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Electrophysiological Studies of Gustation in Lepidopterous Larvae

II. Taste Spectra in Relation to Food-Plant Discrimination

V. G. Dethier*

Department of Biology, Princeton University, Princeton, New Jersey

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Summary. Comparisons were made of the electrophysiological responses of the maxillary gustatory receptors of the following categories of caterpillars: (1) three closely related species (*Papilio polyxenes* L., *P. troilus* L., and *P. glaucus* L.) each of which feeds on a different group of plants; (2) two unrelated oligophagous species (*P. glaucus* L. and *Malacosoma americana* Fabr.) that have one preferred food plant in common; (3) three unrelated monophagous species (*Danaus plexippus* L., *Euchaetias egle* Drury, and *Pygarctia eglenensis* Clemens) that share the same plant. Materials tested included sodium chloride, carbohydrates, amino acids, glycosides, and the saps of *Daucus carota* L. and *Foeniculum vulgare* Mill. (the food plants of *P. polyxenes*), *Sassafras albidum* (Nutt.) and *Lindera Benzoin* (L.) (the food plants of *P. troilus*), *Prunus virginiana* L. (a favored food of *P. glaucus* and *M. americana*), *Asclepias syriaca* L. and *Apocynum androsaemifolium* L. (eaten by *D. plexippus*, *E. egle*, and *P. eglenensis*), and *Brassica oleraceae* L. (food plant of *Pieris rapae*).

The following conclusions were drawn: (1) no species of caterpillar gives a single standard electrophysiological response to all of the plants it rejects; that is, rejection is not a unitary modality; (2) a plant that is unacceptable to several species of caterpillars does not elicit the same pattern of response from each; (3) a food plant that is shared by several species of caterpillars does not elicit the same pattern of response from each; (4) a species of caterpillar that has more than one food plant does not generate the same sensory pattern to each; (5) there is no universal difference between sensory patterns for acceptance and those for rejection.

A model based upon the hypothesis of across-fiber patterning is proposed to explain these results. The essence of this model is that the receptors have unique but overlapping action spectra and that each compound or mixture of compounds in leaf saps that can be discriminated generates a unique total pattern of response. Whether or not a plant is ingested depends, therefore, not on the presence or absence of a single stimulant or deterrent but upon the total sensory impression derived from integrated response to multiple plant components. Prior to the first bite a caterpillar makes its first discrimination on the basis of olfactory clues.

The first phase of a study of the electrophysiological responses of the maxillary taste receptors of ten species of caterpillars revealed marked interspecific differences in sensitivity spectra (Dethier and Kuch, 1971).

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No obvious correlation with the latitude of diet was found. The experiments that are described here were designed to explore further the relation between maxillary gustatory response and food-plant specificity. They are divided into two categories. In the first, a study was made of the responses of three closely related species of caterpillars each of which feeds on a different group of plants. The second study compared (1) the gustatory responses of two unrelated oligophagous caterpillars that have one food-plant in common and (2) three unrelated monophagous species that share the same plant.

Materials and Methods

The experimental approach is described fully in the first paper in this series (Dethier and Kuch, 1971). Seven species of caterpillars were employed in the present investigation. *Papilio polyxenes* L. was collected from parsley (*Petroselinum crispum* Mill.) and fennel (*Foeniculum vulgare* Mill.) in local gardens. *Papilio troilus* L. was collected locally from sassafras (*Sassafras albidum* [Nutt.]) and spicebush (*Lindera Benzoin* [L.]). *Papilio glaucus* L. was collected from choke cherry (*Prunus virginiana* L.). *Malacosoma americana* Fabr. was collected as eggs from choke cherry and reared in the laboratory. *Danaus plexippus* L. was found locally on *Asclepias syriaca* L. *Euchaetias egle* Drury was obtained from *A. syriaca* in Nova Scotia. Another arctiid, *Pygarctia eglenensis* Clemens, was obtained locally on *Apocynum androsaemifolium* L. It also feeds on *Asclepias.*

Materials tested included sodium chloride, carbohydrates, amino acids, glycosides, and the saps of fennel and wild carrot (Queen Anne's Lace) (the food-plants of *P. polyxenes*), sassafras and spicebush (the food-plants of *P. troilus*), cherry (a favored food of *P. glaucus* and *M. americana*), milkweed (the food-plant of *D. plexippus* and *E. egle*), and *Apocynum*, the food-plant of *P. eglenensis.* Although *P. rapae* was not employed in the present study, its food-plant, cabbage, was also occasionally tested on the larvae used.

A minimum of fourteen larvae of each species were tested. In the majority of cases both right and left sensilla were examined. Each stimulation was replicated at least four times. All solutions other than the saps were made up in phosphate buffer (Colowick and Kaplan, 1955) or in 0.05 M NaCl. Thus, on the average, one hundred and twelve records were obtained for each compound or plant sap. The order of presentation was randomized. The records illustrated in figures 1 to 37 are typical responses. Each series illustrated, as, for example, responses by the medial sensillum of *P. troilus*, are from the same sensillum. Accordingly, the responses within a series are strictly comparable. Each caterpillar must serve as its own control because there is some variation from one individual to the next that cannot be accounted for by non-uniformity in the diameter of the electrodes or by variable electrical contact. For example, a sensillum in one preparation might always respond to 0.05 M NaCl with activity from three cells while that in another preparation might respond consistently with activity from only one cell. In this instance the preparation with three active cells would respond to the sap of carrot with activity from three cells while the preparation with one cell responsive to NaCl would respond to sap of carrot with only one cell. Even with these individual variations the *relative* responses to different stimuli by any individual were consistent from one preparation to the next.

Results

Responses to Single Compounds — Related Species of Larvae

The responses of the three species of *Papilio* to salt, sugars, amino acids, and glycosides are summarized in Table 1. A few compounds that were found to be non-stimulating in earlier experiments have now been shown to be effective. It had been predicted that some of the compounds previously recorded as non-stimulating might in fact be slightly effective (Dethier and Kuch, 1971). Additionally, in the case of some compounds, differences were found between buffered and non-buffered solutions.

Not surprisingly the response spectra of the three species of *Papilio* are not identical. A comparison of these data with those in Table 2 and those of Dethier and Kuch (1971) relating to other species shows that differences among the papilios are neither greater nor less than among unrelated species. In the medial sensillum of *P. troilus* a minimum of two cells respond to NaCl; however, the more usual response involves three (Figs. 19 and 50). The cell most sensitive to changes in salt concentration is the one generating the largest spike. It may be considered to be the major salt receptor. In the medial sensillum of *P. glaucus* salt elicits responses primarily from one cell with only infrequent responses from a second one (Figs. 7 and 50). *P. polyxenes* is similar to *P. troilus* (Figs. 27 and 50). In all three species one cell is clearly the primary salt receptor. There is also a sugar receptor in all species. In general, the medial sensillum is not particularly sensitive to amino acids. With *P. troilus* responses were obtained to ten acids. Some of these were effective when buffered and ineffective at the same concentration when unbuffered. *P. glaucus* responded to nine unbuffered acids. *P. polyxenes* responded to six made up in buffer. *P. troilus* and *P. glaucus* each responded to four glycosides, *P. polyxenes* to more. *P. glaucus* did not respond to amygdalin which is found in comparatively high concentration in cherry. Both *troilus* and *polyxenes* responded to apiin which is characteristic of many of the umbelliferous plants upon which *polyxenes* feeds. Other differences in sensitivity are recorded in Table 1. In general, the amino acids and glycosides stimulate one or both of the salt receptors.

The lateral sensillum of *P. troilus* contains one cell that responds actively to salt. Occasionally one or two others also respond (Figs. 12 and 51). In *P. glaucus* response is almost entirely from one cell (Figs. 1 and 51). A similar situation prevails in *P. polyxenes*. In *troilus* there is a sugar receptor that responds to sucrose and fructose. In *P. glaucus* responses were obtained to fructose but not to sucrose. *P. polyxenes* responded to sucrose, glucose, and fructose in buffered solutions. Amino acids stimulated one or two receptors one of which was the salt receptor. With few exceptions there were no responses to glycosides.

Table 1. Responses of related and unrelated species of caterpillars to various compounds occuring in plants. L and M refer to lateral and medial maxillary sensilla respectively. Parentheses indicate that the compound was made up in phosphate buffer. Otherwise compounds were in 0.05 M Nacl

Compound	Species of larva							
	P. troilus		*P. glaucus*		*P. polyxenes*		*M. americana*	
	L	M	L	M	L	M	L	M
PO_4	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
0.005 M NaCl	+	+	?	0	+	+	+	+
0.05 M NaCl	+	+	+	+	+	+	+	+
0.1 M NaCl	+	+	+	+	+	+	+	+
0.1 M sucrose	(+)	(+)			(+)	(+)	(+)	(+)
	+	+	0	+	+	+	+	+
0.1 M glucose	(0)	(0)			(+)	(+)	(0)	(+)
	0		0	0			0	+
0.1 M fructose	(+)	(+)			(+)	(+)	(0)	(+)
	+	+	+	+			0	+
0.1 M inositol	(0)	(+)	(0)		(+)	(+)	(+)	(+)
	0	0	0	0	0	0	+	+
0.1 M sorbitol	(0)	(0)						
							+	+
0.1 M dulcitol	(0)	(?)					0	?
alanine	(0)	(+)	(0)		(0)	(0)	(?)	(+)
	0	—	0	0	+	—	0	?
arginine	(0)	(0)	(0)		(—)	(—)	(0)	(—)
	0	0	0	?			+	0
aspartic acid	(0)	(—)	(0)		(0)	(—)	(0)	(0)
		0	+	+	0		0	0
cysteine	(+)	(+)	(+)		(—)	(—)	(+)	(+)
	+	0	+	+	0	0	+	+
cystine	(0)	(+)	(0)		(0)	(—)	(0)	
	0	+	0	0	0	0	0	0
glutamic acid	(0)		(—)		(—)	(—)	(0)	(+)
	0		0	+	0	0		+
glycine			(?)		(—)	(—)	(+)	(—)
	—	+	0	+	0	0	0	0
histidine	(+)	(+)	(+)		(+)	(+)		
	—	0	0	0			0	+
iso-leucine	(+)	(+)	(0)		(0)	(—)	(0)	(0)
			+	+	+	0	0	0

Table 1 (continued)

Compound	Species of larva							
	P. troilus		*P. glaucus*		*P. polyxenes*		*M. americana*	
	L	M	L	M	L	M	L	M
leucine	(+)	(0)			(0)	(−)	(0)	(0)
			0	+	0	0	0	0
lysine			+	0				
methionine	(+)	(+)	(0)		(+)	(−)	(0)	(0)
	0	+	0	0	0	0	0	0
phenylalanine	(0)		(0)		(0)	(0)	(0)	(0)
	—		0	0			0	0
proline	(0)	(?)			(−)	(−)	(+)	(+)
	0		+	+	0	+	+	+
serine	(+)	(+)			(+)	(?)	(?)	(0)
	0	?	+	?	+	+	0	0
threonine	(+)	(+)			(+)	(0)	(0)	(0)
		0	+	0	+	?	0	0
tryptophane	(0)	(−)			(+)	(0)	(0)	
			0	0	+	+	0	0
tyrosine					(0)	(0)	(0)	(0)
	0		0	0			0	0
valine	(+)		(+)		(0)	(0)	(?)	(0)
			+	?	0	+	0	0
ascorbic acid	(+)							
	+	+	0	+			0	+
malic acid	(+)							
	0	+	0	+			+	+
oxalic acid	(+)							
	+	+	0	+				
succinic acid							+	
0.001 M amygdalin	(0)	(0)	(0)		(0)	(0)	(0)	(0)
							0	0
0.1 M amygdalin	—	—	?	0			0	0
0.001 M apiin	(+)	(+)			(0)	(+)	(0)	(0)
		+	0	0	0	+	0	0
0.001 M apocynin					(0)	(+)		
	—	—	0	0	0	+	0	0
0.001 M glucocapparin	(+)	(0)	(0)	(0)		(0)	(+)	(+)
	0	0	0	0	0	0	+	+
0.001 M glucosinalbin	(0)	(0)			(0)	(?)		
	0	0	0	0	0	?		

Table 1 (continued)

Compound	Species of larva							
	P. troilus		*P. glaucus*		*P. polyxenes*		*M. americana*	
	L	M	L	M	L	M	L	M
0.001 M heliotropin	(0)	(+)	(+)		(0)	(+)	(+)	(0)
	0	+	0	0	0	0	0	0
0.001 M morin	(−)	(−)			(+)	(+)		
	—	—	0	0	0	?	0	0
0.001 M populin	(0)	(0)				(+)		
			0	0			0	+
0.1 M populin	(0)							
		+	+	+		+		
0.001 M rutin						(+)		
	0	0	0	0		?	0	0
0.001 M salicin	(0)	(0)	(+)		(0)	(?)	(?)	(+)
	0	0	?	?			0	0
0.1 M salicin	+	+	+	+		?	0	0
0.001 M sinalbin	(0)	(0)				(+)		
	0	0	0	0		+	0	+
0.001 M sinigrin	(0)	(0)	(0)		(0)	(+)	(0)	(0)
	0	0	0	0	0	0	0	0
0.1 sinigrin	—	—	—	—			0	+
0.001 M tropæolin					(+)			
	—	—	0	+	+		0	+
0.001 M quercitin	(0)	(0)			(0)	(0)	(0)	(0)
	0	0	0	0	0	?	0	0
0.001 M quercitrin	(0)	(0)	(0)		(−)	(+)		
	0	0	+	+			0	+

Responses to Single Compounds — Unrelated Larvae

E. egle and *D. plexippus* feed preferentially on *Asclepias*. *P. eglenensis* prefers *Apocynum*. All three species will eat both plants. The response spectra to single compounds are rather similar, but there are some notable differences. At least three cells in the medial sensillum of *P. eglenensis* respond to NaCl. Occasionally there is a fourth. The most active of these is the major salt receptor. There is also a sugar receptor most sensitive to sucrose. No responses were obtained to 0.1 M fructose or glucose; however, 0.5 M glucose was mildly stimulating. The spike of the sugar receptor characteristically is more nearly monophasic than that of any other receptors (Figs. 34 and 35). No clear response was obtained

Table 2. Responses of three unrelated species of caterpillars that share a food plant to various compounds occuring in plants. L and M refer to lateral and medial maxillary sensilla respectively. Parentheses indicate that the compound was made up in phosphate buffer. Otherwise compounds were in 0.05 M NaCl

Compound	Species of larva					
	D. plexippus		*E. egle*		*P. eglenensis*	
	L	M	L	M	L	M
PO_4	(+)	(+)	(+)	(+)	(+)	(+)
0.0025 M NaCl					+	+
0.005 M NaCl	0	0			+	+
0.05 M NaCl	+	+			+	+
0.1 M NaCl	+	+	+	+	+	+
0.1 M sucrose	(+)	(0)	(+)	(0)		
	+	0			+	+
0.1 M fructose	(0)	(0)	(0)	(0)		
	0	0			0	0
0.1 M glucose	(0)		(0)	(0)		
	0	0			0	0
0.1 M inositol	(+)	(0)	(0)	(0)		
	0	0			0	0
0.1 M sorbitol						
0.1 M dulcitol						
alanine	(?)	(0)	(?)	(?)		
	0	0			0	0
arginine	(?)	(0)	(0)	(0)		
	0	0				
aspartic acid	(+)	(?)	(?)	(?)		
	+	+			0	0
cysteine	(?)	(+)	(0)	(0)		
	0	0				
cystine	(?)	(+)	(0)	(0)		
	0	0			0	0
glutamic acid	(0)	(0)	(0)	(0)		
	0	+			0	0
glycine			(0)	(0)		
	0	0				
histidine			(0)	(0)		
	0	0				
iso-leucine			(0)	(0)		
	0	0				

Table 2 (continued)

Compound	Species of larva					
	D. plexippus		*E. egle*		*P. eglenensis*	
	L	M	L	M	L	M
leucine	(+)	(0)	(0)	(0)		
	0	0				
lysine	0	0				
methionine	(+)	(−)	(0)	(0)		
	0	—			0	0
phenylalanine			(0)	(0)		
	0	0				
proline	(+)	(?)	(0)	(0)		
	0	0			0	0
serine	(?)	(?)	(?)	(0)		
	0	0			0	0
threonine	(+)	(0)	(0)	(0)		
	0	—			0	0
tryptophane			(0)	(0)		
	0	0				
tyrosine	(0)	(0)				
	0	—				
valine	(+)	(−)	(0)	(0)		
	0	0			0	0
ascorbic acid	+	+				
malic acid			(+)	(+)		
	+	+				
oxalic acid			(+)	(+)		
0.001 M amygdalin	(0)	(0)	(?)	(0)		
	0	0				
0.1 M amygdalin	?	0			0	+
0.001 M apiin	(0)	(0)				
	0	0			0	?
0.001 M apocynin	(+)	(+)				
	0	?			—	—
0.001 M glucocapparin	(0)	(0)	(0)	(0)		
	+	0			0	+
0.1 M glucosinalbin	(0)	(0)				
	0	0				
0.001 M heliotropin	(0)	(0)	(0)	(0)		
	0	0			0	0

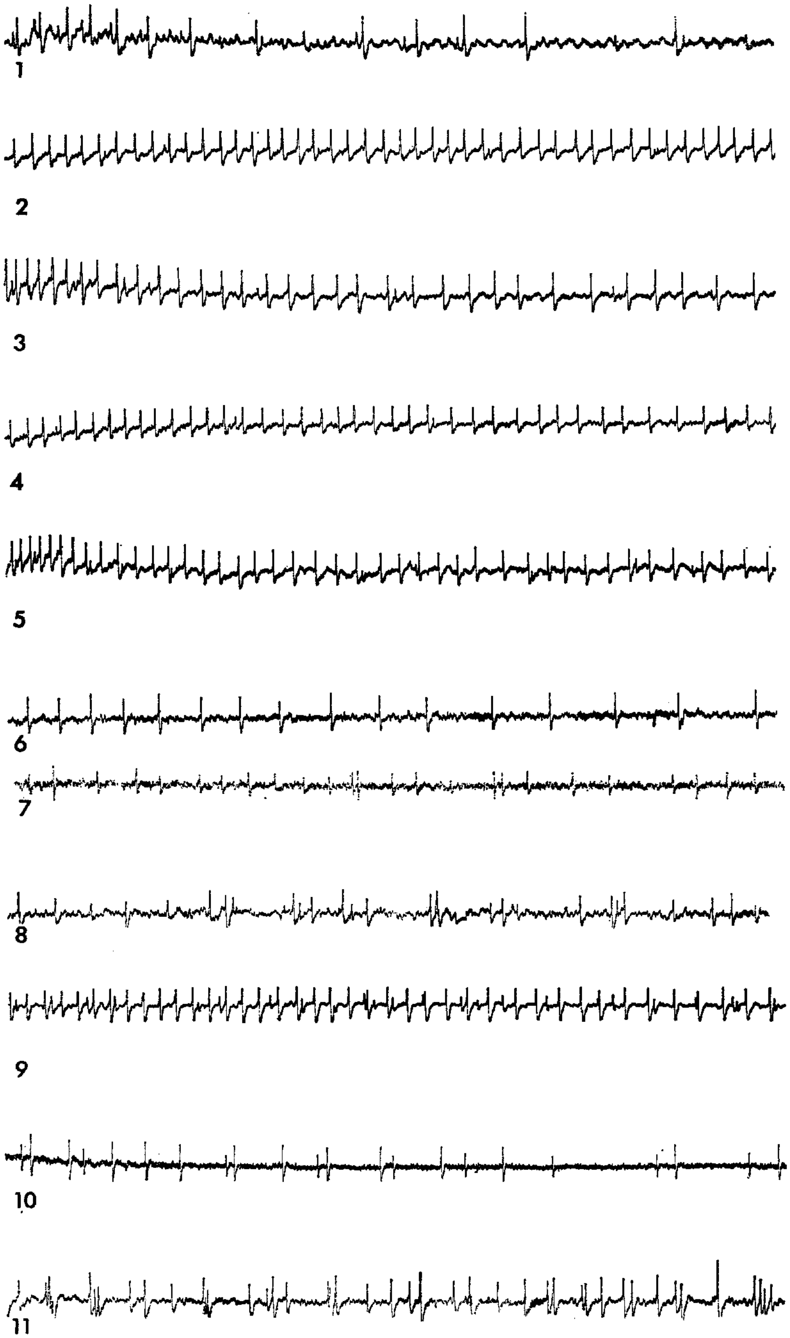
Table 2 (continued)

Compound	Species of larva					
	D. plexippus		*E. egle*		*P. eglenensis*	
	L	M	L	M	L	M
0.001 M morin	(0)	(0)				
	0	0			0	+
0.001 M populin	(+)					
	0	0				
0.1 M populin		(?)				
	0	0			0	0
0.001 M rutin	(0)	(0)				
	0	0			+	0
0.001 M salicin	(?)	(0)				
	0	0				
0.1 M salicin	0	0			0	0
0.001 M sinalbin	(0)	(0)				
	0	0			0	0
0.001 M sinigrin	(0)	(0)	(0)	(0)		
	0	0			0	0
0.1 M sinigrin	+	?			+	+
0.001 M tropaeolin	(+)	(+)				
	+	0			0	0
0.001 M quercitin	(0)	(0)				
	0	0			?	0
0.001 M quercitrin			(+)	(0)		
	0	?			?	0

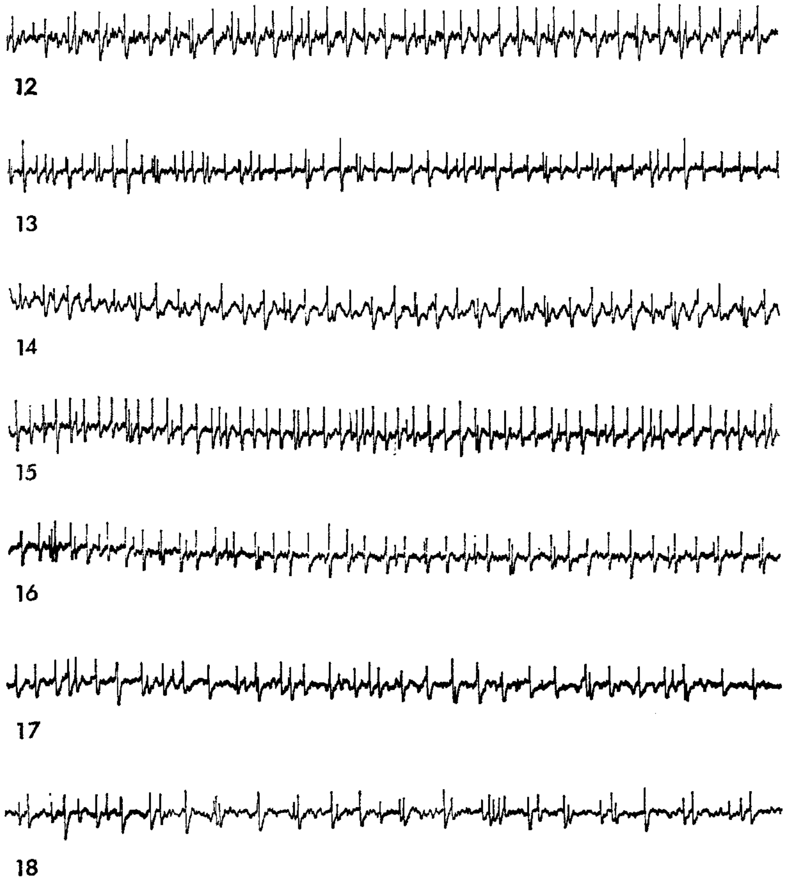
to inositol. Insofar as amino acids are concerned few are effective stimuli. At the concentrations employed none stimulated. Of the glycosides tested the most stimulating is sinigrin. It is especially effective on two of the cells that respond to salt. Of the related glycosides only glucocapparin is effective. Apocynin, a glycoside found in the larva's food plant, does not stimulate and may even be somewhat inhibitory. Amygdalin stimulates the salt cell slightly.

Aside from salt, sucrose, rutin, and sinigrin, few compounds stimulate the lateral sensillum. At least three cells respond to salt.

The medial sensillum of *E. egle* is not markedly responsive. Three cells respond to salt and to phosphate buffer. No responses were obtained to 0.1 M sugars or to inositol. Higher concentrations were not tested. None of the amino acids or glycosides are outstandingly effective.



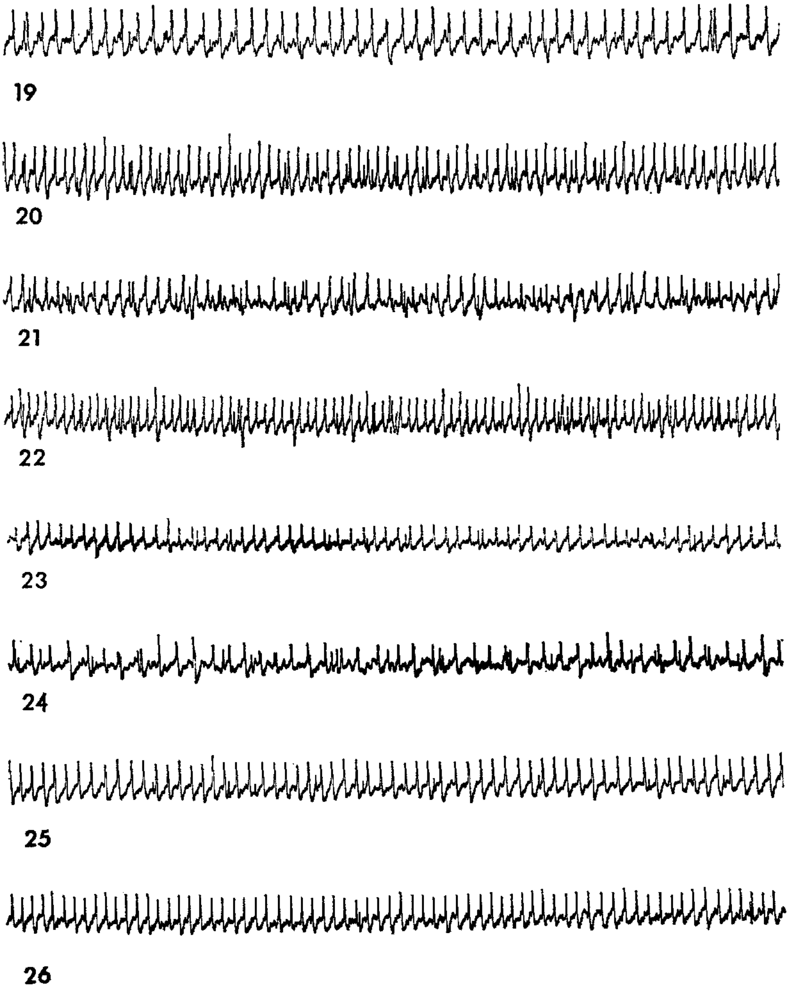
Figs. 1—11



Figs. 12—18. Fig. 12. Sodium chloride (0.15 M) on the lateral sensillum of *P. troilus.* Fig. 13. Sassafras sap (*Sassafras albidum* [Nutt.]) on the same sensillum. Fig. 14. Spicebush (*Lindera Benzoin* [L.]). Fig. 15. Carrot sap. Fig. 16. Fennel sap. Fig. 17. Cherry sap. Fig. 18. Milkweed sap

Figs. 1—6. Fig. 1. Sodium chloride (0.005 M) on the lateral sensillum of *P. glaucus.* Each record begins at the onset of stimulation and continues for 1 sec. Fig. 2. Cherry sap plus 0.05 M NaCl on the same sensillum. Fig. 3. Cherry sap (*Prunus virginiana* L.). Fig. 4. Carrot sap (*Daucus carota* L.). Fig. 5. Fennel sap (*Foeniculum vulgare* Mill.). Fig. 6. Cabbage sap (*Brassica oleraceae* L.)

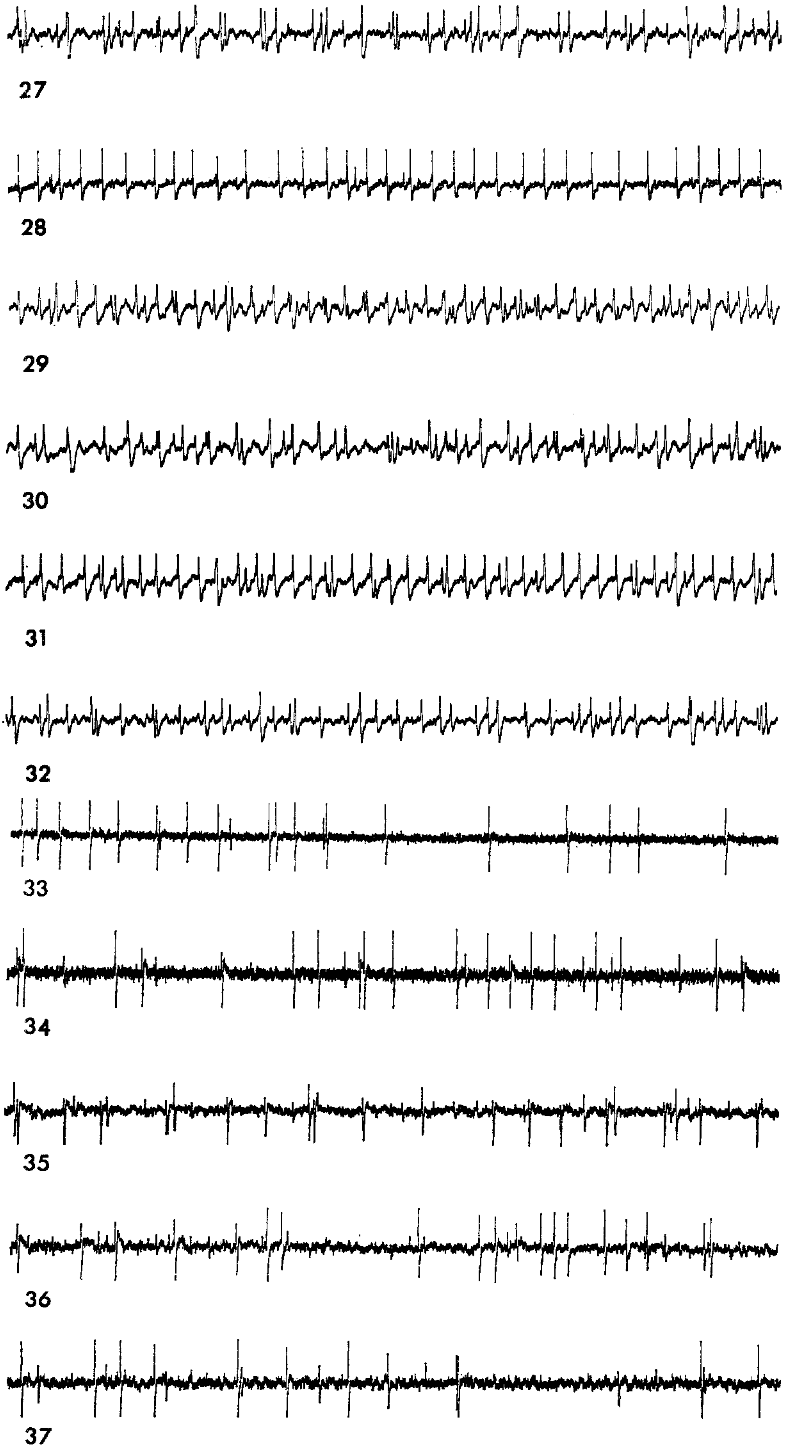
Figs. 7—11. Fig. 7. Sodium chloride (0.05 M) on the medial sensillum of *P. glaucus.* Fig. 8. Cherry sap on the same sensillum. Fig. 9. Carrot sap. Fig. 10. Cabbage sap. Fig. 11. Milkweed sap (*Asclepias syrica* L.)



Figs. 19—26. Fig. 19. Sodium chloride (0.05 M) on the medial sensillum of *P. troilus*. Fig. 20. Sassafras sap on the same sensillum. Fig. 21. Spicebush sap. Fig. 22. Carrot sap. Fig. 23. Fennel sap. Fig. 24. Cherry sap. Fig. 25. Milkweed sap. Fig. 26. Cabbage sap

Figs. 27—32. Fig. 27. Sodium chloride (0.1 M) on the medial sensillum of *P. polyxenes*. Fig. 28. Carrot sap on the same sensillum. Fig. 29. Fennel sap. Fig. 30. Cherry sap. Fig. 31. Sassafras sap. Fig. 32. Spicebush sap

Figs. 33—37. Fig. 33. Sodium chloride (0.25 M) on the medial sensillum of *P. eglenensis* Clemens. Fig. 34. Glucose (0.5 M) on the same sensillum. Fig. 35. Sucrose (0.5 M). Fig. 36. Milkweed sap. Fig. 37. Cabbage



Figs. 27—37

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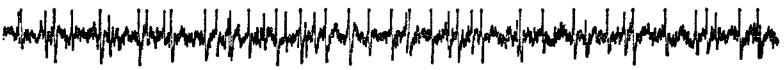

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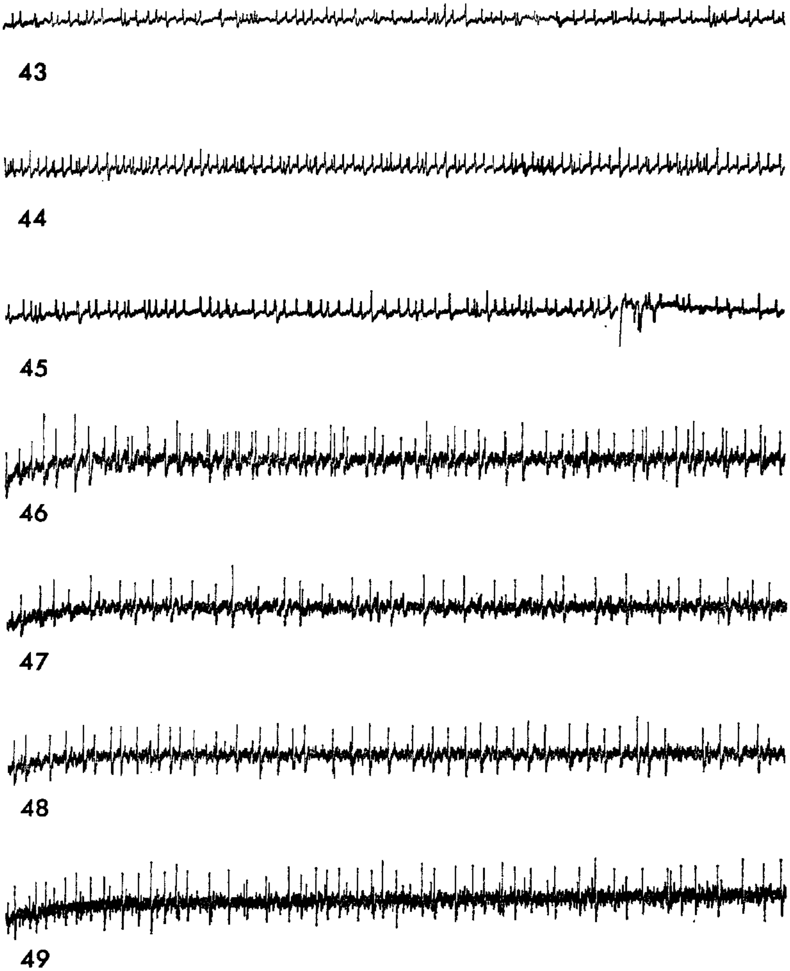
Figs. 38—49. Fig. 38. Phosphate buffer on the lateral sensillum of *E. egle*. Fig. 39. Milkweed sap on the same sensillum. Fig. 40. Carrot sap. Fig. 41. Cabbage sap. Fig. 42. Milkweed sap on the medial sensillum of *D. plexippus*. Fig. 43. Milkweed sap on the lateral sensillum. Fig. 44. *Apocynum* sap on the same sensillum. Fig. 45. Cabbage sap. Fig. 46. Cherry sap on the lateral sensillum of *M. americana*. Fig. 47. Cherry sap on the medial sensillum. Fig. 48. Carrot sap on the same sensillum. Fig. 49. Sodium chloride (0.05 M)

The lateral sensillum behaves similarly except that it has one cell sensitive to sucrose.

D. plexippus is generally more responsive. In the medial sensillum four cells respond well to salt. At the concentrations tested none of the sugars were effective except for an occasional low level response to glucose. The following amino acids buffered with phosphate stimulate: aspartic acid, cysteine, cystine, proline, and serine. Of these only aspartic acid also stimulates when made up in 0.05 M NaCl. Glutamic acid in 0.05 M NaCl stimulates. The cells responding most actively are the two that respond maximally to salt. Methionine, threonine, tyrosine, and valine inhibit. Insofar as the glycosides are concerned some low level activity was obtained in response to 0.001 M apocynin, tropaeolin, and



Figs. 43—49

salicin, and to 0.1 M populin and sinigrin. These compounds tend to stimulate the primary salt cell.

In the lateral sensillum three cells routinely respond to salt. Occasionally there is low level activity from a fourth. Another cell responds to sucrose. No response was obtained to inositol in 0.05 M NaCl. The sensillum also responds to a number of amino acids in buffer as reported earlier (Dethier and Kuch, 1971). Some of these acids stimulate the primary salt cell preferentially; others stimulate both salt cells. Re-

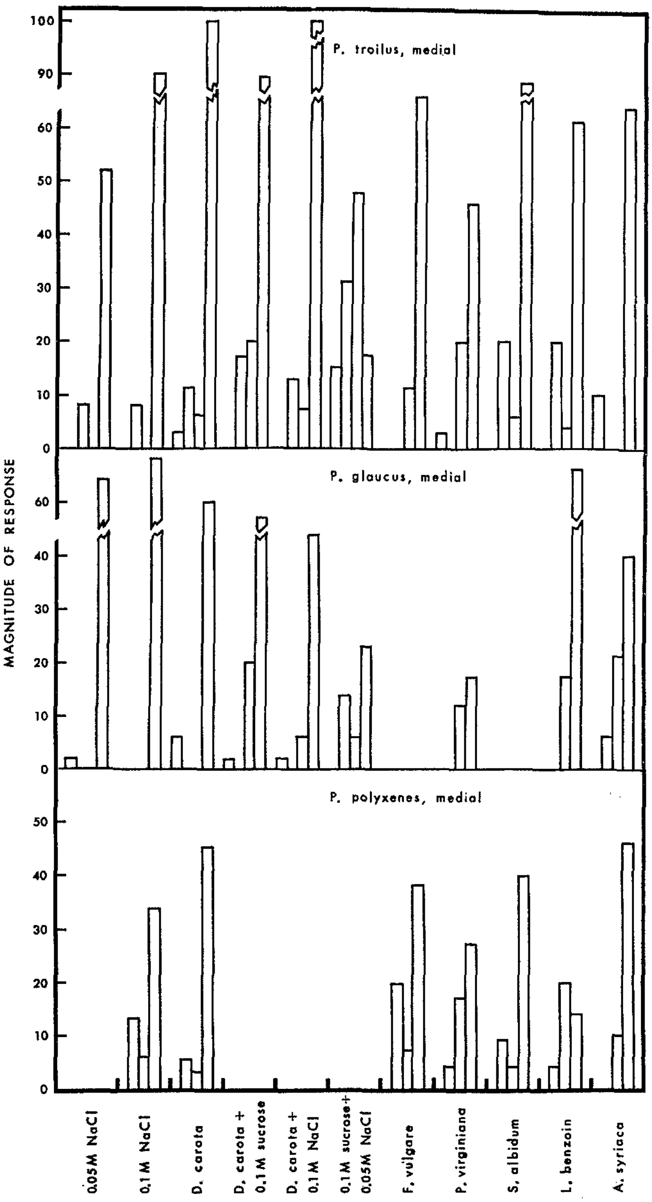


Fig. 50. Response patterns of the medial sensilla of three species of *Papilio* to plant saps. The number of action potentials generated by each receptor in the sensillum during the first second of stimulation by each sap is plotted as a vertical bar (magnitude of response). Receptors were identified by the amplitude of their action potentials. For each stimulus, the impulse with the lowest amplitude is plotted first (reading left to right) and the highest, plotted last. Thus, for example, 0.1 M NaCl caused the receptor of *P. polyxenes* with the lowest amplitude to fire 12 spikes, the cell with the medium amplitude 5 spikes, and the cell with the highest amplitude, 33 spikes. The histograms in all three horizontal rows are aligned vertically so that the salt cells of one species correspond with those of the other

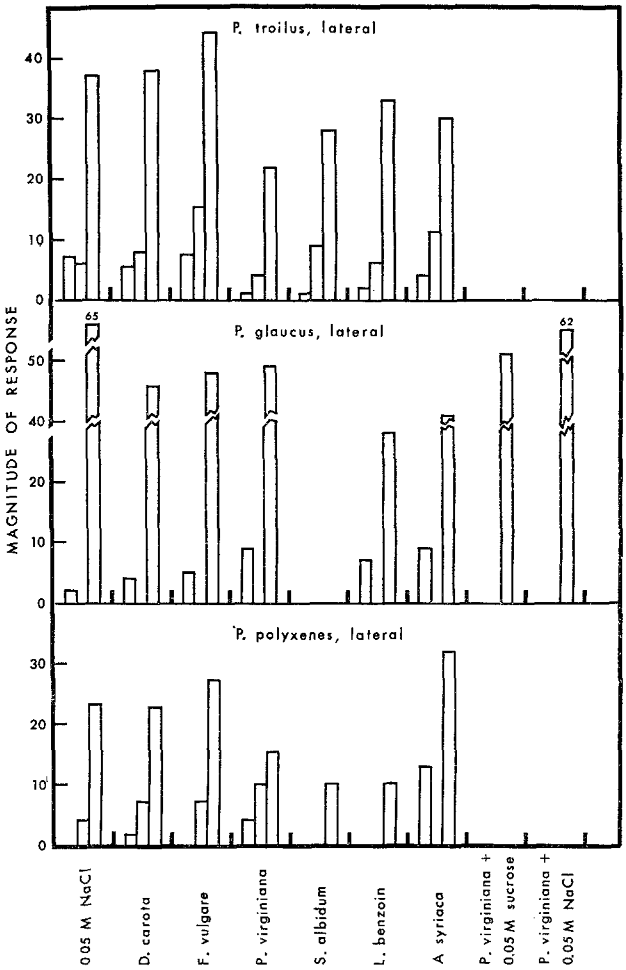


Fig. 51. Response patterns of the lateral sensilla of three species of *Papilio*. For explanation see legend for Fig. 50

sponses were obtained to a number of glycosides. Sinigrin and its relatives are quite effective. The major salt cell is involved.

Another comparison that can be made between unrelated larvae is that between *Papilio glaucus* and *Malacosoma americana*, the tent caterpillar. Although both of these insects feed on a number of plants, cherry is outstandingly preferred in the Princeton area. The differences between the two are of the same degree as the differences among the three papilios.

It is noteworthy that neither caterpillar responds to amygdalin. Other differences may be noted in Table 1.

Responses to Unacceptable Plants — Related Species of Larvae

The responses of *P. troilus* to two unacceptable plants, carrot and fennel, which are the preferred plants of *P. polyxenes*, and cherry, which is the preferred food of *P. glaucus*, are illustrated in Figs. 15–17, 22–24, 50 and 51. Three cells of the lateral sensillum respond in all cases. The cell generating the spike of the highest amplitude was more active than the other two combined. This is the same cell that gives the maximum response to sodium chloride. The sugar receptor appears to be inactive. The spectra of response to these unacceptable plants and to milkweed appears to differ quantitatively rather than qualitatively. This sensillum is unresponsive to apiin, amygdalin, apocynin, and sinigrin, the glycosides that characterize carrot, cherry, milkweed, and cabbage respectively.

The medial sensillum is less uniform in its response. Four cells respond to carrot, two to fennel, two to milkweed, and three to cherry, spicebush, and sassafras; however, in all cases the overwhelming response comes from the cell that gives the spike of the highest amplitude. This is the same cell that responds maximally to NaCl. The addition of salt to the sap of carrot greatly increases the rate of firing of this cell. The same is true when salt is added to cherry. This finding lends support to the view that the cell in question is the major salt receptor. Mixing sucrose with the sap of carrot increases the rate of firing of the receptors that give rise to the spikes of medium amplitude. At the same time sucrose reduces the rate of firing of the salt receptor. Similarly the addition of sucrose to sodium chloride causes the sugar receptor to fire and slightly inhibits the primary salt receptor. One of the four receptors firing in response to carrot sap is therefore the sugar receptor. The response to carrot and to fennel, two plants acceptable to *P. polyxenes* is, therefore, qualitatively different. In general, however, as in the case of the lateral sensillum, the responses to unacceptable plants differ quantitatively, and the major contributing receptor is the salt receptor. This is also the cell that responds to some amino acids, organic acids, and to apiin. There is no response to the glycosides apocynin and amygdalin.

P. glaucus was tested with the saps of five unacceptable plants: carrot and fennel (food plants of *polyxenes*), spicebush (food plant of *troilus*), milkweed (food plant of *plexippus*), and cabbage (food plant of *Pieris rapae*). In the lateral sensillum fewer cells respond than is the case with *P. troilus* (Figs. 4–6 and 51). The response is predominently that of the salt cell. Sometimes it is the only cell responding, but usually there is a small contribution from one other cell.

Responses by the medial sensillum do not differ noticeably from those by the lateral sensillum (Figs. 9–11 and 50). One cell dominantes the response except in the case of milkweed where there is a moderate contribution from another. Mixing experiments indicated that the dominant cell is the salt receptor. For example, no additional cell commences firing upon the addition of salt to carrot sap; with the addition of sucrose an additional cell, the sugar receptor, contributes to the overall pattern (Fig. 50).

P. polyxenes was tested with the saps of cherry (food plant of *P. glaucus*) spicebush and sassafras (food plants of *P. troilus*), milkweed (food plant of *D. plexippus*), and cabbage (food plant of *P. rapae*). In the lateral sensillum three cells respond to cherry and to cabbage. No single cell dominates the response. Spicebush and sassafras elicit activity from one cell; milkweed, from two.

Differences in the responses of the medial sensillum to the various saps are primarily quantitative. Three cells respond in each case except with milkweed, and no one cell dominates. Milkweed elicits responses from two cells.

Responses to Unacceptable Plants — Unrelated Species of Larvae

Just as related species of larvae respond differently to various species of non-preferred plants, so do unrelated larvae. Rejection is not a uniform modality for either. Larvae of *E. egle* respond to carrot and to cabbage with great activity from three cells, and occasionally four, in the lateral sensillum (Figs. 40 and 41). The two cells that generate spikes of the highest amplitude are nearly equal in frequency. The responses to the two plants differ only quantitatively and resemble the response to phosphate buffer (Fig. 38). The response to sassafras involves two cells of which one clearly dominates.

In the medial sensillum three cells respond to carrot and to cabbage. A cell giving a medium-sized spike dominates. The response to sassafras takes the form of activity predominantly from one cell.

In the lateral sensillum of *D. plexippus* the total pattern of response to carrot and to cabbage is similar. Three cells respond; one dominates. In the case of the medial sensillum the response profiles to carrot and to cabbage are again similar; three cells respond; one is dominant (Fig. 45). Fewer cells respond to the sap of sassafras.

Comparison of Response to Host and to Non-Host Plants

An examination of Figs. 50 and 51 shows that there is no marked or consistent difference in the response to acceptable and unacceptable plants for any of the papilios. For example, the medial sensillum of *P. troilus* responds to two food plants and to the unacceptable plants cherry and carrot with activity from three cells of which one clearly dominates. The dominant cell is the salt cell. Although the identity of the other two cells from one stimulus situation to the next cannot be equated, it is highly probable that the differences in the response patterns to the four plants in question are primarily quantitative. A similar situation prevails with *P. polyxenes,* and to a lesser extent, with *P. glaucus.* Milkweed deviates from the pattern in all three instances.

The case is even more marked with respect to the lateral sensillum (Fig. 51). Here the patterns of response to host plant and unacceptable plant are sometimes indistinguishable. Compare, for example, the response of *P. glaucus* to cherry, carrot, and fennel (Figs. 3–5 and 51), or the response of *P. troilus* to sassafras, spicebush, and cherry (Figs. 13, 14, 17 and 50). Other comparisons may be made from the remaining figures. See also the response patterns of *M. americana* to host and non-host plants (Figs. 46–48).

Responses of the lateral sensillum of *E. egle* to milkweed involves three to four cells of which two act at approximately equal frequencies. These are the two that give maximum responses to NaCl and to phosphate buffer (Fig. 38). The total response is not readily distinguishable from responses to carrot and cabbage (Figs. 40 and 41). In the medial sensillum three cells respond to carrot and cabbage. One dominates the pattern. In the response to milkweed two contribute more or less equally.

The lateral sensillum of *D. plexippus* gives responses to milkweed, *Apocynum,* and cabbage that are remarkably similar though not identical (Figs. 43–45).

Comparison of Response of Oligophagous Species to Different Host Plants

Analysis of the responses of *Papilio polyxenes* to two of its several food plants, carrot and fennel, show that the patterns of total response are not identical. This is well illustrated in Figs. 28, 29, 50 and 51. A similar comparison can be made of the responses of *P. troilus* to two of its food plants, sassafras and spicebush (Figs. 13, 14, 20, 21, 50 and 51). The differences here are not so striking; nevertheless, they occur regularly.

Among the milkweed-feeders consistent differences were observed when the responses to *Asclepias* and to *Apocynum* were compared. *P. eglenensis* is a case in point. In the lateral sensillum three cells dominate the response to milkweed. Of these one is active at a higher frequency than all of the others combined. The response to *Apocynum* differs in that there is more nearly equal response from four cells. Comparable differences are observed in the response of the medial sensillum. Differences of similar magnitude are seen in the responses of *D. plexippus* and *E. egle* (Figs. 38–45).

Comparison of the Responses of Unrelated Larvae to the Same Food Plant

In response to 0.1 M NaCl four receptors in the medial sensillum of *D. plexippus* become active. When the sap of milkweed is applied to this sensillum, all four cells again respond but with different frequencies (Fig. 42). Two of the four increase their rate of firing, one shows no appreciable change, one decreases. In the medial sensillum of *E. egle* three cells respond to sodium chloride. Milkweed causes an increase in one cell, no appreciable change in another, and a slight decrease in the third. *P. eglenensis* responds to NaCl with activity from four cells of the medial sensillum. Milkweed also elicits a response from four. Whereas one cell dominates the response pattern to salt, two are very nearly equal in the response to milkweed. The situation is comparable with respect to the sensillum.

Compare also the responses of *P. glaucus* and *M. americana to* cherry (Figs. 3, 46, and 47).

Discussion

The following conclusions may be drawn: (1) no species of caterpillar gives a single standard electrophysiological response to all of the plants it rejects; that is, rejection is not a unitary modality; (2) a plant that is unacceptable to several species of caterpillars does not elicit the same pattern of response from each; (3) a food plant that is shared by several species of caterpillars does not elicit the same pattern of response from each; (4) a species of caterpillar that has more than one food plant does not generate the same sensory pattern to each; (5) there is no universal difference between sensory patterns for acceptance and those for rejection.

Some of these conclusions merely confirm what has long been known or suspected from behavioral studies. Assuming, for the moment only, that the maxillary gustatory sense plays the primary role in assessing the palatability of plants, it is not surprising that rejection may take more than one form because observations of feeding behavior reveal that unacceptability is a matter of degree. Furthermore, it is more than likely that different compounds may form the basis for rejection of different plants. One plant may be rejected because it has a high concentration of organic acid; another, because it has a high glycoside content. If the two compounds in question stimulate different receptors, the modality of rejection is different. This is obviously the situation in some instances. On the other hand, if the acid and the glycoside stimulate the same receptor, the two would be qualitatively indistinguishable, and the modality of rejection would be the same, albeit for different reasons. These results agree with Ishikawa's (1966) conclusion that for the silkworm the modality "unacceptable" is not a homogeneous one.

Conclusion (2) is self evident given the diversity illustrated in Tables 1 and 2. If the sensory capacities of two caterpillars are different, it cannot be expected that they will receive identical stimulation from any particular plant. Conclusion (3) is a corollary of (2). This is a particularly significant conclusion because of its evolutionary connotation. It suggests that a plant in evolving mechanisms to produce chemical compounds that may be of value in protecting it from insect predation would do well to produce a complex array rather than a single compound, and, furthermore, that insects co-evolving with a particular plant each evolve with respect to a different component of that plant's chemical complex.

Conclusion (4) was anticipated long ago by behavioral studies. For example, it was shown that *Papilio polyxenes* could differentiate among its several food plants (Dethier, 1941). More recently, experiments in which *Manduca sexta* and *Heliothis zea* were induced to change their feeding preferences gave further proof that acceptability is not a single modality (Jermy *et al.*, 1968).

The simplest explanation of the way in which taste could act to control feeding would be that after the first bite some particular substance in a plant triggers rejection and some particular substance triggers acceptance. The classical case for a specific taste substance has been sinigrin. It and other cruciferous glycosides have been demonstrated behaviorally and electrophysiologically to be feeding stimulants for *Pieris brassicae, Plutella maculipennis* Curtis, the cabbage aphid (*Brevicoryne brassicae*[L.]), and other insects feeding on cruciferae (Verschaffelt, 1910; Wensler, 1962; Nayar and Thornsteinson, 1963; David and Gardiner, 1966b; and Schoonhoven, 1967). On the other hand, insects that are highly sensitive to these compounds may feed in their absence. For example, larvae of *P. brassicae* will feed and develop on artificial diets lacking mustard glycosides (David and Gardiner, 1966a). There is no doubt, however, that certain compounds individually or mixed enhance feeding.

Correlated with these observations is the evidence that there exist certain receptors more or less specifically sensitive to one or more of these substances and that these receptors signal acceptance to the central nervous system. Schoonhoven (1967) reported a receptor sensitive to cruciferous glycosides in *P. brassicae.* Rees (1969) reported a receptor in *Chrysomela brunsvicensis* that is sensitive to hypericin, a compound present in the food plant *Hyperium hirsutum.* Receptors more or less specific to various sugars and to inositol are of widespread occurrence, and it is well known that the addition of sugar or inositol to the diets of many insects will enhance feeding. For example, sugar induces the silkworm to feed on filter paper (Niimura and Ito, 1964).

Few other gustatory stimulants have been identified (see Schoonhoven, 1972a). The results reported in the present study have not revealed any such gustatory stimulants for the species studied. Some of the likely glycosides (*e.g.*, amygdalin, apiin, apocynin, salicin) have not shown the outstanding effectiveness attributed to sinigrin for cruciferae-feeders. It is, of course, possible that such specific compounds do exist and that they have not been tested. Unfortunately, some of the most likely candidates are not available.

There is also abundant evidence, especially with respect to *Bombyx mori*, of one or more receptors especially sensitive to substances that are known to be feeding deterrents (Ishikawa and Hirao, 1963; Ishikawa, 1966). Feeding by insects can be stopped by adding certain compounds. The silkworm is prevented from feeding on mulberry by painting the leaves with some glycosides and alkaloids (Nakajima, 1939). The Colorado potato beetle is deterred by several alkaloids, saponins (Schreiber, 1958), salts of organic acids, fungicide preparations, copper ion (Jermy, 1961b). Other examples are given by Ma (1969) and Schoonhoven (1972b).

An alternate hypothesis to the one that some particular compound acting as a stimulant or as a deterrent dominates and regulates ingestion is the hypothesis that selection at the first bite is determined by integrating the combined response of several receptors to multiple constituents. This concept has been fore-shadowed by the observations of a number of investigators who have stressed the importance of mixtures of compounds. Ishikawa (1966) found with respect to the silkworm that rejection of a plant does not depend solely on activity of the so-called deterrent receptor. He has suggested that the ratio in amounts of stimulants and deterrents might be significant for food selectivity. He was referring not only to integration of maxillary responses but also to possible contributions from other sensory systems. This latter point will be considered later. Ishikawa, Hirao, and Arai (1969) and Ma (1969) also demonstrated that caterpillars prefer certain *combinations* of taste substances within fairly narrow concentration ratios. House (1966) had previously shown for other insects that particular ratios are important from a nutritional point of view. Haskell and Mordue (1969) emphasized that feeding by acridids is based on receipt of large amounts of information on all qualities of the food. Jermy (1961a) also has pointed out that the host range of a given phytophagous insect is primarily determined by the number and concentration range of chemicals to which the chemoreceptors are tuned in a positive and negative sense respectively. Later he accorded primary to deterrents (Jermy, 1966). Ritter (1967), having searched in vain for a token substance in potato which stimulated feeding by the Colorado potato beetle, concluded that there are a large number of compounds in a potato leaf that can be tasted and that they are present in just the right amount to make this leaf the preferred one.

The hypothesis proposed here is modeled after the across-fiber patterning hypothesis that Erickson (1963) advanced to explain taste discrimination in rats. The essence of this hypothesis is that the receptors have unique but overlaping action spectra and that each compound or combination of compounds that can be discriminated generates a unique total pattern of response. Two of the requisites seem to be met here, namely, that the receptors have spectra of activities rather than unitary specificities, and that the responses to plants involve more than a single receptor. With regard to specificity, the data of Ishikawa (1963, 1966) for the silkworm, of Schoonhoven (1969) for a number of species, of Dethier and Kuch (1971) for ten species, and the data in this study support the idea that few receptors are narrowly specific. There are all degrees of receptor specificity. The so-called deterrent receptor responds to many compounds. The inositol receptor is much more specific, but not absolutely so. With regard to the existence of multireceptor response to plant saps, there are many reports. Ishikawa and Hirao (1963) have shown that different numbers of receptors of *Bombyx mori* respond to different plants. Schoonhoven and Dethier (1966) reported that responses to plant saps were multireceptorial. Many compounds stimulate more than one cell (*e.g.*, terpenoids and some B vitamins [Schoonhoven, 1969], salts, some amino acids, and some glycosides [Dethier and Kuch, 1971; and this study]).

The following model demonstrates how across-fiber patterning can work. Two simplifying assumptions will first be made in order to explain the model after which modifying conditions which more closely approximate actuality will be introduced. The introductory assumptions are: (1) each receptors has a unique spectrum of action which may or may not overlap that of other receptors; (2) no stimulus interaction, inhibition or synergism, occurs. Given these conditions the response characteristics of three hypothetical receptors may be represented by Fig. 52 in which the magnitude of response of each is plotted against the log of concentration of each of four possible stimuli. Consider, for example R_r, the rejection or deterrent receptor, which is represented in Fig. 52 by the dot-dash line. It responds with high activity to low concentrations of glycoside (*G*), moderately well to median concentrations of organic acids *OA*), and minimally to all concentrations of salt (*N*) and amino acid (*AA*) and not at all to sugar. The sugar receptor (solid line) responds well to sugar (*S*), moderately well to an amino acid (*AA*), moderately to high concentrations of organic acid (*OA*), poorly to glycoside (*G*), and not at all to salt. Thus, each receptor has an action spectrum and yet has some degree of specificity even though it overlaps another receptor. Also each receptor

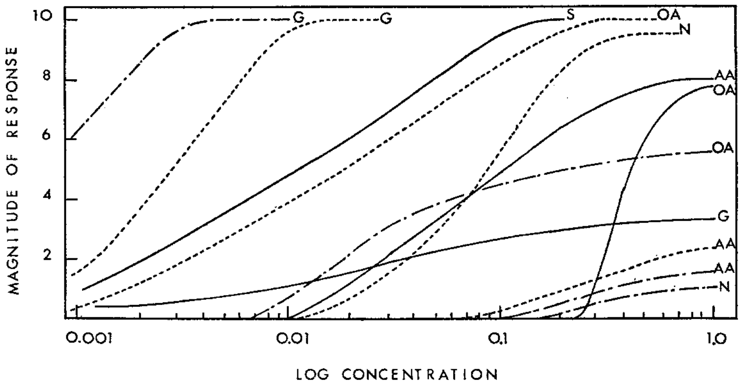
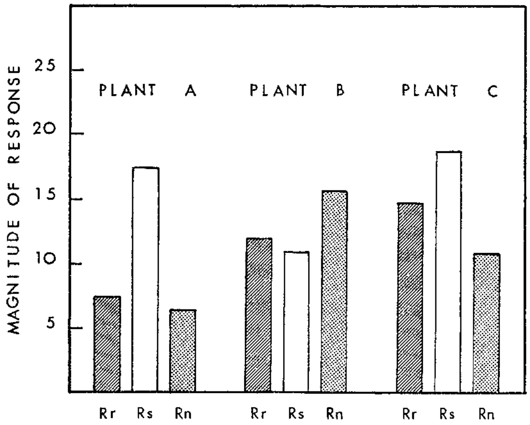


Fig. 52. Concentration-response curves for three hypothetical receptors: ——— a sugar receptor, ----- a salt receptor; ——·—— a rejection or deterrent receptor. Each receptor is postulated as responding to four of five compounds: *G* a glycoside; *S* a sugar; *N* a salt, *OA* an organic acid; *AA* an amino acid. The slopes of the curves are arbitrary but are based on the general characteristics of actual curves



Organic acid	Low	0.0015	High	0.35	Low	0.0015
Salt	Low	0.05	Low	0.05	Low	0.05
Sugar	High	1.0	Low	0.001	Medium	0.5
Glycoside	Low	0.001	Low	0.001	High	0.015
Amino acid	Medium	0.3	Medium	0.3	Medium	0.3

Fig. 53. Three patterns of response of a sensillum made up of the three hypothetical receptors described in Fig. 52: R_r repellent or deterrent receptor; R_s sugar receptor; R_n salt receptor. Each pattern represents the response to a different plant (A, B, C) in which concentrations of five compounds were set arbitrarily. Each vertical bar representing the combined magnitude of response to all constituents of the plant was generated by reading from the response curves in Fig. 52 the magnitude of response given by each receptor to each of the compounds at the concentrations shown

has response curves the slopes of which are different for different compounds. Additionally, a given compound may elicit a differently sloped curve from different receptors. These curves are modeled after actual stimulus-response curves measured for caterpillars. The model takes into consideration the fact that receptors have different sensitivities for different compounds and differ from one another in threshold and sensitivity with respect to any commonly stimulating compound.

From the curves in Fig. 52, it is now possible to construct the total response pattern generated by several hypothetical plant saps. The response to three hypothetical plants are plotted in Fig. 53. The plants were assigned different concentrations of the five constituents for which response curves had been plotted in Fig. 52. Plant A, for example, was given a high concentration of sugar and low concentrations of compounds that might be expected to be deterrent. The total pattern of response to this plant shows activity from three receptors with that of the sugar receptor predominating. Plant B, on the other hand, was given a high concentration of organic acid, a possible deterrent, and a low concentration of sugar. Again three cells contribute to the total response, but the salt and rejection receptors contribute most to the pattern. Plant C depicts a situation intermediate between A and B. It might be predicted that a caterpillar would accept A, reject B, and either accept minimally, or reject C. Theoretically, both B and C could be rejected but clearly for different reasons. This illustrates the non-unitary aspect of the modality rejection. These hypothetical response patterns are not markedly dissimilar from patterns actually recorded from real leaf saps (Figs. 50 and 51).

The concept of across-fiber patterning does not negate the idea that certain acceptable compounds, as, for example, sucrose, or sinigrin, might dominate a mixture and cause the sugar receptor response in turn to dominate the sensory pattern, or that an unacceptable compound such as an alkaloid might cause the deterrent receptor to fire maximally and thus dominate the sensory pattern in a different direction. It has already been pointed out that some pure compounds can drive feeding and others terminate it (Dethier, 1937; Eger, 1937; Frings, 1945; Ishikawa, 1966; Jermy, 1961 b, 1964) and that those compounds added to leaves can render them acceptable or unacceptable (Dethier, 1937; Jermy, 1961 b). What these compounds do electrophysiologically is illustrated in Fig. 50. The addition of sucrose to the sap of carrot alters the response patterns of *P. troilus* and *P. glaucus* as shown and makes this plant very slightly acceptable. The addition of salt renders the leaf less acceptable to *P. polyxenes* (not shown). Obviously, more mixing experiments will have to be conducted before the patterns can be completely understood.

The foregoing discussion involved the assumption that there was no peripheral interaction of stimuli. Obviously this is not true. There are now many examples of synergism and inhibition at the receptor level (Ishikawa and Hirao, 1963; Ishikawa, 1966; Dethier and Kuch, 1971). The histograms in Fig. 53 could be replotted with arbitrary kinds and degrees of inhibition and synergism introduced. The outcome would depend naturally upon what modifications had been introduced. Depending on these there can be masking effects or enhancement or contrast effects. The basic character of the model is not changed.

The hypothesis of across-fiber patterning is compatible with the conclusions stated at the beginning of this discussion. Comparisons of the total sensory response of the various species of caterpillars to the saps of their own and each others plants show that there is no commonality of acceptance or rejection. It would appear that the total "flavor" of a plant, as the term flavor is applied in human experience, is the relevant parameter employed in assessing both absolute and relative acceptability and rejection. Essentially the same idea was expressed by Schoonhoven (1969): "... the ultimate total impression may vary markedly with subtile differences in the food. The decision whether or not a plant is acceptable depends on the degree to which the information received approximates the overall pattern of information which is sought for."

As pointed out earlier (Dethier and Kuch, 1971), sensory analyses give no indication of how the central nervous system interprets the input and acts upon it. The importance of the CNS is dramatically illustrated by the finding of Ishikawa, Tazima and Hirao (1963) that normal electrophysiological sensory patterns are generated by the maxillary sensilla of a mutant of *B. mori* that cannot discriminate mulberry leaves from other leaves. However, some uniformity in CNS interpretation does occur. In general sugars elicit behavioral acceptance, and it is safe to conclude that compounds that stimulate the sugar receptor are interpreted as identical or similar. But it must be remembered that any particular compound may act on the same cell as sugar in one species and on the same cell as salt in other species. This is the essence of the interspecific response differences listed in Tables 1 and 2. The occurrence of a completely identical receptor in two or more species is the exception rather than the rule (Schoonhoven, 1972a).

Finally, it must be reiterated that the foregoing ideas are predicated on the assumption that taste plays the primary role in food plant selection and that the maxillary styloconica dominate in this role. Both of these assumptions are oversimplifications. Dethier (1937) showed that taste in caterpillars was completely abolished only after the epipharynx and hypopharynx were removed. Ma (1969, 1972) has recently discovered gustatory organs on the epipharynx of *P. brassicae*. Pegs on the maxillary palpus were shown to be gustatory by Schoonhoven and Dethier (1971), and Ishikawa and Hirao (1966) demonstrated that the maxillary palpus plays a significant role in food selection.

While there has never been any doubt that taste plays a primary role in determining whether or not, and to what extent, a plant will be ingested and swallowed after it is bitten, the importance of taste in determining whether or not a plant will be sampled in the first place is not so well established. Some insects take indiscriminate exploratory bites of any available leaf, other insects bite selectively. These latter obviously can discriminate before biting. Which sensory system is employed at this juncture is not merely an academic question because its identity and response characteristics will throw some light on the identity of the plant chemicals involved. Various species of caterpillars clearly identify plants before biting them. Götz (1936) observed that larvae of *Vanessa urticae* immediately begin eating nettle even if they are standing on another kind of leaf. He concluded that odor released a feeding reaction. Dethier (1937) concluded that *Danaus plexippus* immediately recognized milkweed among other plants and that odor initiated biting. *Bombyx mori* is attracted by the odor of mulberry (Hamamura *et al.*, 1962; Hamamura, 1965; Ishikawa and Hirao, 1964, 1965). Among herbivorous Coleoptera the Colorado potato beetle employs olfaction for food plant recognition as well as for locating the plant (Chin, 1950; de Wilde, 1958; Bongers, 1970). Olfaction is also employed by Orthoptera. *Schistocerca* detects grass at a distance by its odor (Haskell, Paskin, and Moorhouse, 1962). Having arrived at the food it then palpates with the antennae (Williams, 1954; Goodhue, 1963) and then by the maxillae and labial palpi (Haskell and Schoonhoven, 1969). At this point food can be rejected without biting. It it is not rejected, an exploratory bite may be taken after which the plant may be rejected or accepted.

It is probably a general fact that leaf-feeding insects can discriminate among plants before biting them. Mouthparts and/or antennae are involved. On the one hand there is evidence that taste is the relevant sense because the maxillae and palpi employed by *Schistocerca* are gustatory (Haskell and Schoonhoven, 1969). In the case of *B. mori* Hamamura (1965) has identified the compounds that initiate biting in experimental situations as beta sitosterol, iso-quercitrin, and morin, all compounds that stimulate gustatory organs and compounds that have no appreciable vapor pressure. Since most leaf surfaces are covered with a waxy cuticle and, upon electronmicroscopic examination, appear to be unbroken surfaces, it is difficult to imagine how non-valatile compounds within the leaf could stimulate contact chemoreceptors. On the other hand, volatile compounds would have easy egress from intercellular spaces via the stomata.

There is no evidence other than observational that odors can release biting behavior; however, the observations are fairly convincing. It is reasonable to conclude that odor not only assists the insect in orienting to a plant from a short distance but also is important in bringing about initial discrimination. The fact that insects in experimental situations will ingest artificial food in the absence of specific odors cannot be construed as evidence that odor is not important under normal circumstances. Phytophagous insects will bite many things when hungry and also bite to defend themselves and to escape confinement. That odor is not unimportant in discrimination is also shown by the experiments of Hanson and Dethier (in press) in which discrimination and preference induction by *Manduca sexta* is impaired by removal of olfactory receptors.

All of the foregoing observations together with the findings of this study to the effect that no *unique* taste patterns are associated with acceptance, rejection, or preferences among plants suggest that food plant preference is not exclusively or even primarily a matter of taste and that the non-involvement of *gustatory* token stimuli does not mean that secondary plant substances operating singly or together as token stimuli may not play a vital role in host preference.

At least insofar as lepidopterous larvae are concerned accumulated evidence suggests that an old statement describing the situation comes close to representing the true state of affairs; namely that with respect to chemical senses initial discrimination is made on the basis of olfactory clues and the decision to ingest or not is made on the basis of taste (Dethier, 1937).

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Professor Dr. V. G. Dethier
Department of Biology
Princeton University
Princeton, New Jersey, U.S.A.