Theor. Appl. Genet. 55, 231-238 (1979)

Structural and Functional Analysis of the Scute Locus in *Drosophila melanogaster**

D.P. Furman, S.N. Rodin and V.A. Ratner
Institute of Cytology and Genetics, Siberian Department of the USSR Academy of Sciences, Novosibirsk (USSR)

Summary. The functional expression of 12 scute alleles in homozygotes and compounds of *Drosophila melanogaster* at 14°, 22°, 30°C is analysed. Based on the data obtained, linear maps for bristles and mutations are built. The basic features of the maps, clustering and polarity, are invariable with respect to temperature, scute gene dosage and cross direction. In addition local dominance of the norm over bristle reduction was produced by the scute mutation; different types of complementation reactions were established for each bristle. The gene scute is treated as an operon-like system, composed of 3-4 cistrons with each controlling the formation of bristles on a particular region of the fly's body. This model argues well with the structure of maps constructed and implies a post-translational level of initial events of bristle-formation process.

Key words: *Drosophila melanogaster* – Scute locus – Maps – Operon-like model

Introduction

It has been long realised that the locus scute, which controls the formation of bristles in *Drosophila melanogaster*, has a complex internal structure (Dubinin 1929). Various mutations of this gene affect different groups of macrochaetae on the fly's body.

Comparisons of the phenotypic expression of the numerous step-alleles of the scute locus made it possible to arrange the indices of the reduced bristles in the scute mutants in an orderly manner; the linear series obtained was interpreted as being the genetic map of the scute region (Dubinin 1933).

It was then found that the phenotypic expression of the scute locus alleles is easily modified by a number of factors (Child 1935). The phenotypic patterns were so 'kaleidoscopic' that it seemed doubtful whether the linear arrangement of the scute bristles had the properties of a true genetic map. A definite answer could not be given at that time (Sturtevant and Schultz 1931; Raffel and Muller 1940).

With the development of mapping procedures the search for 'map invariants' was offered a new approach to the problem of step-allelism at the scute locus. This search proceeds in the following manner: if a map faithfully reflects the real topography of the scute locus, analysis of its mutants should reveal some of the map features that are invariable with respect to factors affecting the scute phenotype.

Materials and Methods

12 laboratory scute stocks were used in the experiments: sc1w^a, ysc5, sc6w^a, sc7y f, sc8w^a, sc9 Bx f t w^a, sc3B, y scD1, y scD2, sc28 w^a, sc260-22 w^a and sc$V2^{nh}$.

Bristle mutations, in response to different environmental temperatures (14°, 22°, 30°C), were recorded in the scute homo- and heterozygotes (compounds), obtained in direct and reciprocal crosses. Bristle mutations were estimated as presence or absence of reduction for each of the twenty bristle pairs. In all, 120,000 flies, representing 468 genotypes, at three different temperatures, were examined. The percentages of reduced bristles in homozygotes and compounds were estimated. The values are given in the matrix of functional expression (MFE) 'genotypes × bristles'. Based on the MFE matrices, an attempt was made to identify the structure of the scute locus by mapping bristles and mutants. To form a series of scute alleles the MFE matrix was transformed into a matrix of functional differences between the mutants (MFD) (Ratner and Rodin 1976). The MFD is a matrix in which each item expresses the total difference in bristle reduction percentages (Table 1). The MFD was then rearranged in such a way that the closeness of mutants in the linear series was directly related to the total difference in reduction percentages. In this matrix mutants were found

* This paper is based on the report presented at XIV International Congress of Genetics (Moscow, August 1978)

0040-5752/79/0055/0231/$ 1.60

Table 1. Matrix of functional differences between scute mutants of *Drosophila melanogaster* based on bristle reduction percentages in mutant homozygous females at 14 °C. Clusters with most similar mutants are assigned to four groups

	scD1	sc9	sc7	sc1	scD2	sc6	sc3B	sc28	sc260	sc5	sc8	scV2
scD1	0	2694	3418	4078	5178	6563	7434	11 966	11 162	13 648	15 850	16 971
sc9	2694	0	2506	3136	3388	5877	5484	10 374	10 276	11 714	13 528	14 925
sc7	3418	2506	0	4076	3324	6033	5432	10 208	9584	11 490	13 712	14 601
sc1	4078	3136	4076	0	2528	2863	4744	11 124	11 904	10 330	12 508	13 825
scD2	5178	3388	3324	2528	0	2841	3176	9320	10 344	8742	10 716	12 025
sc6	6563	5877	6033	2863	2841	0	5095	11 243	12 271	9361	10 481	11 922
sc3B	7434	5484	5432	4744	3176	5095	0	6420	7232	6358	8584	10 237
sc28	11 966	10 374	10 208	11 124	9320	11 243	6420	0	1056	1890	4064	6083
sc260	11 162	10 276	9584	11 904	10 344	12 271	7232	1056	0	2918	5092	7107
sc5	13 648	11 714	11 490	10 330	8749	9361	6358	1890	2918	0	2334	4248
sc8	15 850	13 528	13 712	12 508	10 716	10 481	8584	4064	5092	2334	0	2643
scV2	16 971	14 925	14 601	13 825	12 025	11 922	10 237	6083	7107	4248	2643	0

to be clustered. The clusters were grouped so that the maximum total difference of bristle reduction percentages within a cluster was less than the minimum one outside it and so each cluster consisted of a maximum number of mutants. As a result, two culsters of mutants, containing five mutants each, were identified. Mutants sc6 and sc3B form separate clusters (Table 1).

It should be noted that for matrices of the same size consisting of random similarity values the probability for reduction of the matrix to a linear form is null. Hence, the feasibility of such an orderly linear arrangement indicates that it does capture important structural and functional features of the locus.

The second approach was to group bristles with close reduction percentages. The results are summerized in Table 2. It was also found that this grouping of bristles gives rise to clusters. In Table 2 clusters differing sharply in the reduction percentage of at least 1-2 mutant bristles, are separated from each other.

The mutations were aligned first, then the bristles. All these arrays are set out in the maps of functional expression (Table 2) (Furman, Rodin and Ratner 1977a).

Results and Discussion

The conclusions made from analysis of maps built for scute homozygotes (males and females) are as follows:

1) Each linear series has 4 clusters of mutants and bristles. The good correlations between clusters of mutations and bristles indicate that the map has a polar structure. The first cluster consists of sc1, sc7, sc9, scD1, scD2 mutants and pa^1 bristle; the second one is composed of sc6 and n^1 bristle; the allele sc3B and bristles oc^{1-2}, pv^{1-2} and or^{1-2} form the third cluster; alleles sc5, sc8, sc28, sc260-22, scV2 and sc^{1-2} and sc^{3-4} bristles are assigned to the last cluster (Table 2).

2) The number of mutant and bristle clusters, their set and mutual location are invariant with respect to temperature and dosage of the scute gene; however, their linearity within a cluster is affected by these factors.

Table 2a-c. Map of functional expressions of the scute locus of *Drosophila melanogaster* males at 14 °(a), 22 °(b) and 30 °C (c). Continuous vertical lines separate bristle clusters.

a

	pa^1		n^1		or^1		oc^{1-2}		pv^{1-2}		or^2		sc^{1-2}		sc^{3-4}	
	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
scD1	90	92	100	100	100	100	99	99	94	93	80	81	97	98	95	97
sc9	80	79	100	100	100	100	100	100	95	96	64	62	99	99	96	96
sc7	33	35	100	100	99	99	100	100	99	100	65	67	93	91	97	97
sc1	58	58	100	100	100	100	100	100	100	100	94	92	60	61	67	68
scD2	23	24	100	100	100	100	100	100	93	94	68	70	57	65	42	38
sc6	17	18	100	99	99	99	100	100	75	80	92	89			1	2
sc3B	12	11			100	100	95	94	70	71	64	66	70	74	68	69
sc260	1	1											99	100	91	92
sc28													95	96	54	52
sc5	2	2											27	23	43	43
scV2	4	5	6	11	1	3			4	2	6	6	11	15	18	17
sc8	3	3	3	1	1	2			2	1	2	4	8	8	5	5

b

	pa^1		n^1		pv^{1-2}		or^1		oc^{1-2}		or^2		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
scD1	44	47	100	100	92	92	100	100	88	88	83	81	99	98	99	99
sc9	52	52	100	100	95	93	100	100	100	100	96	95	100	100	96	96
sc7	1	2	100	100	94	95	100	100	98	99	78	80	99	98	94	96
sc1	5	6	100	100	97	96	100	100	100	100	98	98	84	88	58	60
scD2			100	100	89	88	100	100	95	96	84	85	64	68	55	56
sc6	1	1	93	89	73	79	100	100	99	99	99	99	2	3	1	
sc3B	1	1			34	38	100	100	76	76	74	71	93	92	62	60
sc260					1	1							100	100	100	100
sc28	2	3	1	1	1	2							99	99	97	94
sc5													69	68	18	17
sc8	3	3	2	1	1	1	2	2			5	4	19	19	37	40
scV2		1	4	4	2	3	6	3			8	9	24	24	23	22

c

	pa^1		n^1		oc^{1-2}		or^2		pv^{1-2}		or^1		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
sc9	42	43	93	99	99	100	84	87	100	100	99	97	100	100	99	99
sc1	2	1	100	100	91	92	96	95	100	100	99	99	99	100	96	98
sc7			100	100	71	70	74	72	100	99	99	100	100	100	96	98
scD2			92	91	86	85	39	35	100	100	98	99	92	94	72	70
scD1	1	1	97	97	49	49	43	43	97	96	93	95	99	99	97	97
sc6			77	74	97	97	99	97	99	99	93	93	17	16	8	8
sc3B					17	17	36	37	92	89	97	97	99	99	86	91
sc260			1	1		1						1	100	100	100	100
sc28	1		1	1		1			1	1	1	2	80	79	79	79
sc5									1	1	5	6	87	88	48	47
sc8	2	2	3	3		1	1		1		1		53	54	83	81
scV2			1	1		1		1	1				8	9	11	11

This means that linearity and clustering are essential features of the system and, hence, the maps constructed reflect real structures of the locus or its product(s) with a precision corresponding to the internal structure of clusters.

Matrices for the bristle reduction in compounds were treated in the same way. The basic data, the genotypes, having a common allele derived from a parent of one sex, were assigned to groups. This common allele was the reference allele (Furman, Rodin and Ratner 1977b).

It was found that map building, based on non-reference alleles, depends on the cluster of homozygotes to which the reference allele is assigned in the map. Depending on the reference allele, three types of assignments are possible:

1) The reference allele belongs to the first cluster of homozygotes. The maps of bristles and non-reference mutations are easily built. They do not differ from the respective maps of homozygotes: the same clusters of mutants and bristles are identified, the number, set and order of clusters are also invariable under different temperature conditions (Tables 3, 4).

2) The reference allele belongs to the second or third cluster of the map of homozygotes. While some details of cluster structure are reproduced faithfully, map building for the whole set of mutations and bristles is impossible (Table 5).

3) Alleles of the fourth cluster on the map of homozygotes serve as references. The non-reference alleles cannot be mapped. The bristles retained on the map of bristles are sc^{1-2} and sc^{3-4} (Table 6).

Thus, the reference mutations show a strong polarity in their influence on the cluster-polar structure of the scute map. This is additional evidence that the cluster series identified has real meaning.

Comparisons of the reduction percentages of a bristle in homozygotes and compounds demonstrate that interallelic relationships are irreducible to dominance of the

Table 3. Matrix of functional differences between scute mutants of *Drosophila melanogaster* based on bristle reduction percentages in compounds with reference allele sc1

	scD1	sc9	sc7	sc1	scD2	sc6	sc3B	sc28	sc260	sc5	scV2	sc8
scD1	0	1719	1839	2058	2867	3582	4717	7836	7447	9147	5750	8649
sc9	1719	0	1930	1437	2282	4178	3253	7557	7482	8688	5619	8290
sc7	1839	1930	0	1283	1676	3221	3436	6611	6206	7892	4755	7410
sc1	2058	1437	1283	0	1559	2518	3375	7288	7211	7861	4788	7357
scD2	2867	2282	1676	1559	0	1753	2176	6511	6416	6460	4931	6148
sc6	3582	3253	3221	2518	1753	0	2537	7480	7385	6271	5700	5921
sc3B	4717	4178	3436	3375	2176	2537	0	5301	5704	4558	5435	4672
sc28	7836	7557	6611	7288	6511	7480	5301	0	563	1379	2986	1657
sc260	7447	7482	6206	7211	6416	7385	5704	563	0	1770	2891	1886
sc5	9147	8688	7892	7861	6460	6271	4558	1379	1770	0	3807	664
scV2	5750	5619	4755	4788	4931	5700	5435	2986	2891	3807	0	3323
sc8	8649	8290	7410	7357	6148	5921	4672	1657	1886	664	3323	0

Table 4a-c. Map of functional expressions of the scute locus based on bristle reduction percentages in compounds at 14 °(a), 22 °(b) and 30 °C (c). The reference allele is sc1

a

	pa^1		n^1		or^1		oc^{1-2}		pv^{1-2}		or^2		sc^{1-2}		sc^{3-4}	
	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
scD1	44	46	100	100	100	99	98	99	70	78	68	72	74	75	58	58
sc9	11	13	100	100	100	100	100	100	90	92	60	70	43	36	65	71
sc7	24	31	100	100	100	100	100	100	80	82	23	23	53	55	36	33
sc1	35	37	100	100	100	100	100	100	89	88	54	57	26	25	37	34
scD2	8	8	100	100	100	100	100	100	73	70	32	36	32	23	6	8
sc6	17	18	100	100	100	100	100	100	56	52	88	90				
sc3B		1			100	100	100	100	58	61	5	5	6	7	12	12
scV2	28	28	52	52	34	36	23	18	17	20	36	38	33	34	38	38
sc260-22			35	27		1	1		1				52	52	27	20
sc28			6	6									43	46	20	28
sc8	15	18	16	13	8	6		2			6	5	8	7	2	2
sc5	1	3											2	1	2	6

b

	pa^1		n^1		or^1		oc^{1-2}		pv^{1-2}		or^2		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
scD1	1	2	100	100	100	100	99	96	64	57	78	80	80	86	68	76
sc9	3	1	100	100	98	99	100	100	83	80	77	76	98	97	36	34
sc7	1	2	100	98	100	100	96	94	58	51	52	51	90	91	54	58
sc1	2	4	100	100	100	100	98	99	81	82	88	86	70	69	28	30
scD2			100	100	100	100	98	98	67	71	49	55	67	56	18	29
sc6			97	98	100	100	97	98	52	48	81	78		1		
sc3B					100	99	76	76	38	34	44	46	88	86	10	12
scV2	11	8	78	77	41	44	16	20	16	12	62	67	76	70	54	61
sc8	4	4	16	14	4	8	3	1	2	2	22	19	42	44	38	38
sc260-22	1											1	82	86	61	63
sc28													88	88	46	44
sc5													60	64	6	8

c

	pa^2		oc^{1-2}		n^1		pv^{1-2}		or^1		or^2		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
sc9	2	2	94	94	86	89	99	98	91	93	81	81	100	99	74	68
sc1	1	2	94	92	100	100	97	98	99	99	74	76	100	99	84	83
sc7			75	74	98	98	99	99	99	99	84	81	99	100	94	95
scD2	2	1	78	79	88	85	98	98	98	96	30	24	80	76	34	44
scD1	2		12	13	82	82	96	96	93	96	66	58	98	100	87	80
sc6	2		34	37	54	49	98	99	90	91	83	81	19	20	7	7
sc3B			17	20	1		63	59	92	93	48	49	97	94	31	28
sc260-22													100	100	93	96
sc28				2			1						77	77	74	72
sc8						1	2		1				46	54	60	64
scV2					2					2			30	32	27	30
sc5	1							1	2	1			94	96	9	10

Table 5a-c. Map of functional expressions of the scute locus of *Drosophila melanogaster* based on bristle reduction percentages in compounds at 14 °(a), 22 °(b) and 30 °C (c). The reference allele is sc3B

a

	or^2		pv^{1-2}		oc^{1-2}		or^1		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r
scD2	9	7	65	67	99	99	100	100	20	16	14	14
sc7	21	22	47	43	98	98	100	100	24	28	40	32
scD1	31	31	65	62	99	99	100	100	37	36	42	43
sc1	45	53	45	34	98	97	100	100	53	48	9	11
sc9	23	23	80	80	100	100	99	99	75	73	37	45
sc6	25	25	43	43	97	97	100	100	1			
sc3B	13	12	61	60	91	94	100	100	34	36	43	43
sc260-22									61	73	38	40
sc28									67	68	41	41
scV2		1			2	2	1	1	8	7	3	7
sc8	1	1				2	1		2	2	5	6
sc5									4	7	7	7

b

	or^2		pv^{1-2}		oc^{1-2}		or^1		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r
sc9	41	47	58	48	98	98	100	100	92	93	32	31
sc1	20	23	26	23	70	78	100	100	85	85	18	20
scD1	7	7	36	32	47	49	100	100	84	82	70	69
sc7	16	16	30	30	84	85	99	99	60	55	24	22
scD2	9	9	36	36	81	82	100	100	38	45	9	4
sc6	18	26	24	32	82	83	100	100				
sc3B	26	25	17	17	71	70	100	100	68	70	19	18
sc28									91	93	54	50
sc260									87	85	18	25
scV2	15	10			2	2	11	8	50	51	27	27
sc5							1	1	49	48	2	1
sc8									8	7	3	2

c

	or^2		oc^{1-2}		or^1		pv^{1-2}		sc^{3-4}		sc^{1-2}	
	l	r	l	r	l	r	l	r	l	r	l	r
sc9	13	13	83	84	97	97	98	97	95	94	15	11
scD2	21	21	31	26	96	96	88	84	87	85	20	20
scD1	17	18	19	20	98	97	91	92	93	91	33	29
sc7	26	26	23	20	97	97	90	86	87	88	59	54
sc1	23	23	17	14	94	94	88	84	99	98	27	31
sc6	36	36	13	13	86	86	91	95	5	5	1	1
sc3B	15	16	14	12	97	97	82	79	89	91	48	52
sc260-22									95	95	58	61
sc28			1		1	3			96	95	48	54
sc5					10	5	2		63	71	12	9
sc8									5	6	13	12
scV2					3	3	1	1	10	10	7	6

Table 6. Matrix of functional differences between scute mutants of *Drosophila melanogaster* based on bristle reduction percentages in compounds with reference allele sc8. Mutants cannot be assigned to clusters in this matrix

	scD1	sc9	sc7	sc1	scD2	sc6	sc3B	sc28	sc260	sc5	scV2	sc8
scD1	0	380	385	304	368	439	339	280	388	332	509	1364
sc8	380	0	369	362	432	537	549	370	562	446	535	1464
sc7	385	369	0	483	377	600	648	521	665	543	672	1613
sc1	304	362	483	0	448	337	271	288	316	214	335	1288
scD2	368	432	377	448	0	633	669	562	688	608	695	1648
sc6	439	537	600	337	633	0	174	323	261	221	368	1229
sc3B	339	549	648	271	669	174	0	229	135	129	348	1137
sc28	280	370	521	288	562	323	229	0	248	168	403	1216
sc260	388	562	665	316	688	261	135	248	0	164	319	1152
sc5	332	446	543	214	608	221	129	168	164	0	297	1168
scV2	509	535	672	335	695	368	348	403	319	297	0	1209
sc8	1364	1464	1613	1288	1648	1229	1137	1216	1152	1168	1209	0

norm over scute mutation. Three types of complementation reactions were distinguished: (1) positive complementation (the reduction percentage is lower in compounds), (2) negative complementation (compounds are predominantly formed by homozygotes with large percentage of bristle reduction), (3) anti-complementation (the bristle reduction percentage in the compound unexpectedly exceeds that in the respective contributing homozygotes). One of these three complementation types are observed for one-two bristles in virtually all the crosses. Mutants in compounds show most clearly the complementation for bristles assigned to the same clusters on the map of homozygotes; i.e., they show polarity and clustering of complementation (Table 7).

Despite its seeming complexity, four essential features may be identified in the diverse mutational expressions at the scute locus (Furman, Rodin and Ratner 1977c). These features make genetic-molecular models of the locus workable: (1) map linearity, (2) invariance of clusters (their number, set and mutual location) with respect to temperature and the dosage of the scute gene, (3) instability of the internal structure of clusters, (4) variability of the functional expression of the scute gene in compounds. This variability depends on the allele chosen as reference.

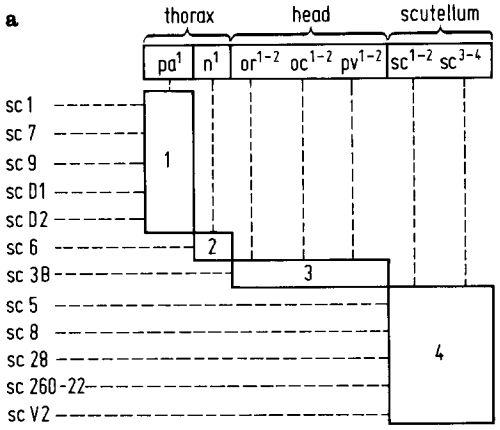
From this analysis a model was developed in which the locus scute is envisaged as an operon-like system (Furman, Rodin and Ratner (1977c). This suggested system may consist of several cistrons, corresponding to clusters on the map of mutational expression. Transciption is thought to propagate wave-like from one cistron to another. The products of these cistrons are homomultimers that trigger bristle formation in a particular region of the fly's body (Fig. 1). In the framework of this model, map linearity is determined by the linear arrangement of cistrons; mutations, inactivating the formation of bristle groups, are

Table 7. Types of complementation reactions in scute compounds at 14 °C*

	sc9	scD1	sc1	sc7	scD2	sc6	sc3B	sc28	sc260-22	sc5	sc8	scV_2
sc9	–	pa^1 ⊕	pa^1 ⊕	pa^1 +	or^2 + pa^1 –		$sc^{1,2}$ or^2 –	$sc^{3,4}$ •	$sc^{3,4}$ –	sc –	sc –?	ps•?
scD1	pa^1 ⊕	–	pa^1 +?	pv ⊕		pv + or^2 +		sc ⊕	$sc^{3,4}$ +	$sc^{3,4}$ + $sc^{1,2}$ –	$sc^{1,2}$ –	
sc1	pa^1 ⊕	pa^1 +?	–			or^2 –	pv ⊕ sc ⊕	$sc^{3,4}$ –	sc + n^1 –	sc +		
sc7	pa^1 ⊕	pv ⊕		–	or^2 + pv –		pv ⊕ $sc^{3,4}$ +	$sc^{3,4}$ –	$sc^{3,4}$ +	$sc^{3,4}$ + $sc^{1,2}$ –	$sc^{1,2}$ – pa^1 –?	
scD2	or^2 + pa^1 –			or^2 + pv –	–	pv + pa^1 +	$sc^{1,2}$ ⊕		$sc^{1,2}$ –	$sc^{3,4}$ +		ps• pa• sc•
sc6		pv + or^2 +	or^2 –		pv + pa^1 +	–	pv ⊕	oc –	oc –?			pa^1 • or^3 •?
sc3B	sc +? or –		pv ⊕ sc ⊕	pv ⊕ $sc^{3,4}$ +	$sc^{1,2}$ ⊕	pv ⊕	–	$sc^{1,2}$ + $sc^{3,4}$ –		$sc^{3,4}$ +		
sc28	$sc^{3,4}$ •?	sc ⊕	sc +	$sc^{3,4}$ –		oc –	$sc^{1,2}$ + $sc^{3,4}$ –	–	$sc^{3,4}$ ⊖	sc ⊖		sc ⊙
sc260-22	$sc^{3,4}$ +	$sc^{3,4}$ –	sc + n^1 –	$sc^{3,4}$ ⊕	$sc^{1,2}$ –	oc –		$sc^{3,4}$ –	sc ⊖	sc ⊖		
sc5	sc –	$sc^{3,4}$ + $sc^{1,2}$ –	sc +	$sc^{3,4}$ + $sc^{1,2}$ –			$sc^{3,4}$ +	sc ⊖	–	–	$sc^{1,2}$ •?	sc ⊙
sc8	sc –?	$sc^{1,2}$ –		$sc^{1,2}$ – pa^1 –?	$sc^{3,4}$ +					$sc^{1,2}$ •?	–	
scV_2	ps•?				ps• pa• sc•	pa^1 • or^3 •?		sc ⊙		sc ⊙		–

* Brackets indicate strong complementation, + = positive; – = negative; • = anticomplementation

polar. The identified sequence of clusters is a reliable genetic map of the locus and, consequently, the map is invariable with respect to external factors and gene dosage. Instability of the internal ordering of mutants and bristles, as well as complementation, indicates that the cistron products are active as homomultimers. The instability of the internal structure of clusters may be explained by the thermal sensitivity of protein. Differences in the expression of compounds with different reference alleles are also easily explained. Polar mutations of cluster 1 on the map of homozygotes have deeper consequences and do not hinder the expression of non-reference alleles in compounds. The reference alleles of cluster IV affect solely the last cistron, the products of the preceding ones interact with those of the non-reference mutants, thereby giving rise to an intricate pattern of the functional expression of the scute gene.



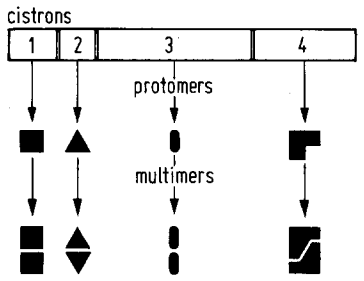


Fig. 1a and b. A model for the structural and functional organization of the scute locus in *Drosophila melanogaster*. a the map of functional expression of the scute locus; four invariant clusters are separated in this map; b a tentative model of the locus derived from the map

Acknowledgement

The authors express their gratitude to Dr. Irwin I. Oster (Bowling Green State University, Ohio, USA) and Dr. E.B. Lewis (California Institute of Technology, California, USA) for kindly providing them with stocks of scute mutants, and to colleagues at the Laboratory of Population Genetics for helpful discussion. Gratitude is also expressed to A.N. Fadeeva for translation of their paper from Russian into English.

Literature

Child, G.P.: Phenogenetic studies on scute-I *Drosophila melanogaster*. 1. The association between the bristles and modifiers and temperature. Genetics **20**, 109-126 (1935)

Dubinin, N.P.: Allelomorphentreppen bei *Drosophila melanogaster*. Biol. Zbl. **49**, 328-339 (1929)

Dubinin, N.P.: Step allelomorphism in *Drosophila melanogaster*. J. Genet. **27**, 443-464 (1933)

Furman, D.P.; Rodin, S.N.; Ratner, V.A.: Investigation of the genetic topography of the locus scute in *Drosophila melanogaster*. 3. Thermal effect on the maps of functional manifestation of homozygotes. Genetics (Russ.) **XIII**, 1042-1053 (1977a)

Furman, D.P.; Rodin, S.N.; Ratner, V.A.: Investigation of the genetic topography of the locus scute in *Drosophila melanogaster*. 4. Thermal effect on the functional manifestation in heterozygotes. Genetics (Russ.) **XIII**, 1220-1232 (1977b)

Furman, D.P.; Rodin, S.N.; Ratner, V.A.: Investigation of the genetic topography of the locus scute in *Drosophila melanogaster*. 5. Maps of the functional manifestation of heterozygotes and the model for the scute locus. Genetics (Russ.) **XIII**, 1387-1397 (1977c)

Ratner, V.A.; Rodin, S.N.: Theoretical aspects of genetic complementation. In: Progress in Theoretical Biology (eds. Rosen, R.; Snell, F.M.), Vol. 4, pp. 1-63. New York-London: Academic Press 1976

Ruffel, D.; Muller, H.J.: Position effect and gene divisibility considered in connection with three strikingly similar scute mutations. Genetics **25**, 541-583 (1940)

Sturtevant, A.H.; Schultz, J.: The inadequacy of the sub-gene hypothesis of the nature of the scute allelomorphs of *Drosophila*. Proc. Nat. Acad. Sci. (USA) **17**, 265-270 (1931)

Received February 23, 1979
Communicated by D.K. Belyaev

Dr. D.P. Furman
Dr. S.N. Rodin
Dr. V.A. Ratner
Institute of Cytology and Genetics
Siberian Department of the USSR Academy of Sciences
Novosibirsk 90 (USSR)