ratio discrimination based on two or more receptor systems even when detecting a single chemical compound. The adaptive advantage for the insect is clearly specificity in detection. The greater the number of specific conformations of a single molecule required to satisfy the different chemoreceptors, the lower the probability that an incorrect molecule will satisfy the chemoreceptor requirements. We consider it probable that other highly selective chemical communication systems, such as hormones, also use multiple chemoreceptor systems to achieve a high degree of chemical specificity.

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4. The 2-(2-cyclopenten-1-yl)ethyl tosylate was prepared from optically pure 2-(2-cyclopenten-1-yl)ethanol (*5*). The syntheses are described in (*6*).
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7. A plot of specific rotation as a function of molecular weight for the well-characterized acids of chaulmoogra oil and their esters is linear (*6*). Even (+)-(*S*)-2-cyclopenten-1-yl acetic acid and (+)-(*S*)-2-(2-cyclopenten-1-yl)ethanol fall on the plot. Linear regression analysis (*6*) of these data gives a predicted rotation for (+)-(*R*)-(2)cyclopenten-1-yl)nonyl acetate of +68.6°. The data plotted are from (*5*) and (*8*). The linearity of the plot is a consequence of the fact that the rotation in the 2-cyclopenten-1-yl system depends only on the molecular weight of the side chain when $n \geq 1$.
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9. Resolution of 2-cyclopentenecarboxylic acid was accomplished by using the enantiomers of α-phenethylamine. The (+)-(*R*)-cyclopentenecarboxylic acid, $[\alpha]^{25}_{\mathrm{D}} = +262°$, was obtained with (+)-$\alpha$-phenethylamine. Use of (−)-α-phenethylamine gave the (−)-(*S*) enantiomer. The syntheses are described in (*6*).
10. All compounds used in sex stimulation bioassays were analyzed on a glass open tubular column (60 m by .05 mm) coated with SP-1000 (J & W Scientific). The chromatography indicated that the compounds were chemically pure. The details of the syntheses, resolutions, and characterizations have been described (*6*).
11. Pupae of the European corn borer (Iowa) and the red-banded leaf roller were isolated individually. As the adult moths emerged, males were selected from the culture and placed in respective cages for the bioassay. The males were conditioned for 96 to 120 hours at constant light, 80 percent relative humidity, and 27°C. The bioassay consisted of exposure of a set of ten males in a screened cage positioned in a 20° to 22°C airflow (1.5 to 1.8 m/sec) to 0.5 μg of compounds for 30 seconds on the tip of a glass rod held 4 to 5 cm upwind of the caged moths. The number of males that responded to the stimulus with wing vibration, extension of genitalia, and clasper responses in the 30-second exposure period were recorded. The assays were conducted in a randomized complete-block design with 30 replicates; each set of ten males was exposed to only one stimulus, and then the moths were discarded. Variation of the amount of stimulus (nanograms to micrograms) did not alter qualitatively the relative response to (+)-(*R*)-, (−)-(*S*)-, and (±)-9-(2-cyclopenten-1-yl)nonyl acetate.
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Regulative Interactions Between Cells from Different Imaginal Disks of *Drosophila melanogaster*

Abstract. *The regulative behavior of cells from the imaginal wing disk of* Drosophila melanogaster *can be modified by interaction with cells from different disk types. Both thoracic and nonthoracic disks are able to interact, but there are major differences in the effectiveness of interaction. The finding lends experimental support to the idea that cells in different fields within the same organism use the same mechanism for specifying positional information. A similar conclusion has been reached by Wilcox and Smith based on studies of the mutation* wingless.

The spatial patterns of differentiation which arise during animal development are thought to be generated by cell interactions that occur before differentiation. These interactions appear to assign different states (positional information) to cells according to their locations relative to other cells in the same cell population (*1*). Although Wolpert (*1*) proposed some time ago that the mechanism for specifying positional information may be the same for different fields, it has only recently been shown (*2*) that pattern formation and regulation (a term we use to designate developmental responses to surgical intervention) in several different systems can be understood in terms of a single set of rules for cell behavior. In the experiments reported here, we tested the idea that cells in different imaginal disks of *Drosophila* larvae use the same kind of cellular signals in establishing

Table 1. Structures derived from 02 wing fragments (identified by wild-type genotype) mixed with irradiated (15,000 R) genetically marked whole disks and wing disk fragments and cultured for 7 days in adults before transfer to larvae for metamorphosis. Occurrence of structures below the axillary cord indicates regeneration.

	Wing disk fragment 02 mixed with										
	Wing* 02	Wing* 68	Wing	Antenna	Eye	Leg			Haltere	Genital	
						1	2	3		Male	Female
N†	61	15	81	68	58	43	41	37	64	44	53
Notum	61	15	80	68	58	42	41	31	64	44	53
Tegula	7	10	44	30	14	21	11	9	34	11	19
Axillary cord	3	11	42	12	2	21	11	14	29	10	1
Regeneration											
Costa	1	1	31	9	4	8	4	7	12	4	3
Triple row	1		14	5	2	7	1	4	5	3	1
Double row		2	20	7	2	7	5	6	6	1	1
Posterior row		6	37	15	1	18	8	12	25	8	3
Alar lobe		8	40	12	4	20	9	13	27	6	4
Dorsal radius		1	51	15	6	23	16	14	42	8	1
Ventral hinge		2	14	1	3	9	1		2	4	
Wing blade	1	6	69	25	8	30	18	19	53	12	7
Regenerated											
Number	1	8	71	28	9	34	22	19	54	12	7
Percentage	2	53	88	41	16	79	53	51	84	27	13

*Data from (*9*) are incorporated. †*N* = total number of mixtures examined.

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their quite different patterns of differentiation.

When a piece is removed from the edge of the imaginal wing disk and the remaining fragment is given time for growth by culturing it in an adult host before metamorphosis, the fragment is often able to regenerate the missing parts of the disk (*3*). The complementary fragment from the edge of the disk usually does not regenerate the missing parts when similarly cultured, but instead produces a mirror-image duplication of the pattern normally produced by that part of the disk (*3*). However, it was recently shown that the regulative behavior of duplicating fragments can be altered by mixing them with fragments from different disk regions. Fragments from opposite edges of the disk, when grafted together, were able to produce the missing pattern elements from the central part of the disk by intercalary regeneration (*4*). This made it possible (*2*) to understand the different types of pattern regulation displayed by cultured intact fragments, in terms of intercalation between different parts of the disk which come together during wound healing (*5*).

In the experiments reported here we tested the ability of different imaginal disks (eye, antenna, first leg, second leg, third leg, wing, haltere, and male and female genital) to stimulate regeneration by the wing disk fragment designated 02 (*3*), whose normal fate is to produce the dorsal surface of the thorax (mesonotum) (Fig. 1). The capacity of wing disk fragments 02 and 68 to stimulate regeneration by 02 fragments was also tested.

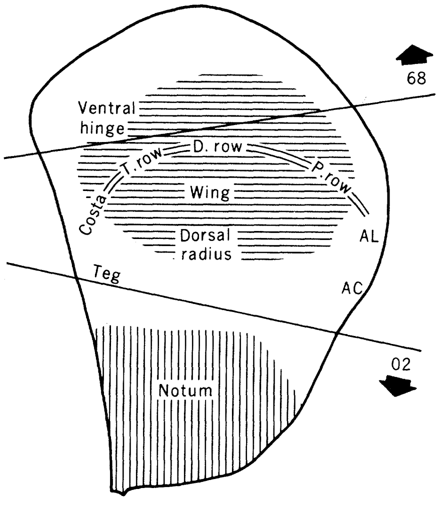

Fig. 1. Schematic diagram of the wing disk showing the location of presumptive adult cuticular structures, after Bryant (*3*). Abbreviations: *Teg*, tegula; *T. row*, triple row of wing margin bristles; *D. row*, double row of wing margin bristles; *P. row*, posterior row of wing margin hairs; *AL*, alar lobe; and *AC*, axillary cord. Horizontal hatching indicates the presumptive wing blade, whereas vertical hatching indicates presumptive mesonotum. The two straight lines indicate the location of cuts on the wing disk yielding the fragments designated 02 and 68. Because of their proximity to the cut line, the presence of tegula or axillary cord in implants was not considered to be evidence of regeneration.

Table 2. Comparison of effectiveness of irradiated and unirradiated imaginal disks or fragments in stimulating regeneration by the notum (02) fragment of the wing disk. The data for the irradiated series are from Table 1. The experiments in the unirradiated series were carried out and scored as described for irradiated mixtures except that *y w* sn^3; *mwh* tissue was not irradiated before mixing.

Wing disk fragment 02 mixed with	Percentage of regeneration*	
	Irradiated	Unirradiated
Wing 68†	53 (15)‡	48 (27)‡
Third leg	51 (37)‡	26 (19)‡
Antenna§	41 (68)‡	18 (33)‡
Male genital‖	27 (44)‡	7.1 (56)
Female genital	13 (53)‡	7.1 (28)
Eye	16 (58)‡	5.3 (19)
Wing 02	1.6 (61)	3.7 (191)
Total‖	25 (336)	10.2 (373)

*The number of mixtures examined is given in parentheses. †Data from (*4*) and (*9*) are incorporated. ‡$P < .01$ compared to wing 02 control (chi-square). §$.05 > P > .01$ for irradiated compared to unirradiated mixtures (chi-square). ‖$P < .01$ for irradiated compared to unirradiated mixtures (chi-square).

The 02 wing disk fragments were taken from wild-type *Ore-RC* larvae and mixed with whole disks or disk fragments from *y*; *mwh* or *y w* sn^3; *mwh* (*6*) larvae that had been irradiated just before dissection with 15,000 R from a gamma-ray source. The irradiation was performed to limit growth and transdetermination (*7*) in the disk tissue that was mixed with the 02 wing disk fragment (*8*). This treatment does not destroy the ability of fragments to induce intercalary regeneration in fragments with which they are mixed (*9*, *10*). After the 02 wing disk fragment and the other component of the combination had been mixed, using tungsten needles, the combinations were transplanted into adult female hosts, where they remained for 7 days before transfer to larval hosts for metamorphosis [for details of the methods, see (*3*) and (*4*)]. The differentiated implants were then mounted between cover slips and examined microscopically. Pattern elements showing the wild-type phenotype were derived from the 02 fragments; the yellow, singed, multiple wing hair (and white in the case of the eye disk) phenotype identified any surviving derivatives of the tissues of this genotype.

As a control (Table 1), 02 wing disk fragments were mixed with irradiated 02 fragments from other wing disks. These combinations usually produced only those structures (chiefly notum) expected from the fate map (*3*), as had already been shown (*4*). Only one of 61 combinations produced structures usually derived from other parts of the disk. Irradiated wing 68 fragments, however, caused the unirradiated 02 fragments to regenerate other pattern elements at a high frequency (*4*). In the combinations with whole disks, all of the tested disks caused regeneration of wing structures by the 02 fragment, but with marked differences in effectiveness. Wing, haltere, and foreleg disks were best able to stimulate regeneration, but the other thoracic disks (second and third leg disks) were also quite effective. In addition, substantial stimulation of regeneration was evident in the mixtures of 02 wing disk fragments with antenna and, to a lesser extent, male genital disks. In contrast, the eye and female genital disks stimulated regeneration only minimally, although the regeneration frequency was significantly greater than in the controls (*11*).

We have obtained qualitatively similar results in experiments with unirradiated whole disks or fragments, as shown by the data in Table 2, in which the frequency of regeneration in mixtures of 02 fragments with various irradiated disks is compared with that obtained in mixtures with unirradiated disks. For the seven disks or fragments compared, it is clear

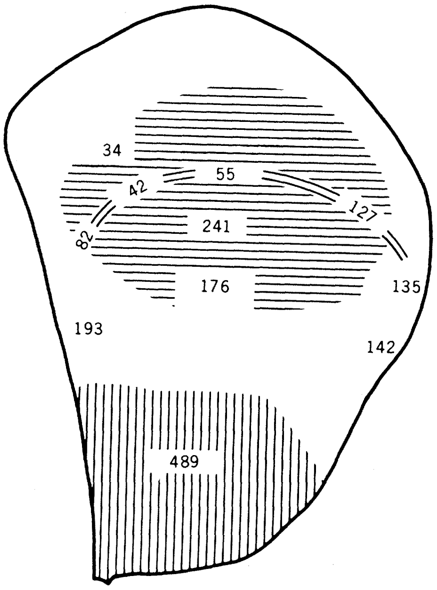

Fig. 2. Number of cases in which specific pattern elements were formed by 02 wing disk fragments mixed with irradiated whole disks and cultured for 7 days before transfer to larvae for metamorphosis. The data from all of the different mixtures with whole disks in Table 1 have been pooled.

that the relative effectiveness in stimulating regeneration by the 02 fragment is not altered by the irradiation. However, mixture with unirradiated male genitalia, female genitalia, and eye disks, which are minimally effective when irradiated, yielded regeneration frequencies insignificantly different from that of the wing 02 control. When all of the data are considered together, the frequency of regeneration obtained in irradiated mixtures is significantly greater than that in unirradiated mixtures. However, when the different mixtures are considered individually, only two of the seven disks or disk fragments compared (antenna and male genital) showed a statistically significant increase in effectiveness when irradiated.

Our results demonstrate a significant interaction of the wing 02 fragment with all thoracic and at least one nonthoracic disk, and this result, as well as the differences in effectiveness of different disks, appears to be independent of irradiation of the tissue. Evidently, the interactions between cells which lead to intercalary regeneration can occur between wing disk cells and cells of other disks. The result agrees with the recent finding that dissociated and reaggregated cells of the male foreleg disk can interact with wing or antenna disk cells present in reaggregates, leading to a pronounced change in the regulative behavior of the leg disk cells (*12*).

These findings could be explained if imaginal disks were organized by similar pattern-forming mechanisms, such that specific regions of one disk were homologous to specific regions of other disks (*1, 2*). However, such homological relationships cannot be deduced directly until specific parts of each disk are tested for interactions with specific parts of other disks. Even though all of the imaginal disks tested showed interaction with the wing disk test piece, at least in the irradiated series, the obvious differences in effectiveness call for some explanation. One possibility is that the homology between disks may in some cases be incomplete: one entire disk may be homologous to only a part of another disk. If, for example, in one imaginal disk most of the positional field were homologous to that of the 02 wing disk fragment, then it would be expected to stimulate regeneration of that fragment only minimally. Our data do not support this possibility, since even with the least effective combinations most of the wing disk markers were regenerated at least once from the 02 fragment. In fact, the data from whole disks are rather uniform with respect to the relative frequency of different markers: in every case except eye and female genitalia (for which the number of cases of regeneration is too small for meaningful comparisons) the wing blade is the most frequent, dorsal radius second most frequent, alar lobe or posterior row third most frequent, and ventral hinge, triple row, or double row least frequent of the regenerated markers. When all of the data are combined (Fig. 2), it is clear that the probability of regeneration of a pattern element is simply a function of the proximity of that element to the 02 fragment in the fate map; distant markers are regenerated less frequently than are nearby ones. The only inconsistent frequency is that of the wing blade itself, but its atypically high frequency is probably due simply to the large area of the fate map occupied by presumptive wing blade, providing a larger "target size" for regeneration than is the case with the other markers. The ordered frequencies of marker regeneration should not be taken to imply that markers are regenerated in sequence with different stopping points; in fact, the data are clearly against this possibility since there are many cases of regeneration of distant markers in the absence of many of the closer elements. Rather, the distribution of frequencies is probably a result of the random tissue-mixing procedure. Many of the confrontations generated in the combinations would be expected to lead to regeneration of the nearby markers, but in order for the distant markers to be regenerated a rare confrontation between maximally disparate positional values in the two components of the mixture would be required.

An alternative explanation for the different abilities of different disk types to stimulate regeneration from the 02 wing disk fragment (Table 1) may be that they differ in adhesiveness (*13*) or in the ability to form cell junctions with wing disk cells. The low frequency of regeneration obtained in mixtures with the eye disk may indicate that disk cells which have already completed proliferation and begun terminal differentiation, as is true of much of the ommatidia-forming region of the eye disk (*14*), are unable to communicate positional information effectively. These possibilities are now being examined.

Results similar to those reported here have recently been obtained by Wilcox and Smith (*10*). The test piece used in their experiments was the duplicated presumptive notum represented by the abnormal wing disks of the *wingless* mutant, rather than the wild-type presumptive notum used here. Wilcox and Smith found interactions only with thoracic disks (wing, haltere, leg). In our experiments interactions with nonthoracic disks were also observed. Perhaps the *wingless* mutation decreases the frequency of effective interaction between wing and nonthoracic imaginal disk cells.

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