}(3\text{R})\text{P}$ are given in table II. Due the absence of homozygotes for $\text{In}(2\text{L})\text{t}$, only 6 karyotypic combinations could be ascertained in north Indian populations. The differences between observed and expected numbers are significant in most of the populations. The karyotypes in 2L and 3R are associated randomly only in 3 populations (Shillong, Tirupati and Fort Cochin). The values obtained by the correlation coefficient analysis also show a similar pattern of statistical significance for different karyotypic associations (table IV).

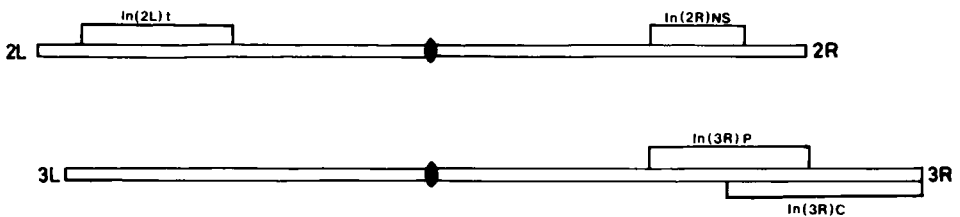


Fig 2. Location of $\text{In}(2\text{L})\text{t}$, $\text{In}(2\text{R})\text{NS}$, $\text{In}(3\text{R})\text{P}$ and $\text{In}(3\text{R})\text{C}$ inversions in different chromosomes of *D. melanogaster*.

The observed and expected numbers of different interchromosomal associations involving $\text{In}(2\text{R})\text{NS}$ and $\text{In}(3\text{R})\text{C}$ are given in table III. As $\text{In}(3\text{R})\text{C}$ occurs only in south Indian populations, the study is limited to only 8 populations. The homozygotes for $\text{In}(3\text{R})\text{C}$ could not be found in certain populations and as a result of this only 6 karyotypic combinations could be ascertained in all the populations. The deviation from randomness is highly significant in all the populations. The individuals which are either doubly homozygous for ST (standard) or doubly heterozygous are in significant excess. On the other hand, there is a deficiency of those individuals which are homozygous in one arm and heterozygous for inversion in the other arm. An identical pattern has been found in all the populations and deviation from randomness is highly significant. Statistically significant positive correlations obtained from differential karyotypic associations produced by these 2 inversions (see table IV) further strengthen the suggestion that the karyotypes in 2R(NS) and 3R(C) are associated non-randomly in natural populations of *D. melanogaster* from India.

Table II. Observed and expected numbers of different interchromosomal combinations (In(2L)t and In(3R)P) in Indian natural populations of *D. melanogaster*.

Population	Total No of larvae examined	Karyotype combinations																χ^2	P		
		2L		ST/ST		ST/ST		ST/ST		ST/ST		ST/ST		ST/ST		ST/ST				ST/ST	
		Obs	Exp	ST/ST	ST/In	ST/ST	ST/In	ST/ST	ST/In	ST/ST	ST/In	ST/ST	ST/In	ST/ST	ST/In	ST/ST	ST/In			ST/ST	ST/In
Jammu	61	Obs	28	8	13.70	2	1.87	8	13.57	14	8.30	1	1.13	-	-	-	-	9.98 (2)	< 0.01*		
Guwahati	100	Exp	22.43	16	19.60	1	3.20	9	14.40	8	4.80	3	0.80	-	-	-	-	12.76 (2)	< 0.01*		
		Obs	63	6	9.76	1	0.81	5	8.58	6	2.24	0	0.19	-	-	-	-	9.83 (2)	< 0.01*		
Patna	59	Obs	41	10	12.12	2	2.27	9	11.39	6	3.88	1	0.73	-	-	-	-	2.32 (2)	> 0.30		
Shillong	66	Obs	38	11	15.23	1	0.85	5	9.08	7	2.77	0	0.15	-	-	-	-	9.98 (2)	< 0.01*		
Ghazipur	78	Exp	49.92	12	16.92	1	0.89	1	5.81	7	2.08	0	0.11	-	-	-	-	17.66 (2)	< 0.001*		
Mirzapur	73	Obs	52	9	12.67	2	3.33	4	8.89	5	6.3	3	1.48	1	1.11	0	0.19	9.39 (4)	> 0.05		
Tirupati	54	Exp	20.00	8	11.85	1	1.32	2	6.66	10	5.71	1	0.63	1	0.51	0	0.05	10.25 (4)	< 0.05*		
Madras	41	Obs	18	10	18.97	2	2.71	9	9.19	8	5.8	2	1.23	0	0.48	0	0.06	28.11 (4)	< 0.001*		
Bangalore	62	Exp	20.33	9	19.62	1	1.96	22	22.53	9	9.52	2	0.95	1	2.05	2	0.09	21.87 (4)	< 0.001*		
Mysore	104	Obs	58	7	12.32	2	1.64	2	6.27	7	2.41	0	0.32	0	0.69	1	0.04	17.64 (4)	< 0.01*		
Ernakulam	56	Exp	32.04	10	14.23	3	2.71	7	10.74	10	6.09	1	1.16	1	1.19	0	0.13	6.09 (4)	> 0.10		
Fort Cochin	62	Obs	29	11	16.84	1	1.40	8	8.16	13	6.32	1	0.53	2	1.09	0	0.07	19.37 (4)	< 0.001*		
Trivandrum	57	Exp	25.07	26	15.47	2	2.69	8	8.14	12	6.69	3	1.02	1	0.84	0	0.15	19.29 (4)	< 0.001*		
Kanniya Kumari	55	Obs	26	10	18.84	1	2.69	8	8.14	12	6.69	3	1.02	1	0.84	0	0.15	19.29 (4)	< 0.001*		

* Significant. Values in parentheses indicate degrees of freedom.

Table III. Observed and expected numbers of different interchromosomal combinations (In(2R)NS and In(3R)C) in Indian natural populations of *D melanogaster*.

Population	Total No of larvae examined	Karyotype combinations												χ^2	P				
		2R		3R		ST/ST		ST/ST		ST/ST		ST/ST				ST/ST		ST/ST	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp			Obs	Exp	Obs	Exp
Tirupati	54	Obs 30	5	Obs 30	5	Obs 30	5	Obs 30	5	Obs 30	5	Obs 30	5	Obs 30	5	Obs 30	5	15.04 (4)	< 0.01*
Madras	41	Exp 23.98	10.37	Exp 23.98	10.37	Exp 23.98	10.37	Exp 23.98	10.37	Exp 23.98	10.37	Exp 23.98	10.37	Exp 23.98	10.37	Exp 23.98	10.37		
		Obs 26	0	Obs 26	0	Obs 26	0	Obs 26	0	Obs 26	0	Obs 26	0	Obs 26	0	Obs 26	0	21.00 (2)	< 0.001*
Bangalore	62	Exp 20.29	5.71	Exp 20.29	5.71	Exp 20.29	5.71	Exp 20.29	5.71	Exp 20.29	5.71	Exp 20.29	5.71	Exp 20.29	5.71	Exp 20.29	5.71		
		Obs 39	4	Obs 39	4	Obs 39	4	Obs 39	4	Obs 39	4	Obs 39	4	Obs 39	4	Obs 39	4	17.23 (4)	< 0.01*
Mysore	104	Exp 33.35	9.94	Exp 33.35	9.94	Exp 33.35	9.94	Exp 33.35	9.94	Exp 33.35	9.94	Exp 33.35	9.94	Exp 33.35	9.94	Exp 33.35	9.94		
		Obs 63	4	Obs 63	4	Obs 63	4	Obs 63	4	Obs 63	4	Obs 63	4	Obs 63	4	Obs 63	4	46.20 (4)	< 0.001*
Ernakulam	56	Exp 48.38	18.31	Exp 48.38	18.31	Exp 48.38	18.31	Exp 48.38	18.31	Exp 48.38	18.31	Exp 48.38	18.31	Exp 48.38	18.31	Exp 48.38	18.31		
		Obs 32	0	Obs 32	0	Obs 32	0	Obs 32	0	Obs 32	0	Obs 32	0	Obs 32	0	Obs 32	0	31.05 (2)	< 0.001*
Fort Cochin	62	Exp 22.86	9.14	Exp 22.86	9.14	Exp 22.86	9.14	Exp 22.86	9.14	Exp 22.86	9.14	Exp 22.86	9.14	Exp 22.86	9.14	Exp 22.86	9.14		
		Obs 35	5	Obs 35	5	Obs 35	5	Obs 35	5	Obs 35	5	Obs 35	5	Obs 35	5	Obs 35	5	9.59 (2)	< 0.01*
Trivandrum	57	Exp 30.32	9.68	Exp 30.32	9.68	Exp 30.32	9.68	Exp 30.32	9.68	Exp 30.32	9.68	Exp 30.32	9.68	Exp 30.32	9.68	Exp 30.32	9.68		
		Obs 30	2	Obs 30	2	Obs 30	2	Obs 30	2	Obs 30	2	Obs 30	2	Obs 30	2	Obs 30	2	14.67 (2)	< 0.001*
Kanniya Kumari	55	Exp 24.14	7.86	Exp 24.14	7.86	Exp 24.14	7.86	Exp 24.14	7.86	Exp 24.14	7.86	Exp 24.14	7.86	Exp 24.14	7.86	Exp 24.14	7.86		
		Obs 32	1	Obs 32	1	Obs 32	1	Obs 32	1	Obs 32	1	Obs 32	1	Obs 32	1	Obs 32	1	25.17 (2)	< 0.001*
		Exp 24.00	9.00	Exp 24.00	9.00	Exp 24.00	9.00	Exp 24.00	9.00	Exp 24.00	9.00	Exp 24.00	9.00	Exp 24.00	9.00	Exp 24.00	9.00		

*Significant. Values in parentheses indicate degrees of freedom.

Table IV. Correlation coefficients (r) between 2 inversion karyotypes in different chromosome arms (interchromosomal associations) of *D melanogaster*.

Population	<i>In(2L)t/In(3R)P</i>			<i>In(2R)NS/In(3R)C</i>		
	r	df	P	r	df	P
Jammu	0.267 1	59	< 0.05*	—	—	—
Guwahati	0.348 3	98	< 0.001*	—	—	—
Patna	0.318 3	57	< 0.02*	—	—	—
Shillong	0.064 6	64	> 0.10	—	—	—
Ghazipur	0.299 5	76	< 0.01*	—	—	—
Mirzapur	0.562 2	71	< 0.001*	—	—	—
Tirupati	0.250 8	52	> 0.05	0.513 9	52	< 0.001*
Madras	0.309 1	39	< 0.05*	0.714 0	39	< 0.001*
Bangalore	0.564 2	60	< 0.001*	0.420 4	60	< 0.001*
Mysore	0.619 8	102	< 0.001*	0.531 7	102	< 0.001*
Ernakulam	0.393 6	54	< 0.01*	0.738 1	54	< 0.001*
Fort Cochin	0.179 7	60	> 0.10	0.324 6	60	< 0.02*
Trivandrum	0.325 7	55	< 0.02*	0.506 1	55	< 0.001*
Kanniya Kumari	0.360 6	53	< 0.01*	0.674 1	53	< 0.001*

*Significant.

DISCUSSION

The results of the present study indicate that Indian populations of *D melanogaster* are highly polymorphic for chromosome inversions and several inversions have widespread geographical distribution. When it was possible to analyze chromosome interactions, no evidence for non-random associations between linked inversions was found in any of the populations studied. Based on this, it is suggested that evidence for epistatic interaction between linked inversions is lacking in Indian populations of *D melanogaster*. Similar results were reported earlier by the present authors (Das and Singh, 1990) who studied this phenomenon in 6 natural populations of *D melanogaster* from north India. Non-random associations (linkage disequilibrium) between linked inversions resulting from interaction have been found in certain populations from Japan, Greece, Australasia, America, Korea, Tunisia and Congo (Alahiotis *et al*, 1976; Choi, 1977; Langley *et al*, 1977; Inoue and Watanabe, 1979; Yamaguchi *et al*, 1980; Knibb *et al*, 1981; Aulard and Lemeunier, 1985) but not in others (Mukai *et al*, 1974; Stalker, 1976; Mukai and Voelker, 1977; Voelker *et al*, 1977; Paik and Yang, 1983; Yamazaki *et al*, 1984; Aulard and Lemeunier, 1985). It is believed that linkage disequilibrium is most easily produced under a 2-allele system and its occurrence becomes more difficult as the number of alleles present in the populations increases (Yamazaki *et al*, 1984). Also, it is possible that most polymorphic loci are of multiple allele systems (Singh *et al*, 1975). Therefore, it is highly likely that the non-occurrence of linkage disequilibrium between inversions in natural populations of *D melanogaster* in the majority of studies may be to its

highly developed chromosome inversion system. However, non-random associations of linked inversions occur in other species of *Drosophila* (Levitan, 1958; Levitan and Salzano, 1959; Brncic, 1961; Mather, 1963; Stalker, 1964; Prakash, 1967; Sperlich and Feuerbach-Mravlag, 1974; Singh, 1983, 1984; Shyamala *et al.*, 1989). In most cases it is maintained in the populations by natural selection involving epistatic interaction between linked gene arrangements. However, in the absence of selection, recombination over years will lead to a random association causing linkage equilibrium between the 2 physically linked inversions, if present for a long time in a population. Linkage disequilibrium may also occur due to suppression of crossing-over (Sperlich and Feuerbach-Mravlag, 1974) and genetic drift (Singh and Singh, 1990a, b).

In *Drosophila melanogaster* all the 4 major autosomal arms are highly polymorphic for inversions and 4 common cosmopolitan inversions are located in each of them. Besides the 4 common cosmopolitan inversions, 2 rare cosmopolitan inversions in 3R and 1 recurrent endemic inversion in 3L are widespread in Indian natural populations. Thus, it offers a good opportunity to test epistatic interaction between unlinked inversions. In our earlier study (Das and Singh, 1990), no evidence for interaction between unlinked inversions in 6 natural populations of *D. melanogaster* was found as various interchromosomal associations occurred randomly. During the present study it has been found that karyotypes of different chromosomes in several comparisons are associated randomly in 14 Indian natural populations of *D. melanogaster*. However, epistatic interaction between unlinked inversions could be detected between IN(2R)NS and IN(3R)C in 8 populations from south Indian and between In(2L)t and In(3R)P in 11 populations coming from both north and south. Thus, our results from Indian populations clearly show that certain inversions on different chromosomes may show epistatic interaction (interchromosomal interaction). Furthermore, the same inversions may show interaction in some populations but not in others.

Choi (1977) tested interchromosomal interaction in a Korean population of *D. melanogaster* but could not find significant deviation from expectation in any of the combinations tested. However, he detected an excess of double heterozygotes in all cases. Inoue and Watanabe (1979) also found no evidence for interchromosomal interaction in Japanese populations of *D. melanogaster* as various karyotypes on different chromosomes were associated randomly. Knibb *et al.* (1981) studied 50 individual comparisons of associations between pairs of unlinked inversions in 19 Australasia samples and detected only 2 significant associations (In(2L)t–In(3L)P and In(2L)t–In(3R)P) in the 2 populations. Interestingly, they found that the northern populations were characterized by a consistent deficiency of gametes with inversions in both autosomes whereas the populations from the south had an excess of gametes having inversions in both autosomes. Thus, our results are in agreement with those of Knibb *et al.*, (1981) that certain unlinked inversions may show epistatic interactions in certain populations which may be considered adaptive. Yamazaki *et al.* (1984) also obtained data on interchromosomal associations in 2 Japanese populations of *D. melanogaster* which do not indicate the existence of interchromosomal interaction. Aulard and Lemeunier (1985) analysed 3 populations of *D. melanogaster* from France, Tunisia and Congo and found significant non-random association between second and third chromosomes bearing inversions (data

of different inversions combined) in the French and Congolese populations but not in the Tunisian populations. However, when inversions were tested independently, no significant deviation was detected in any of the populations studied.

It is evident from the results obtained in *D melanogaster* populations from different regions of the world (including Indian populations) that various intra- and interchromosomal associations occur randomly in the majority of cases. However, there are cases in which certain intra- and interchromosomal associations occur non-randomly, resulting from selection involving epistatic interaction. Thus, certain chromosomal associations may be adaptive in a given set of environments. The variation in the result in different populations may be due to the fact that genetic factors may vary in different populations of the same species.

The intra- and interchromosomal interactions have been tested in various species of *Drosophila* and different situations exist when results from different species are compared. In *D robusta*, evidence for both intra- and interchromosomal interactions have been presented (Levitan, 1958, 1961, 1973; Prakash, 1967). In *D subobscura* intrachromosomal interaction is found but evidence for interchromosomal interaction is lacking (Sperlich and Feuerbach-Mravlag, 1974). *D ananassae* is also characterised by linkage disequilibrium between independent inversions resulting from epistatic interaction as well as suppression of crossing-over but interchromosomal interaction could not be found (Singh, 1982, 1983, 1984; Singh and Singh, 1989, 1990a,b). On the other hand, in most of the cases, evidence for intra- and interchromosomal interactions is lacking in natural populations of *D melanogaster*. However, in certain populations adaptive interactions could be detected between certain pairs of linked as well as unlinked inversions. Thus, the genetic structure of different species may be different and different species may achieve success by different modes of adjustment within their gene pools.

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