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INTERACTIONS OF ALKALOIDS WITH GALEAL CHEMOSENSORY CELLS OF COLORADO POTATO BEETLE

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Abstract—The galeal chemosensory system of the adult Colorado potato beetle was used as a model to study the effects of alkaloids on insect gustation. Nine alkaloids, representing a wide range of structural types, were used. Their ability to stimulate chemosensory cells when presented in isolation and their ability to interfere with normal chemosensory processes were emphasized. None of the alkaloids stimulated chemosensory cells in a dose-dependent manner, although a few stimulated low-level activity from some cells. There was no evidence for a general "deterrent receptor" in these beetles. Some of the alkaloids had a marked inhibitory effect on normal chemosensory responses. Tomatine, solanine, papaverine, and sparteine significantly inhibited responses to amino acids (represented by GABA) while quinine and papaverine inhibited responses to sucrose. An attempt was made to correlate neurophysiological action of some alkaloids with their effects on feeding behavior. It was clear from this correlation that even a dramatic inhibition of sensory input by an alkaloid does not necessarily lead to measurable effects on behavior. The results are discussed in the context of current theories on the mode of action of alkaloids and other secondary plant compounds which may be involved in host recognition by phytophagous insects.

Key Words—*Leptinotarsa decemlineata*, Coleoptera, Chrysomelidae, Colorado potato beetle, deterrent receptor, feeding deterrents, alkaloids, sugar receptor, amino acid receptor, chemoreception, steroidal alkaloids, antifeedants.

INTRODUCTION

Alkaloids represent one class of plant compounds that have come to be considered secondary because of the difficulty encountered in discovering a role for them in primary plant metabolism. The idea that secondary plant compounds

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might be important in protecting plants against natural enemies has generated a working hypothesis which suggests that insect herbivores will not feed on most plant species because of the presence of secondary compounds which inhibit feeding. One of the earliest and most comprehensive statements of this hypothesis came from Jermy (1961, 1966). More recently, several review papers have been published in which the relationships among secondary compounds, feeding deterrency, and chemoreception are discussed (Dethier, 1980, 1982; Jermy, 1983; Schoonhoven, 1982).

While it is clear from these papers that we now realize chemical messages signaling acceptance and nonacceptance are complex, the ideas of "specific deterrent receptors" (Schoonhoven, 1982); generalist receptors for deterrents, with the central nervous system responsible for decoding a complex message (Dethier, 1980); and an "inhibitory biochemical profile" for recognition of nonhost plants (Jermy, 1983) are given prominence. Implicit in each of the above hypotheses is the existence of receptors (in the pharmacological sense) evolved to interact with secondary plant compounds. These receptors may be found primarily on a cell which sends a negative message to the central nervous system (the so-called deterrent receptor) or they may be found spread variously over the membranes of a number of sensory cells requiring the central nervous system to decode the complex message. These ideas are largely based on data obtained from larvae of a number of lepidopteran species.

An additional hypothesis, which appears to better fit existing data on chrysomelid beetles, puts more emphasis on the general bioactive nature of many plant secondary compounds. Mitchell and Sutcliffe (1984) suggest that these compounds may not normally require a particular receptor type (specific or general) in order to have an effect. Instead, they may only need to be "capable of interfering with processes that are generally found in excitable membranes." These processes include receptors (in the pharmacological sense) for feeding stimulants as well as basic membrane properties associated with maintenance of a resting potential and production of a generator potential or an action potential.

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) has been important in the development of ideas concerning the role of plant secondary compounds as feeding deterrents. Considerable effort has so far failed to reveal specific feeding stimulants which could account for the clear recognition of several solanaceous species as host plants by this insect (Ritter, 1967; Hsiao, 1968). On the other hand, the steroidal glycoalkaloids of the Solanaceae are well known, and the concept of host-plant selection by avoidance of deterrents has been associated with the Colorado potato beetle for some time. Because the suggested influence of alkaloids on plant avoidance by this beetle is generally accepted, its chemoreceptors provide an excellent system on which to test the various hypotheses discussed above.

In an earlier study (Mitchell and Harrison, 1985), we attempted to determine if the galeal chemosensory system of the adult Colorado potato beetle had cells sensitive to steroidal glycoalkaloids which could be interpreted as deterrent cells. Such cells were not found in this sensory field, instead the alkaloids elicited nonspecific responses from many cells, and caused at least short-term loss of sensitivity. The effect was similar to that caused by other surfactant chemicals such as saponins, and no differences were observed among effects of tomatine, solanine, and chaconine. In this paper, the possibility of alkaloid interactions with the stimulants sucrose and α-amino butyric acid (GABA) is addressed, together with an extension of the search for specific responses to alkaloids in this chemosensory system. In addition, an attempt is made to relate observed effects of some of these compounds on chemosensilla to their influence on feeding behavior in a complex sensory environment.

METHODS AND MATERIALS

Adult insects of both sexes were used for sensillar recording. To keep variability to a minimum, recordings were always made from adults which had emerged within 24 hr of the time of the experiment. Beetles were from a laboratory colony that is continuously maintained on fresh cut leaves of *Solanum tuberosum.* Wild *L. decemlineata* are collected each summer in the Edmonton area and added to this culture. Details of the rearing technique are provided in Mitchell and Harrison (1984) and in Harrison (1985).

Only the apical chemosensitive pegs on the galea of the maxilla were considered. This chemosensory field consists of 11–15 peg-like sensilla, usually with four chemosensory cells per peg (Sen and Mitchell, 1987). One of the sensilla in this field was termed the α-sensillum by Mitchell and Harrison (1984) because its sensitivity to amino acids was much greater than that of other galeal sensilla. Because of this sensitivity difference, the study of alkaloid interaction with GABA was conducted using the α-sensillum exclusively. All galeal chemosensilla have equal sensitivity to sucrose (Mitchell and Harrison, 1984). The tip-recording method originally described by Hodgson et al. (1955) was used throughout. The galeal sensilla studied have a very low sensitivity to NaCl and KCl, with concentrations as high as 150 mM stimulating very little activity. This feature allows a wide choice of saline concentrations for the carrier solution in the stimulating–recording electrode. In this study 50 mM NaCl was used. This concentration of salt rarely stimulates any activity from galeal chemosensilla in this insect. Alkaloids were dissolved in 50 mM NaCl made up in deionized water (pH approx. 6.7). When necessary (e.g., solanine and tomatine) solvent pH was lowered to 2 in order to dissolve the alkaloid, following which the pH was raised to 5 before testing. No effect related to pH alone in the range

5–7 has been observed (unpublished observations and Mitchell and Harrison, 1985).

Cell injury is always a possibility when working with alkaloids at the concentration used in this study (1 mM). Consequently, no more than three alkaloids were tested on any particular sensillum. In addition, regular applications of 10 mM GABA or sucrose were used to confirm that at least one of the cells in the sensillum was functioning normally during the entire experiment. Deterioration in response or signal-to-noise ratio terminated experiments on a preparation. In tests of alkaloid effect on responses to GABA or to sucrose, paired stimuli (e.g., GABA followed by GABA + alkaloid) were used to keep variability to a minimum. Responses were recorded on magnetic tape using a TEAC four-channel recorder and a Vetter FM recording adapter. Segments of each response were digitized using an Apple II computer fitted with an analog to digital card, and plotted on a Hewlett-Packard digital plotter for analysis and presentation. This system is described in Mitchell and McIntyre (1986).

Adult feeding on water-infused and alkaloid-infused potato leaves was measured using an assay described in Harrison (1985). Briefly, this method uses video analysis of prefeeding behavior and aspects of first meal consumption of individual, newly emerged adult beetles of both sexes. Care was taken to ensure that leaves maintained turgor pressure and other visible characteristics of good health during infiltration and during the feeding test. Analysis of the video data produced a number of measures related to plant acceptance and feeding (Harrison, 1985). For this study the following four were chosen: (1) time (seconds) spent in prefeed maceration activity, this is the first behavior that brings the plant sap into contact with mouthpart sensilla, probably the epipharyngeal sensilla in the upper part of the buccal cavity; (2) percent of beetles which rejected the leaf after some time spent in prefeed maceration behavior; (3) area of leaf consumed during first meal (mm^2, measured with a leaf-area meter), end of a meal was defined as more than 3 mm without feeding following some period of feeding; and (4) feeding rate (area/feeding time). Ten beetles were used in each experiment.

RESULTS

Stimulation with Alkaloids Alone. All the alkaloids shown in Figure 1 were tested at 1 mM for their effects on galeal sensilla. They were each applied to several sensilla on six preparations (four for atropine) using short (1–3 sec) application times. In no cases were there responses resembling the phasic–tonic responses normally obtained from insect chemoreceptors. In some cases a more or less regular, low-level response was elicited from a single cell. This was most consistent for strychnine (six of six animals) and occurred in three of six cases with arecoline, sparteine, and quinine. Atropine, papaverine, caffeine,

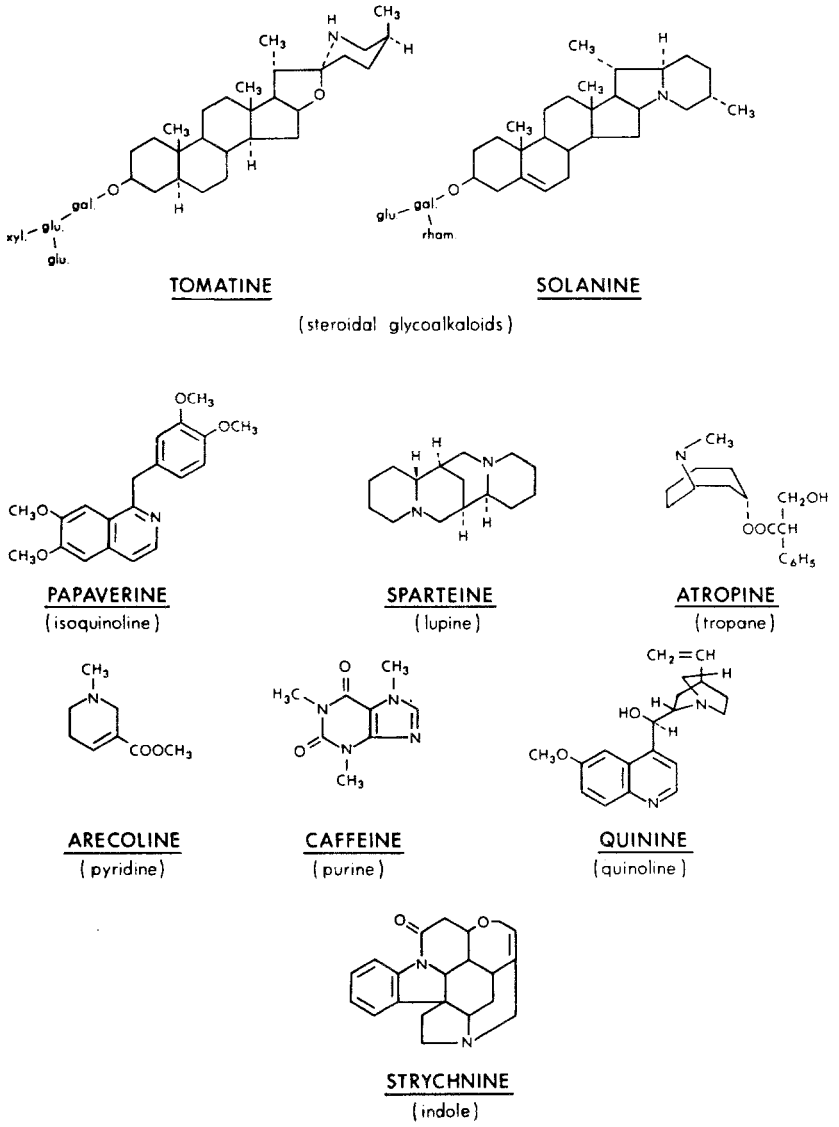

FIG. 1. Structures of the nine alkaloids used in this study.

tomatine, and solanine did not stimulate any cell in this manner. Irregular, bursting patterns of firing from one or more cells during short applications was seldom observed (four of 52 cases).

Because of the single-cell response in some preparations to 1 mM strychnine, arecoline, sparteine, and quinine, a limited dose–response study was con-

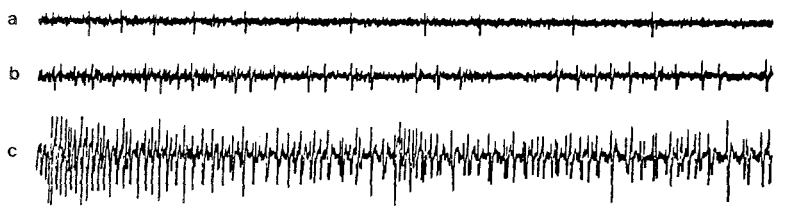

FIG. 2. (a, b) Response to sparteine sulfate (10 mM) from two sensilla on the same preparation. First second of response is shown. (c) burst of multicell activity after 4 sec of stimulation with 5 mM strychnine nitrate. Time bar = 100 msec.

ducted with these compounds. There was no increase in the low-level response over several concentrations between 1 and 10 mM for any of the compounds. Figure 2a and b shows a typical response to 10 mM sparteine sulfate from two preparations. The same four alkaloids were tested in long-term applications (approximately 30 sec). Strychnine and quinine, at 5 mM and 10 mM, elicited bursting activity after several seconds of application (Figure 2c). This activity is reminiscent of the delayed responses caused in this system by 1 mM concentrations of steroidal glycoalkaloids and saponins (Mitchell and Harrison, 1985). The high concentrations necessary to obtain this response with strychnine and quinine make it unlikely that the effect is behaviorally significant.

Inhibition of Responses to GABA and Sucrose. Table 1 documents the ac-

TABLE 1. INHIBITION OF RESPONSE TO GABA BY NINE ALKALOIDS[a]

Alkaloid	Response to GABA (10 mM)	Response to GABA (10 mM) plus alkaloid (1 mM)	Relative decrease in response	*N*
Tomatine	13.9 ± 3.9	3.8 ± 4.0	3.7[b]	6
Solanine	12.8 ± 3.2	7.3 ± 2.1	1.8[b]	4
Papaverine	15.8 ± 2.3	9.7 ± 5.1	1.6[b]	6
Sparteine	15.7 ± 3.4	11.2 ± 3.5	1.4[b]	6
Atropine	17.8 ± 5.4	12.4 ± 2.5	NS	5
Arecoline	16.3 ± 3.9	13.3 ± 1.9	NS	6
Caffeine	20.2 ± 3.1	17.8 ± 4.0	NS	6
Quinine	14.8 ± 3.9	13.5 ± 2.6	NS	6
Strychnine	15.3 ± 6.5	14.5 ± 4.5	NS	6

[a] Data represent impulses from α-sensillum occurring during 250–750 msec of 1-sec stimulations. Responses are expressed in impulses per 0.5 sec. Errors are ±SD.

[b] $P < 0.05$ Mann-Whitney U test. This survey was conducted using 18 adult *L. decemlineata.* Two to three alkaloids were tested per preparation. Multiple amino acid stimulations were distributed throughout the test period and each response to a mixture of GABA and alkaloid was compared to the preceding response to GABA alone.

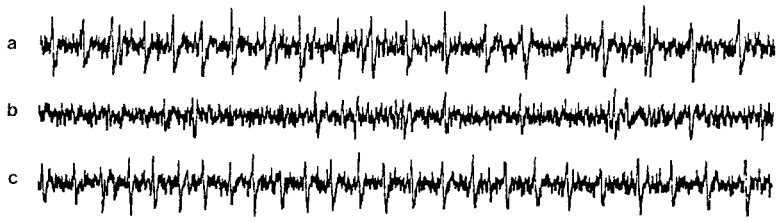

FIG. 3. Response of an α-sensillum to three sequential stimulus applications. (a, c) 10 mM GABA; (b) 10 mM GABA + 1 mM tomatine. Records show responses from 250 to 750 msec following stimulus application. Time bar = 100 msec.

tion of nine alkaloids when applied to the α-sensillum (Mitchell and Harrison, 1984) in the presence of 10 mM GABA. This sensillum contains a cell which is particularly sensitive to GABA and L-alanine, and Mitchell (1985) presents evidence that the same receptor is activated by both of these amino acids. Four of the alkaloids, when present at 1 mM, significantly reduced the response to 10 mM GABA. Tomatine was especially effective, reducing the response nearly fourfold (Table 1 and Figure 3).

The same cell in the α-sensillum responds to sucrose (Mitchell and Harrison, 1984), presumably involving a different receptor site (see Discussion). Most of the alkaloids tested at 1 mM had no significant effect on the response to sucrose, but quinine and papaverine were strong inhibitors (Table 2).

Stimulation of Additional Cells. The ability of these alkaloids to stimulate

TABLE 2. INHIBITION OF RESPONSE TO SUCROSE BY NINE ALKALOIDS[a]

Alkaloid	Response to sucrose (10 mM)	Response to sucrose (10 mM) plus alkaloid (1 mM)	Relative decrease in response	N
Quinine	11.8 ± 5.2	2.2 ± 3.5	5.4[b]	6
Papaverine	10.6 ± 4.2	3.2 ± 3.4	3.3[b]	5
Solanine	10.0 ± 4.8	5.6 ± 3.2	NS	5
Strychnine	10.4 ± 2.2	6.2 ± 7.6	NS	6
Sparteine	11.5 ± 3.2	8.3 ± 3.9	NS	4
Tomatine	11.1 ± 5.5	9.2 ± 4.4	NS	7
Caffeine	14.8 ± 7.4	12.3 ± 4.8	NS	4
Arecoline	10.2 ± 4.4	11.4 ± 6.1	NS	5
Atropine	10.0 ± 3.4	9.4 ± 3.3	NS	7

[a] Data represent impulses from α-sensillum occurring during 250–750 msec of 1-sec stimulations. Responses are expressed in impulses/0.5 sec. Errors are ±SD.
[b] $P < 0.05$ Mann-Whitney U test.

cells when presented alone may not necessarily predict their action on additional cells when one cell in the sensillum is already active. Therefore, the ability of alkaloids to stimulate additional cells when the amino acid-sensitive cell was already active was tested using mixtures of 10 mM GABA and 1 mM alkaloid. In some preparations, some alkaloids markedly stimulated additional cells when the amino acid-sensitive cell was active. This type of response was quite variable, but it occurred often enough and was of sufficient intensity when it occurred to warrant quantification. The data are presented in two ways: (1) average activity in non-amino acid-sensitive cell(s) during stimulation with GABA and GABA plus alkaloid are compared (Table 3); and (2) responses from preparations which showed a marked effect of alkaloid on non-amino acid-sensitive cell(s) under these conditions are presented alone (Table 4).

A marked effect was defined as a firing rate >20 impulses/sec from the non-amino acid-sensitive cell(s). During stimulation with GABA alone, spikes from cells other than the amino acid-sensitive cell were sometimes seen. These usually occurred at low frequencies ranging from one to five impulses in the 500-msec sample period (Table 3). Paired applications of 10 mM GABA and 10 mM GABA + 1 mM alkaloid on the same sensillum were used to keep variability to a minimum. Several alkaloids, notably atropine, did stimulate considerable activity in a second cell under these experimental conditions. Ref-

TABLE 3. AVERAGE RESPONSE FROM NON-AMINO ACID-SENSITIVE CELL(S) WHEN STIMULATED WITH 10 mM GABA (COLUMN 1) AND MIXTURE OF 10 mM GABA AND 1 mM ALKALOID (COLUMN 2)[a]

Response of additional cell(s) during stimulation with GABA	Response of additional cell(s) during stimulation with GABA + alkaloid[b]	Alkaloid used	Relative increase	*N*
0.9 ± 1.1	6.5 ± 6.6	Atropine	7.2	7
1.5 ± 1.7	6.8 ± 4.3	Arecoline	4.5	4
1.5 ± 0.8	6.2 ± 2.7	Quinine	4.1	6
2.7 ± 1.4	8.2 ± 3.7	Strychnine	3.0	6
2.2 ± 2.6	4.3 ± 4.1	Sparteine	2.0	9
2.8 ± 2.1	3.3 ± 1.0	Solanine	1.2	4
5.3 ± 3.5	3.5 ± 1.9	Papaverine	0	6
1.2 ± 1.0	1.2 ± 1.2	Tomatine	0	6
2.0 ± 0	1.5 ± 2.1	Caffeine	0	2

[a] Note increase in average response from these cells with some of the test mixtures. Errors are ±SD.

[b] Impulses counted between 250 and 750 msec of response and expressed as impulses per 0.5 sec.

TABLE 4. DATA FROM TABLE 3 TO EMPHASIZE RESPONSES FROM NON-AMINO ACID-SENSITIVE CELLS IN EIGHT PREPARATIONS PARTICULARLY IN COMBINATION WITH 10 mM GABA.[a]

Alkaloids	Number/total *N*	Response of additional cell(s)[b]
Atropine	3/7	13.3 ± 1.5
Strychnine	2/6	12.5 ± 2.1
Sparteine	1/9	14
Arecoline	1/4	11
Quinine	1/6	10

[a] A sensitive preparation is defined as one where the non-amino acid-sensitive cell(s) fired at a rate greater than 20 impulses/sec. during stimulation with the GABA–alkaloid mixture.
[b] Impulses counted between 250 and 750 msec of response and expressed as impulses per 0.5 sec.

erence to Table 4, however, shows that most of this additional activity, with atropine present, was produced in the α-sensilla of three of seven preparations. In these three animals, the response of the second cell averaged 26 impulses/sec. Figure 4 shows an example of this type of response. Two of the six preparations also had this kind of sensitivity to strychnine.

Behavioral Response to Alkaloid-Treated Food. Adult beetles, offered healthy leaves infiltrated with one of five different alkaloids, showed a variety of responses. The video bioassay used measured a number of parameters (Harrison and Mitchell, 1988), four of which are given in Table 5. Only atropine and papaverine had significant effects, with atropine being the most potent. Forty percent of adults refused the atropine-treated leaves after a significantly prolonged prefeed maceration time. The 60% which fed did not differ from controls in amount consumed or in feeding rate. Papaverine caused only a re-

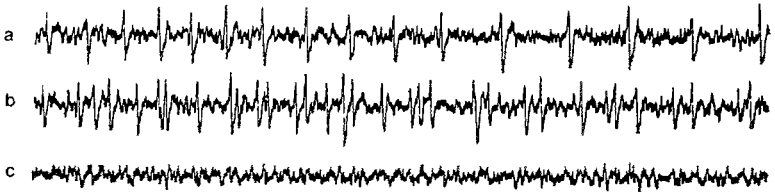

FIG. 4. Response of an α-sensillum to three sequential stimulus applications. (a) 10 mM GABA; (b) 10 mM GABA + 1 mM atropine sulfate; (c) 1 mM atropine sulfate. Note activity of a second cell during stimulation with GABA + atropine. Records and time as in Figure 3.

TABLE 5. FEEDING PARAMETERS MEASURED FOR ADULT BEETLES OFFERED ALKALOID-TREATED POTATO LEAVES, EXPRESSED RELATIVE TO BEETLES OFFERED WATER-TREATED CONTROL LEAVES[a]

Alkaloid (2 mM)	Relative prefeed maceration time	Rejection (%)	Relative amount consumed	Relative feeding rate
Water	1.00	0	1.00	1.00
Solanine	0.88	0	1.19	0.97
Tomatine	1.28	0	1.00	0.94
Atropine	2.62[b]	40[b]	1.00	0.63
Quinine	2.20	0	1.16	0.96
Papaverine	1.64	10	0.52[b]	0.81

[a] Data on solanine, tomatine, and atropine adapted from Harrison and Mitchell (1987) ($N = 10$).
[b] Significant at 5% level or less.

duction in amount consumed; other parameters remained indistinguishable from control beetles.

DISCUSSION

Deterrent Receptors. This study and a previous one on steroidal alkaloids and saponins (Mitchell and Harrison, 1984) provide no evidence for a receptor cell, which is sensitive to a wide range of potentially distasteful secondary plant compounds, in the galeal chemosensory field of the Colorado potato beetle. The idea of a deterrent-sensitive cell comes from work on several caterpillar species (Schoonhoven, 1982), and the best evidence for such a cell comes from *Bombyx mori* (Ishikawa, 1966) and *Pieris brassicae* (Ma, 1972; Blom, 1978). A variety of compounds stimulates these cells at concentrations in the micromolar range, and there is some evidence for a positive dose–response relationship. These two features strongly support the idea of high sensitivity to a number of structurally different secondary compounds in at least some lepidopterous species, but detailed studies are lacking on all but two species. Dethier (1980) questions the idea of a generalized deterrent receptor in lepidopterous larvae, stressing instead the fact that secondary compounds stimulate several cells in 59% of the cases he has studied.

The actions of repellents on mosquito antennal sensilla provide an interesting parallel to the situation in phytophagous insects. Davis (1985) reviewed the mosquito work and presented a list of possible actions of repellents which is remarkably similar to the one proposed by Schoonhoven (1982) for plant feeders. With the evidence to date in both systems, it is not possible to identify

any single mechanism that explains the effects of repellents or feeding deterrents. Given the vast array of chemical structures represented by these compounds, and the large number of potential molecular sites of action in a chemoreceptive system, each situation will require detailed study.

Comparative Aspects of Alkaloid Action. When the effects of a number of compounds on the same system are compared, some preliminary conclusions regarding mechanisms of action can be drawn. The evidence to date strongly suggests that sucrose, GABA, and L-alanine stimulate the same cell in the α-sensillum of the Colorado potato beetle (Mitchell and Harrison, 1984). Because of the difference in molecular structure of the amino acids and sucrose, and because of the high specificity of the amino acid response (Mitchell, 1985), there are probably at least two receptor sites on the same cell, one for the amino acids and one for sucrose.

The actions of the nine alkaloids given in Tables 1 and 2 can be interpreted against this background. Interestingly, except for papaverine, the compounds which significantly inhibit the response to GABA do not affect the response to sucrose. This suggests that tomatine, solanine, and sparteine have their effect on some site related to the amino acid receptor which is separate from the sucrose-receptor site. This observation also supports the hypothesis that the amino acid and sucrose receptors are separate entities. The fact that papavarine inhibits both responses does not exclude the possibility that it interacts with both receptor sites, but it is also possible that this alkaloid acts at sites other than the receptor site causing the entire cell or even all cells in the sensillum to be less sensitive. It is possible that the mode of action of papaverine, at the molecular level, is quite different from that of tomatine, solanine and sparteine. The data do not provide any information on the possible differences between the actions of the latter three compounds. It should be noted that the effect of tomatine and solanine described here is distinctly different from the long-term effects of these compounds which involve all cells in the sensillum (Mitchell and Harrison, 1985).

There are very few data on other phytophagous insect species with which to compare these results. Dethier (1982) emphasized the importance of peripheral integration in the context of host-plant recognition. He cited unpublished data from work on several lepidoptereous larvae which showed that tannic acid, quinine, piperidine, and caffeine inhibit electrophysiological responses to sugars. Apparently there is some variation in effects of these compounds across lepidopterous species. Frazier (personal communication) finds that caffeine excites a candidate "deterrent" cell in *Manduca sexta* confirming a similar result reported by Schoonhoven (1972). Caffeine was ineffective in all experiments reported here. Such differences in activity across orders may reflect differences in receptor mechanisms, and it should be possible to gain additional insight into the role of these compounds and the mechanisms underlying their action by

using a comparative approach. Interestingly, quinine has so far proven to be an effective inhibitor of sucrose stimulation in Diptera (Morita, 1959), Lepidoptera (Dethier, 1982), and Coleoptera (Mitchell and Sutcliffe, 1984, and present study). The fact that quinine inhibits the response to sucrose in the Colorado potato beetle, while leaving the response of the same cell to GABA unaffected, suggests that this alkaloid acts at a site specifically involved with sugar reception.

Correlation of Sensory Physiology and Behavior. The adult bioassay was limited to five alkaloids, because the results suggest that little is to be gained by looking at the remaining alkaloids which were studied electrophysiologically. It is assumed that the alkaloids introduced into the potato leaf remained intact for the duration of the test and that they were accessible to the beetle's chemosensory system. Only papaverine and atropine caused significant reduction of any of the feeding parameters measured (Table 5). Papaverine strongly inhibited responses to GABA and to sucrose, suggesting these effects may be causally related to its effect on feeding. It would be interesting to test papaverine more thoroughly. Solanine, tomatine, and quinine, although clearly effective at the cellular level, did not significantly disrupt consumption when presented in the whole-leaf context.

The lack of clear correlations between physiological and behavioral results in these, admittedly limited, data, is not altogether surprising. First, only the galeal sensilla are represented in the physiological study. Epipharyngeal sensilla are present in adult beetles (unpublished data) and probably in larvae as well. These sensilla may, in fact, contact leaf sap before the galeal sensilla, and their input is probably important in regulating feeding behavior as it is in lepidopterous larvae (de Boer et al., 1977). Unfortunately these sensilla are technically difficult to record from, making their inclusion in a general survey such as this a daunting task. Second, we still know very little about the nature of sensory codes in sensilla which mediate host-plant recognition. In a pioneering study, Dethier and Crnjar (1982) suggested a number of possible types of codes whereby lepidopterous larvae may recognize different hosts and nonhost plants. Their data did not allow firm conclusions, but they did indicate that detailed analyses of complex interactions at the chemosensory level will be required to make progress in this area. The results presented here lead to the same conclusion.

An interesting study by Derby et al. (1984) on *Homarus americanus* illustrates the generality and the complexity of the action of secondary compounds on sensory systems and their influence on behavior. They demonstrated that a number of chemosensilla on antennules and walking legs were sensitive to several of 14 secondary plant compounds tested. They also had difficulty in correlating the sensory effect with behavioral results. For example, ferulic acid stimulated a large response from leg and antennular sensilla but had no effect

on behavior, while tannic acid reduced food intake while only stimulating antennular sensilla.

It seems clear that future progress in this area will require in-depth study of a few well-chosen model systems. Prerequisites will be a good understanding of the basic responses of the chemosensory system in each preparation, an easily interpretable behavioral bioassay, and a thorough study of interactions of a few ecologically relevant secondary compounds with the sensory system in question. Success in correlating sensory and behavioral data will likely be enhanced if comparisons are made on an individual plant (defined substrate) and an individual insect basis.

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