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Pattern mosaicism for behaviour controlled by the *yellow* locus in *Drosophila melanogaster*

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SUMMARY

Some *yellow* alleles which show full expression of the mutant phenotype have behavioural defects, including reduced locomotor activity and a low level of male competitive mating success. Other *yellow* alleles produce pattern mosaics in which some cuticular structures are *yellow* and others wild type within the same individual. The pattern mosaic expression of these alleles extends to behaviour. Mosaicism in respect of the different pleiotropic effects reveals something about the possible mode of action of this locus on behaviour.

1. INTRODUCTION

Mutant alleles at the *yellow* locus (*y*-1 : 0·0) differ in their effects on the cuticular pigmentary phenotype. Green (1961), Nash & Yarkin (1974) and Nash (1976) distinguish two major classes. Type-1 mutant alleles express the mutant phenotype throughout the larval and adult cuticle. Type-2 mutant alleles display pattern mosaicism, in which some larval or adult cuticular structures are mutant and others are wild type in phenotype. According to Nash (1976) these *y* pattern mosaics have the appropriate phenotypic expression of regulatory mutants which alter the time or place of gene expression. The alleles in these two classes appear to represent mutations in functionally distinct regions of the *yellow* locus. Fine-structure mapping indicates that alleles of type-1 are located in a region to the left of alleles of type-2. The latter would constitute the regulatory region controlling the expression of the structural gene to which the type-1 alleles cluster.

Some type-1 alleles are known to have pleiotropic effects on behaviour (Wilson *et al.* 1976). The *yellow* mutants show a reduced level of locomotor activity and low male competitive mating ability. Whilst it may be a contributory factor, lower locomotor activity is not the principal reason for the decrement in mating success of *yellow* males, and different suggestions have been made as to how this may be caused. Bastock (1956) concluded that *yellow* males have a lower level of sexual motivation than normal males. Burnet & Connolly (1974) have suggested that the *yellow* gene is involved in the control of tyrosine and 3,4-dihydroxyphenylalanine utilization, and affects the pathways leading to the synthesis of both

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the pigment melanin and catecholamines affecting neural transmission. The absence of melanin results in the yellow body colour, and the impairment of catecholamine production could imply that the behavioural effects of the *yellow* gene have a neurochemical basis. An alternative explanation, offered by Wilson *et al.* (1976), is that impairment of the mating ability of mutant males is a consequence of the effects of the gene on the cuticle, affecting the efficiency of the secondary sexual structures, the sex-combs and genital apparatus, which are required for copulation.

The pattern mosaicism of type-2 *yellow* alleles affords a direct method for testing the effects upon male mating success of *yellow* mutant gene expression in different external cuticular structures, and so of testing the effect on a male of having mutant sex-combs in combination with wild-type external genitalia, and *vice versa*. At a more fundamental level, investigating the effects of type-2 alleles may shed some light on the control network regulating the action of a gene affecting behaviour.

2. MATERIALS AND METHODS

(i) *Stocks*

The *yellow* alleles referred to here fall into two groups according to whether the mutant phenotype is fully or partially expressed in the adult body cuticle and its associated structures. The allele y^{59B} is a type-1 mutant which shows complete expression of the *yellow* phenotype. Alleles y^2, y^{b1} and y^{bab} are type-2 mutants which determine the *yellow* phenotype in some cuticular structures and the wild type phenotype in others. The pattern of expression of these alleles is indicated in Table 1. More detailed description is given by Nash & Yarkin (1974).

(ii) *Experimental procedures*

Special care was taken to control for the effects of residual genetic variation within stocks used for behavioural studies by crossing each *yellow* allele into an isogenic wild type stock. The isogenic stocks used were Novosibirsk and Oregon. Repeated backcrossing and re-isolation of the mutant in the inbred background was performed for at least 25 generations before experiments were begun. Observations were made using adult male flies obtained from the backcross of $+/y$ heterozygous females to hemizygous wild type males. The male offspring consist of equal numbers of wild type and *yellow* mutants which were collected daily and transferred to fresh feeding vials. For behavioural tests the wild type and mutant males to be compared were always full sibs raised in the same cultures to control for environmental variables.

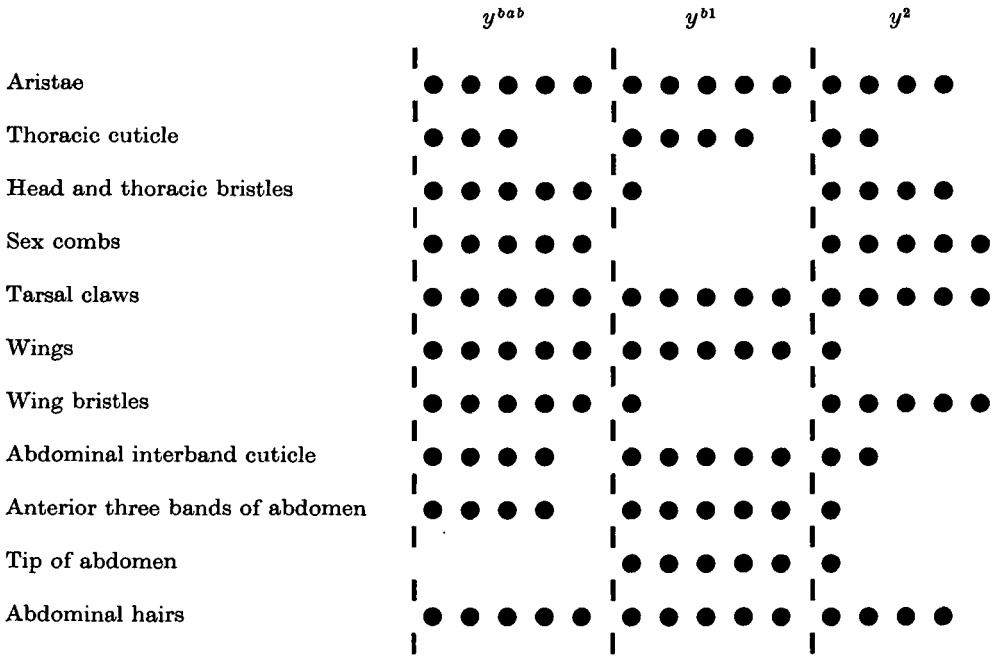
All experiments were performed at 25 °C under standardized conditions of illumination, and unless stated to the contrary all flies were aged 3 days after eclosion, and were transferred to the apparatus for observation without anaesthetization.

Locomotor activity was observed using single individuals in a $10 \times 10 \times 0{\cdot}8$ cm deep white Perspex box fitted with a clear lid on which was engraved a lattice of

1 cm squares. Each fly was observed under a binocular dissecting microscope and its behaviour recorded using a multichannel serial time/event recorder with continuous time base. Unless otherwise indicated each fly was observed for 100 s beginning 2 min after the fly entered the apparatus. Further details of the method are given by Wilson, Burnet & Connolly (1976).

Table 1. *The pattern of phenotypic expression for type-2 mutant alleles in adult male flies*

(The scale of expression for each structure varies from wild type (five points) to completely *yellow* (zero points). The allele y^{59B} has a score of zero for every structure on this scale. (Modified from Nash & Yarkin, 1974.)



Courtship behaviour was observed in 19 mm diameter, 7 mm deep, white plastic cells fitted with a clear Perspex lid using single pair matings. The elements of courtship behaviour were recorded, using the multichannel event recorder with continuous time base. Measures were made manually from the permanent ink traces on the chartrolls. Courtship latency was measured from the time of entry of the pair of flies into the chamber until the beginning of courtship by the male. Competitive matings were observed using a single female and two competing males of different genotype. The female always entered the cell after the two competing males. The genotype of the successful male was confirmed by inspection after rapidly immobilizing and removing the pair *in copula*.

The sex-combs were removed by amputating the foretarsi of the prothoracic legs just above the level of the combs. Amputations were carried out on the day of hatching from the pupa and the operated males were then kept in the usual way in

fresh vials and used for competitive mating experiments at age 3 days. The females used were y^{bab}/y^{b1} virgin heterozygotes. Competitions took place in $3'' \times 1''$ vials containing yeasted medium for a period of 5 days at the end of which females were removed and placed singly in fresh vials. The genotype of the successful male was determined by inspecting the daughters of each individual female. No double impregnations were found to have occurred.

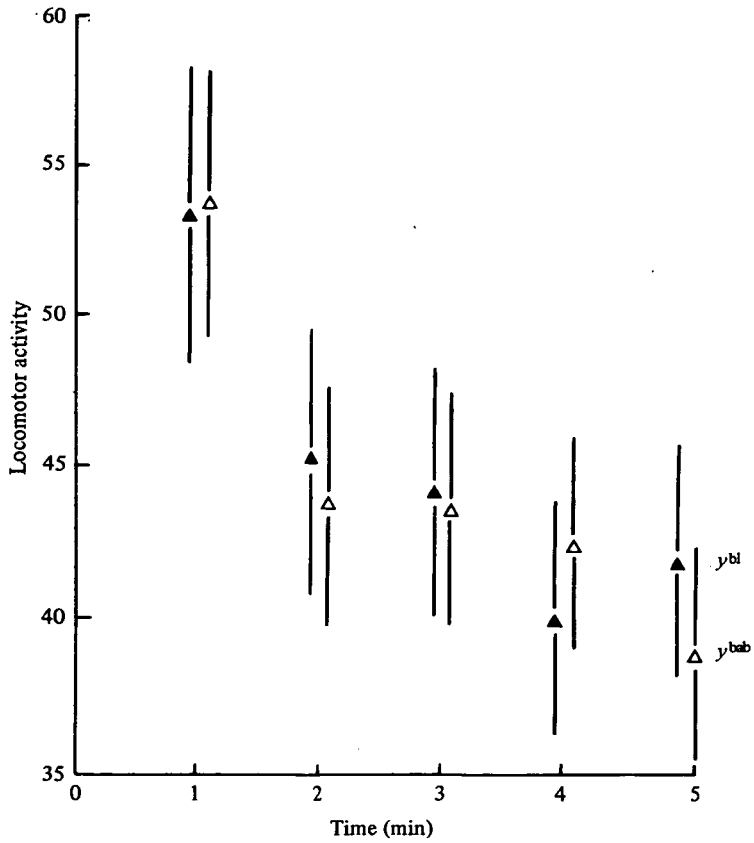


Fig. 1. Comparison of the locomotor activity of 3-day-old y^{b1} and y^{bab} mutant males, measured as the number of squares in the activity chamber entered per min (n = 50 for each genotype group)

3. RESULTS

(i) *Adult locomotor activity*

A single fly placed in an activity chamber shows an initially high level of locomotor activity which rapidly decays to a more stable value. The effect is caused by the initial reactivity of the fly to its surroundings (Fig. 1). The stable value to which the activity score tends over the first 4–5 min is a reflection of the spontaneous locomotor activity of the fly (Connolly, 1967).

A reduced level of locomotor activity may contribute to the decrement in mating

success shown by *yellow* mutant males. Since most wild type males successfully copulate within 4–5 mins, any differences in the pattern of locomotor activity relevant to mating success would have to be expressed during this period in which the two components, reactivity and spontaneous activity, are confounded.

A further distinction has to be made between the amount of time spent moving and the speed of movement. Two measures were made on flies within the activity chamber. The amount of time that each individual spent moving, and the number of squares entered whilst moving (Table 2).

Table 2. *The amount and speed of locomotor activity of* yellow *mutant males*

(The table shows the deviation of the mean score for the mutants from that of their corresponding wild type male sibs. The amount of time spent standing (including preening), and moving, was measured in s. Speed of movement was measured as the distance travelled in cm during an observation period of 100 s.)

	y^{59B}	y^{2}	y^{b1}	y^{bab}
Standing	+63·3**	+25·5**	+6·0	+5·6
Moving	−60·2**	−25·0**	−6·0	−5·6
Speed of movement	−33·5**	−19·2**	+1·7	+4·2

** Denotes deviations significant at the 1% level of probability.

The *yellow* mutants fall into two discrete groups with respect to their locomotor activity. Males hemizygous for y^{b1} or y^{bab} show a pattern of activity indistinguishable from that of wild type males. Fig. 1 shows that y^{b1} and y^{bab} are similar in their initial reactivity and in the level of spontaneous locomotor activity measured at five min. They are indistinguishable from their wild type sibs in both amount and speed of locomotor activity (Table 2).

Males hemizygous for y^{59B} and y^{2} are significantly less active than wild type males at each age at which observations were made (Fig. 2), and significantly different from each other. The most severely affected is y^{59B} which also shows full expression of the cuticular mutant phenotype. There are no significant differences in preening behaviour, but the mutants spend more time standing motionless than their wild type sibs (Table 2). The difference in locomotor activity is, for both mutants, the consequence of a reduction in the amount and the speed of locomotor activity. There was no difference in the occurrence of dyskinesis such as could indicate a disturbance of motor co-ordination in the mutant males (Burnet, Connolly & Mallinson, 1974).

(ii) *Competitive mating ability*

Competitive mating tests in which two males of different genotype compete for a single virgin female are a sensitive and discriminating measure. The outcome is unambiguous and the inferences with regard to relative fitness are quite straightforward. Males hemizygous for different *yellow* alleles differ strikingly in competitive mating ability (Table 3). The most severely impaired y^{59B} and y^{b1} have a

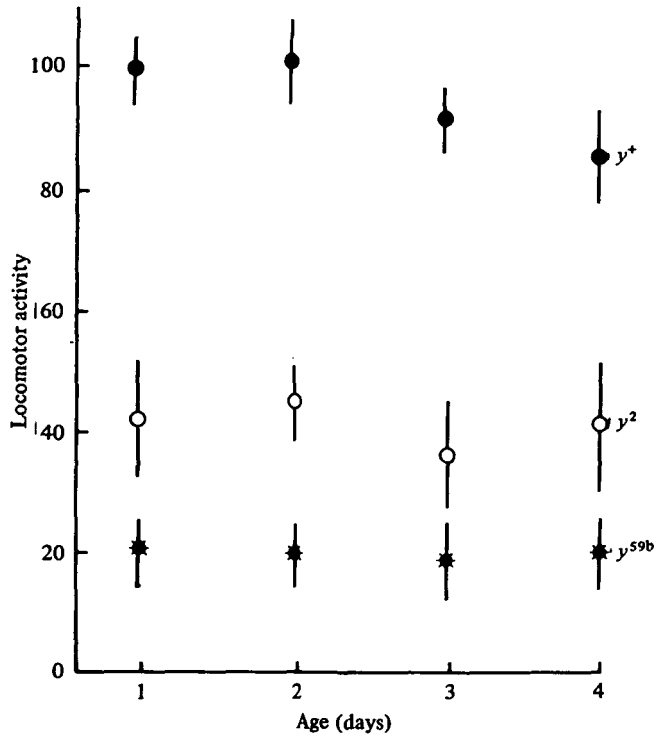


Fig. 2. Locomotor activity measured as the number of squares in the activity chamber entered during a period of 100 s. The mean activity score is shown for the same number of individuals (n = 30) of each genotype group measured on successive days after eclosion from the pupa on day 0. The vertical bars indicate the 95 % confidence interval for each mean score.

Table 3. *Competitive mating success of wild-type and* yellow *mutant males*

(Two males of different genotype competed for a single wild-type virgin female. Each competition was observed until copulation occurred or for a period of 20 min.)

	Contests observed	Not mated	Successful					P
			y^+	y^{59B}	y^2	y^{b1}	y^{bab}	
y^+ versus y^{59B}	100	5	95	0				< 0·01
y^+ versus y^2	100	4	75		21			< 0·01
y^+ versus y^{b1}	100	8	92			0		< 0·01
y^+ versus y^{bab}	105	10	45				50	N.S.
y^{bab} versus y^{b1}	108	15				2	91	< 0·01

relative success rate which is less than 1 % of that of their wild type sibs. Males hemizygous for y^2 are significantly less successful than wild type males, but a substantial proportion do succeed in achieving copulation. The y^{bab} mutants show no decrement in competitive mating ability relative to wild type, and the outcome here is indistinguishable from that expected due to chance. The y^{b1} males show the same severe competitive disadvantage in relation to y^{bab} as to y+ males.

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The difference in competitive mating ability of the two mosaic alleles y^{bab} and y^{b1} is striking. The y^{bab} males are as successful as the wild type, whilst the y^{b1} males are as severely impaired as the fully expressed type-1 mutant y^{59B}. Although reduced locomotor activity may be at least a contributory cause of the low competitive ability of y^{2} and y^{59B} this is unlikely to account for the difference between the mosaic alleles y^{bab} and y^{b1} because both have normal activity. A possibility for consideration is that the difference in mating success between these mutants is a consequence of the differences between them in the pattern of expression of the mutant phenotype in those external cuticular structures essential for the successful

Table 4. *Competitive mating success of* y^{b1} *and* y^{bab} *mutant males after removing the sex-combs*

Group	Contests observed	Contests with no mating	Successful male	
			y^{b1}	y^{bab}
a	131	78	8	45
b	99	62	3	34
c	110	80	3	27
Total	340	220	14	106

completion of mating by the male. Males hemizygous for y^{b1} differ from both of the other type-2 mutants in having *yellow* sex-combs. The functional importance of the sex-combs for achieving genital contact and successful copulation was demonstrated by Cook (1977), who observed that surgical removal of these structures from wild type flies causes a marked impairment of mating success. Removal of the sex-combs does not completely prevent copulation but greatly retards its occurrence. If *yellow* sex-combs are in some way responsible for reducing courtship success of y^{b1} males, by failing to provide adequate traction during grasping perhaps, removal of them from both y^{b1} and y^{bab} males should, *ceteris paribus*, remove the difference in their competitive mating ability.

The results of four such experiments involving competition between y^{b1} and y^{bab} males which have had the foretarsus, including the sex-combs, amputated are shown in Table 4.

Removal of the foretarsi reduces the speed of mating in both genotype groups so that a period of five days was necessary to ensure that a sufficient number of successful matings took place. Although the speed of mating was greatly reduced in both genotype groups y^{bab} males were nevertheless superior in competitive mating success to y^{b1} males. This evidence contradicts the notion that copulation by y^{b1} males is impaired by structural differences in their sex-combs.

(iii) *Courtship behaviour*

A descriptive account of the courtship behaviour of *D. melanogaster* is given by Bastock & Manning (1955) and Burnet & Connolly (1974). The courting male approaches the female with his body axis oriented directly towards her. If she

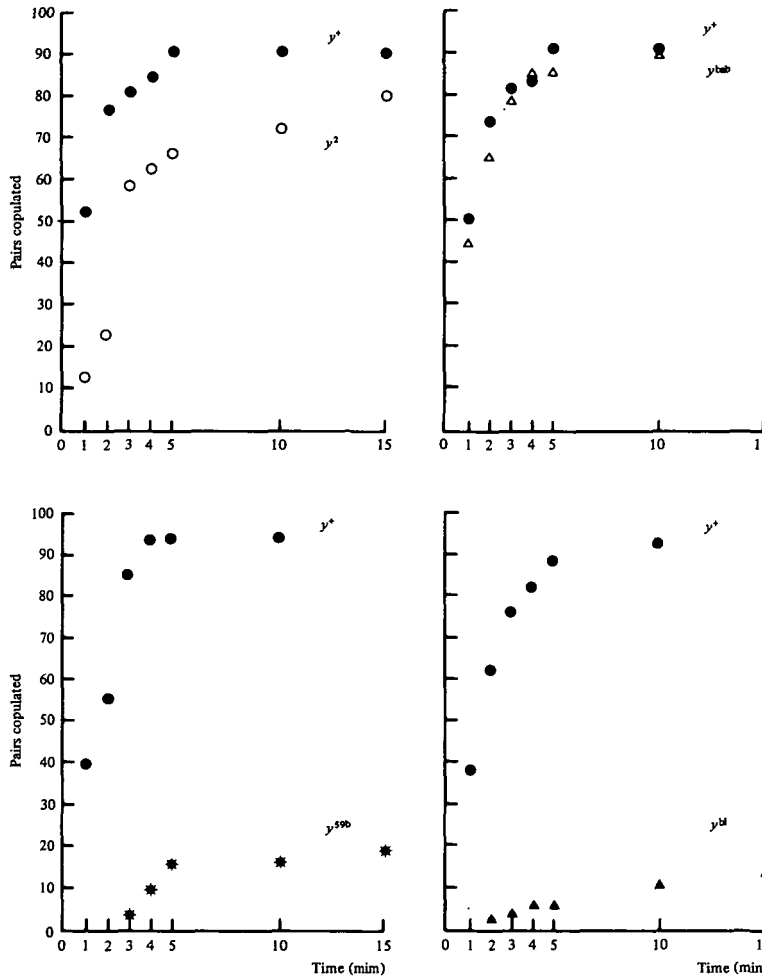

Fig. 3. Mating speed for wild-type and *yellow* mutant males. The cumulative percentage of matings is shown as a function of time for 3-day-old males with wild-type virgin females tested in the single pair mating situation.

moves, he follows. The male then extends his wing nearest the female and vibrates it up and down for brief periods, and may frequently repeat this wing display. Moving to the posterior end of the female, he licks her genitalia, and attempts to copulate. Males differ in both the latency, and duration of courtship and these together determine their mating speed (Eastwood & Burnet, 1977). The latency period affords some indication of the speed of sexual response of a male, whereas the duration of courtship required to achieve successful copulation reflects the quality and intensity of his courtship.

The results for single pair mating trials summarized in Fig. 3 show that mating speed of y^{bab} males is closely similar to that of their wild type sibs. The courtship behaviour of the two genotype groups is qualitatively, and quantitatively, indistinguishable. Mating speed of y^2 males is significantly slower than that of y^+

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males. This is probably because the y^2 males are slower to initiate courtship as is indicated by their significantly longer latency scores (Table 5). Once begun, the courtship behaviour of y^2 males is indistinguishable from that of the wild type males within the Novosibirsk background, although on the Oregon background y^2 males show a significant deficit in the proportion of time spent oriented, and a lower frequency of attempted copulation.

Table 5. *Comparison of the courtship behaviour of wild type* (y^+) *and* yellow *mutant* (y^2, y^{59B}) *males in single pair matings with wild type virgin females*

(Twenty-five single pair matings were observed for each male genotype group until copulation occurred or for a total observation period of 1000 s. Courtship latency is measured in s. Orientation is expressed as the mean percentage (angular transformation) of the total courtship time during which the male was oriented to the female. Wing vibration is expressed as the mean percentage (angular transformation) of orientation time. Licking and attempted copulation are each expressed as the mean number of events per bout of orientation.)

Novosibirsk background	y^+	y^2	P	y^+	y^{59B}	P
Latency	40·2	155·6	< 0·01	83·3	142·2	< 0·01
Orientation	58·0	55·3	N.S.	59·0	35 2	< 0·001
Vibration	49·9	50·2	N.S.	53·4	27·9	< 0·001
Licking	1·9	1·7	N.S.	1·1	0·3	< 0·001
Attempted copulation	1·1	0·9	N.S.	1·3	0·3	< 0·001
Oregon background						
Latency	54·3	127·7	< 0·01	61·6	201·8	< 0·01
Orientation	63·8	57·9	< 0·05	56·5	29·7	< 0·001
Vibration	44·6	40·9	N.S.	54·9	21·7	< 0·001
Licking	1·5	0·9	N.S.	1·6	0·6	< 0·001
Attempted copulation	1·0	0·5	< 0·05	1·8	0·2	< 0·001

The mating speed of y^{59B} males is severely impaired. The y^{59B} males are slow in starting to court, and their courtship is less intense than that of wild type males. The mutants spend less time oriented to the female, offer less wing vibration and licking stimuli, and are less persistent in their attempts to achieve copulation (Table 5).

Males hemizygous for y^{b1} exhibit a decrement in mating speed comparable in severity to that shown by the type-1 mutant y^{59B} (Fig. 3). The y^{b1} males show no reduction either in locomotor activity or in courtship latency, and the courtship elements of y^{bab} and y^{b1} males differ significantly only in the proportion of their courtship time oriented to the female, that is, actively engaged in courtship (Table 6). Wing vibration, together with licking and attempted copulation measured as a proportion of orientation time are similar in the two mutants. The proportion of wing vibration is apparently lower than in wild type males (see Table 6) but this may be because the amount of vibration in courtship increases with time, and measurements were made over different periods in the two experiments, (120 s, Table 6 and 1000 s, Table 5). Wing vibration, licking, and attempted copulation are superimposed on orientation, but y^{b1} males are oriented for a

Table 6. *Comparison of the courtship behaviour of* yellow *mutant* y^{b1} *and* y^{bab} *males in single pair matings with wild type virgin females*

(Fifty single pair matings were observed for each male genotype group until copulation occurred or for a total observation period of 120 s. from the beginning of courtship. Other details are given in Table 5.)

Novosibirsk background	y^{bab}	y^{b1}	P
Latency	42·7	47·9	N.S.
Orientation	69·8	53·9	< 0·01
Vibration	26·5	24·5	N.S.
Vibration bout length	1·02	1·07	N.S.
Licking	1·46	1·67	N.S.
Attempted copulation	0·70	0·77	N.S.

Table 7. *Summary comparison of the pigmentary and behavioural effects of different alleles at the* yellow *locus*

(Results for the *y* allele are from Wilson *et al.* (1976), and unpublished data.)

	Cuticle pigment	Locomotor activity	Courtship latency	Mating ability
y^{+}	+	+	+	+
y^{2}	±	−	−	+
y^{bab}	±	+	+	+
y^{b1}	±	+	+	−
y	−	−	−	−
y^{59B}	−	−	−	−

significantly reduced proportion of overall courtship time. Consequently they perform these elements at a relatively lower intensity than y^{bab} males, and may be unable to bring the female to a threshold of acceptance so rapidly.

4. DISCUSSION

The pleiotropic effects of *y* mutants are summarized in Table 7. Some of their separate phenes, notably locomotor activity and mating success, are controlled independently. Locomotor activity and courtship latency time may not be independent, but observations on additional pattern mosaic *y* mutants should clarify this point. The present evidence gives no support to the suggestion that the behavioural effects of *yellow* are a secondary consequence of the action of the locus on pigmentation, or a mechanical consequence of changes in the structure of the cuticle. These behavioural effects evidently arise through some other route, including possible direct action of the locus on the functions of the nervous system.

Nash (1976) has concluded from his observations on temperature sensitive mutants that the *yellow* gene functions at different times in cells which form the various structures of the cuticle and therefore must be controlled independently in each cell type. Our observations on the apparent independence of the pigmentary and behavioural effects of the *yellow* locus can be explained on the assumption that pattern mosaicism in the expression of the gene extends to the internal tissues,

and that independent foci are involved. The situation is analogous to that observed in the somatic mosaics generated by chromosomal aneuploidy by Hotta & Benzer (1976), and Hall (1979). Loss of a chromosome carrying the y^+ allele during one of the early nuclear divisions in a y/y^+ heterozygote results in a mosaic individual in which the cells of some areas of tissue are heterozygous and phenotypically normal, whilst the other areas are hemizygous for the mutant allele and phenotypically mutant. This technique used in conjunction with external morphological and internal biochemical markers has led to the mapping of discrete foci of mutant gene action, and to recognition of those parts of the nervous system which control the elements of male courtship behaviour (Hall & Greenspan, 1979). Regional absence of wild type function in the aneuploid somatic mosaics is caused by actual loss of the y^+ structural gene. Absence of y^+ gene function in the type-2 y mosaics is brought about by mutation in the regulatory region of the locus and represents non-induction, or repression, of the function of the structural gene in the cells of a particular tissue. Burnet & Connolly (1974) have argued that the yellow gene is involved in controlling utilization of tyrosine and 3,4-dihyroxyphenylalanine in the biosynthetic pathways leading to synthesis of melanin, sclerotin, and the catecholamines. Melanin and sclerotin are concerned with the hardening and darkening of the cuticle whereas the catecholamines dopamine and noradrenalin are important in neural transmission. This suggestion is supported by the observations of Wilson (in manuscript) that *yellow* males have significantly lower titres of noradrenaline than wild type males, which may account for the reduced activity of the mutants. The behavioural effects of the locus could arise if type-2 y gene expression causes abnormal catecholamine balance in different regions of the nervous system.

The mode of expression in respect of the pigmentary and behavioural effects of the *yellow* gene gives rise to two categories of *yellow* mutants. (i) type-1 have completely yellow cuticles, reduced locomotor activity and low mating success. (ii) type-2 mutants have partially yellow cuticles, with or without changes in locomotor activity and/or mating success. The mutants listed in Table 7 fit into one or other of these categories, but pattern mosaic expression of the type-2 mutants suggests the possible existence of other *yellow* mutants, which are wild type in their cuticular phenotype but nevertheless show some of the behavioural effects of the mutant gene. These would be type-2 mutants in which mosaic expression of the y gene affected only internal tissues but not the external body cuticle. They could be recognized as *yellow* mutants only on the basis of their map location and complementation tests.

Not all the *yellow* mutants show a decrement in male mating success, and the mutants which show reduced mating ability do so for different reasons.

The type-1 mutant y^{59B} shows a generalized impairment of male courtship ability which combines a high threshold of sexual response with a less intense performance of all the courtship elements including the failure to complete copulation and intromission, which would seem to be a consequence of complete expression of the mutant gene at all behavioural foci. The apparently uncompro-

mising effect of y^{59B} on all of the elements of male courtship on each of the genetic backgrounds differs from what is observed with the undesignated y allele described by Wilson *et al.* (1976). This is similar to y^{59B} on the Oregon background, whereas on the Novosibirsk background there is extended latency and reduced ability to complete copulation. The elements of courtship behaviour are otherwise normal. Although assumed on the basis of the cuticular phenotype to be a type-1 mutant, the absence of type-1 mutant expression for some of the behavioural elements may indicate that this was actually a type-2 mutant.

A higher sexual response threshold, reflected by abnormally long courtship latency, is an important cause of the deficiency in the competitive mating performance of y^2 mutant males, which otherwise exhibit normal courtship behaviour and also complete copulation. This indicates that the behavioural focus for control of courtship latency must be separate from those controlling the elements of male courtship behaviour.

The threshold for male sexual response is normal in y^{b1} males, and they show a normal repertoire of male courtship elements. In this case, reduced mating success has a different cause. The y^{b1} males spend a significantly lower proportion of courtship time oriented to the female so that, even though performance of the superimposed elements of wing vibration, licking, and attempted copulation are normal whilst they are oriented, these elements are performed at a reduced overall intensity. Courtship stimuli from the male are summated by the female. If summation of courtship stimuli is subject to decay in the female the y^{b1} males may simply have difficulty bringing the females to their threshold of acceptance.

Although y^{b1} males spend significantly less time oriented they continue to court for lengthy periods making repeated attempts to copulate. Like the type-1 mutants y^{b1} males usually fail to achieve successful genital engagement and intromission, suggesting that there may be some failure in the terminal sequence of mating behaviour similar to that in *fruitless* and *celibate* mutants (Hall, 1978, 1979). Somatic mosaic analysis shows that attempted copulation is controlled from a diffuse behavioural focus in the thoracic ganglion (Hall, 1979). Impaired performance of y^{b1} males could arise from localized expression of the mutant at this focus, resulting in impairment rather than a complete block of the ability to complete copulation, because some of the mutant males eventually succeed in achieving genital engagement and are fertile.

REFERENCES

Bastock, M. (1956). A gene mutation which changes a behaviour pattern. *Evolution* **10**, 421–439.

Bastock, M. & Manning, A. (1955). The courtship of *Drosophila melanogaster*. *Behaviour* **8**, 85–111.

Burnet, B. & Connolly, K. (1974). Activity and sexual behaviour in *Drosophila melanogaster*. In *The Genetics of Behaviour* (ed. J. H. F. van Abeelen). Amsterdam: North-Holland.

Burnet, B., Connolly, K. & Mallinson, M. (1974). Activity and sexual behavior of neurological mutants of *Drosophila melanogaster*. *Behavior Genetics* **4**, 227–235.

Connolly, K. (1967). Locomotor activity in *Drosophila*. III. A distinction between activity and reactivity. *Animal Behaviour* **15**, 149–152.

Cook, R. (1977). Behavioral role of the sexcombs in *Drosophila melanogaster* and *Drosophila simulans*. *Behavior Genetics* **7**, 349–357.

Eastwood, L. & Burnet, B. (1977). Courtship latency in male *Drosophila melanogaster*. *Behavior Genetics* **7**, 359–372.

Green, M. M. (1961). Complimentation at the *yellow* locus in *Drosophila melanogaster*. *Genetics* **46**, 1385–1388.

Hall, J. C. (1978). Courtship among males due to a male-sterile mutation in *Drosophila melanogaster*. *Behavior Genetics* **8**, 125–141.

Hall, J. C. (1979). Control of male reproductive behavior by the central nervous system of *Drosophila*: dissection of a courtship pathway by genetic mosaics. *Genetics* **92**, 437–457.

Hall, J. C. & Greenspan, R. J. (1979). Genetic analysis of *Drosophila* neurobiology. *Annual Reviews of Genetics* **13**, 127-195.

Hotta, Y. & Benzer, S. (1976). Courtship in *Drosophila* mosaics: sex-specific foci for sequential action patterns. *Proceedings of the National Academy of Sciences, U.S.A.* **73**, 4154–4158.

Nash, W. G. (1976). Patterns of pigmentation and color states regulated by the *y* locus in *Drosophila melanogaster*. *Developmental Biology* **48**, 336–343.

Nash, W. G. & Yarkin, R. J. (1974). Genetic regulation and pattern formation: A study of the *yellow* locus in *Drosophila melanogaster*. *Genetical Research* **24**, 19- 26.

Wilson, R., Burnet, B., Eastwood, L. & Connolly, K. (1976). Behavioural pleiotropy of the *yellow* gene in *Drosophila melanogaster*. *Genetical Research* **28**, 75–88.