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Chapter

Deterrents and Their Effects on the Feeding Behavior and Sensory Physiology of Insects

Vonnie D.C. Shields

Abstract

The gustatory system of insects is a prominent model in neuroscience. This important sensory system allows insects to detect, encode, and process gustatory information. This important sensory modality allows insects to perceive their environment. All animals detect and react to chemicals in their environment. Using insects as model systems allows us to obtain fundamental information regarding the processing of sensory information in the brain of the animal. Stimuli, associated with taste and smell, are responsible in insects being able to locate and select food sources, mates, and egg-laying sites. One line of research can be directed to better understanding gustatory cues in the selection of food sources by insects. Experimentally, this will involve feeding behavioral and electrophysiological testing in insects. Examining the structural organization of the gustatory organs using transmission electron and scanning electron microscopy will shed more light on the detailed structure of these taste sensory organs, the sensilla. During feeding, these taste organs sample the plant sap that contains a multitude of phytochemicals. Gustatory sensory input is encoded as patterns of nerve impulses by gustatory receptor cells which are housed in these taste sensory organs. Taste information gathered by these receptor cells will allow the insect to determine if the food is palatable or should be rejected.

Keywords: gustation, taste, glucosinolates, deterrent, feeding behavior, insect

1. Introduction

Our ability to taste is crucial for our survival and is central in our nutrition. The sense of taste determines the palatability of food and beverages. It provides early warning alerts for the detection of spoilage. Taste disorders affect the quality of life, daily living, psychological well-being and can change body weight or appetite. Having an appreciation of basic gustatory mechanisms in animals, including humans, allows us to have a better understanding and promises to contribute toward an explanation of taste disorders.

Using caterpillars as insect models allows us to increase our understanding of taste recognition and coding and to unravel some of the principles that govern food selection behavior. One feature that makes these larvae ideal candidates for such studies is their recognizable gustatory behaviors. In addition, they have relatively

simple gustatory systems with relatively low numbers of sensory cells located in sensory organs (sensilla) on their mouthparts that mediate taste mechanisms. These cells are individually identifiable, show strong electrophysiological responses, and are relatively easy to access for experimental manipulation. All these features make the larval gustatory system amenable to structural, behavioral, and electrophysiological approaches, respectively.

2. Ultrastructure of main taste sensory organs: styloconic sensilla

Caterpillars bear a pair of uniporous styloconic sensory organs or sensilla (i.e., lateral and medial styloconic sensilla) on the maxillae, and more specifically, maxillary galeae. These are the main organs involved in feeding and detect plant phytochemicals by being in constant contact with plant sap during feeding. Each sensillum appears as a small cone inserted into a fibrous cuticular socket of a cylindrical projection or style of insensitive cuticle. The cone bears a terminal pore (**Figure 1**) [1]. In each styloconic sensillum, four bipolar taste neurons extend toward the tip of the cone. Receptors bound to these neurons interact with plant sap as the caterpillar is feeding. These receptors respond to salt, one or more sugars, and bitter compounds [2, 3]. One bipolar neuron, a putative mechanosensory neuron, terminates near the base of the cone and lies near the dendritic sheath [4, 5]. Here, many microtubules lie parallel to one another within a dense matrix. This location is thought to be the site of sensory transduction of mechanical stimuli [6]. Each styloconic sensillum bears a single apical or terminal pore. Gustatory sensory input gathered from the receptor cells within the sensory organs is encoded as patterns of nerve impulses which ultimately determine if relevant information is accepted or rejected in the brain of the animal (**Figure 2**).

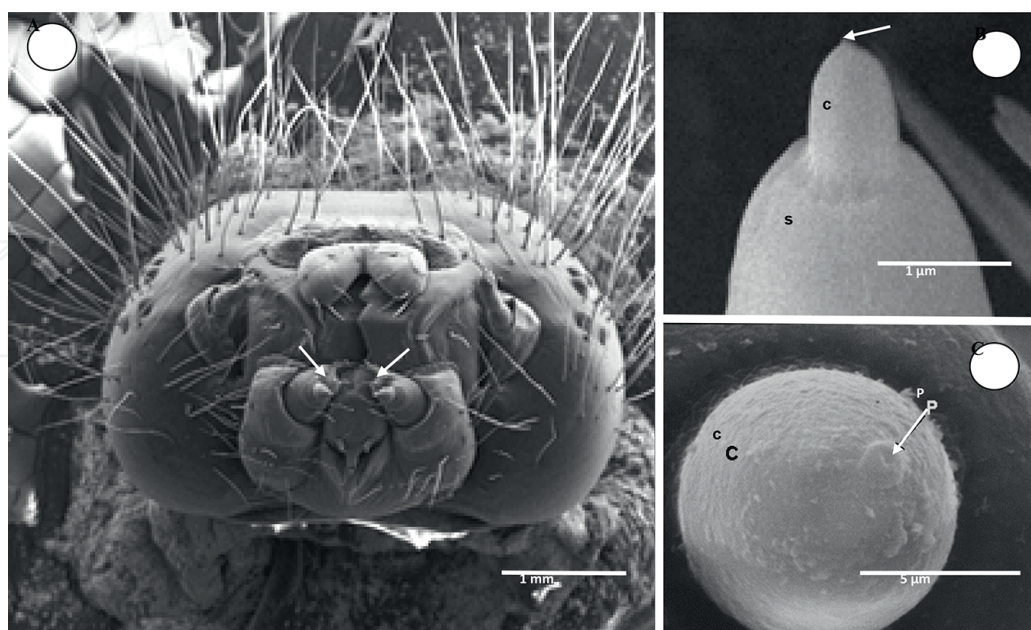


Figure 1. A–C, Scanning electron micrographs of *Lymantria dispar* (L.) fifth instar larvae. The specimens were critical point dried. (A) Frontal view, whole head. The arrows denote the galeae, components of the maxillae. Bar = 1 mm. (B) Side view of a medial styloconic sensillum. The cone is inserted into the style or cylinder. The arrow shows the location of the pore at the tip of the cone. Bar = 1 μm. (C) Higher magnification view of the cone (c) from a lateral styloconic sensillum showing the pore (p with arrow) at the tip of the cone. Bar = 5 μm. This figure was adapted from [1].

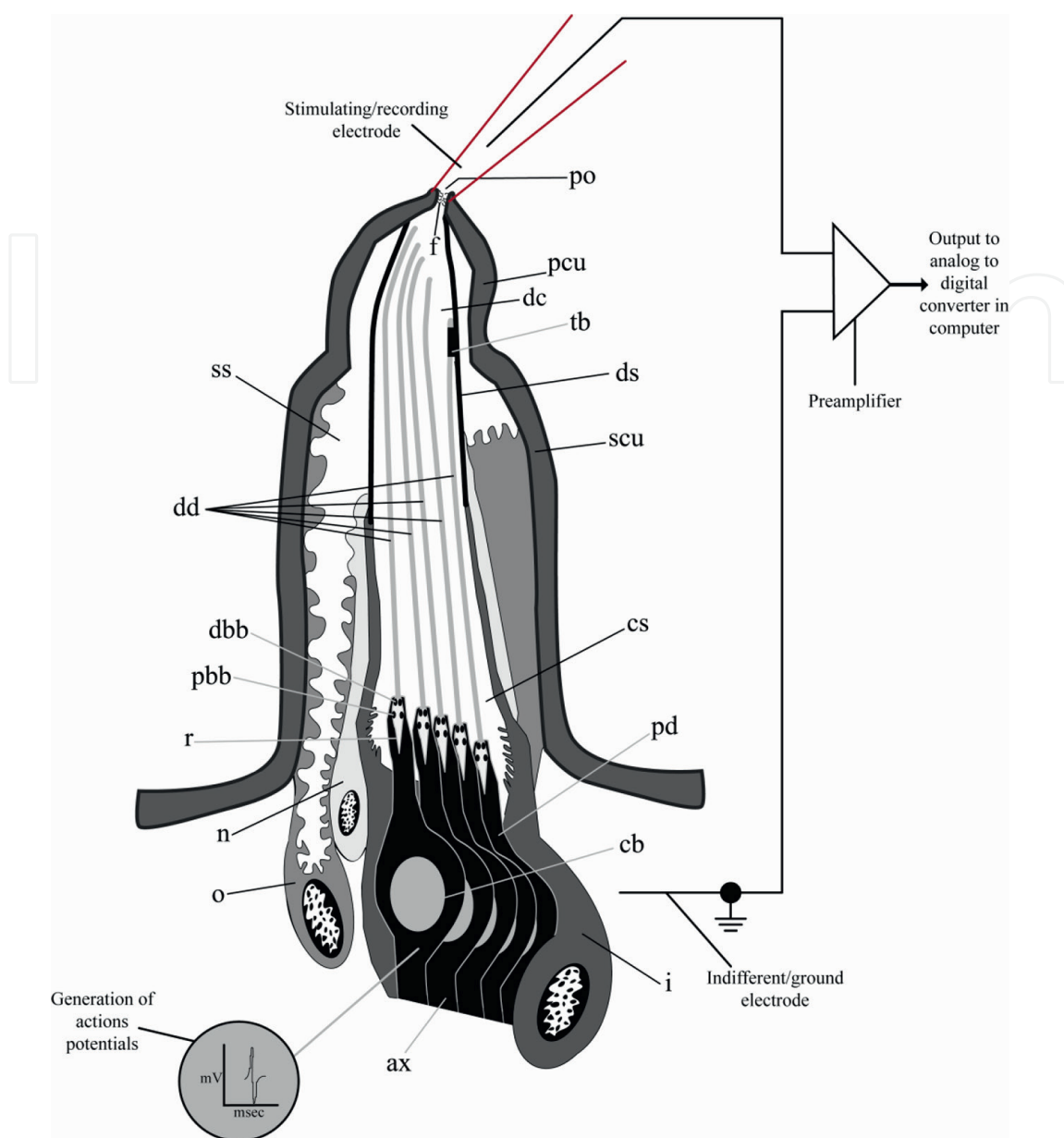


Figure 2. Diagrammatic reconstruction of a uniporous styloconic sensillum shown in longitudinal section with five bipolar neurons innervating this sensillum: four gustatory and one mechanosensory. This illustration also shows the electrophysiological tip recording method. This method is useful for recording the neurophysiological responses from taste cells in a styloconic sensillum [7]. A taste stimulus is dissolved in an electrolyte solution (e.g., 0.1 M KCl dissolved in deionized water) contained within the stimulating or recording electrode. This electrode is placed over the tip of the pore of the sensillum. The solution diffuses through the pore. Taste compounds bind to dendritic taste receptors which transduce the quality and quantity of the stimulus into a neural code of action potentials. The indifferent or ground electrode contains a similar electrolyte solution except for the taste stimulus. Each electrode contains a silver wire. The solution and wire allow contact to be made with the internal environment of the insect (e.g., body). The excitatory responses recorded are amplified, digitized, and analyzed using a computer software program. ax, axon; cb, cell body; cs, ciliary sinus; dbb, distal basal body of proximal dendritic segment; dc, dendritic channel; dd, distal dendritic segment; ds, dendritic sheath; f, fibrils; i, inner sheath cell; n, intermediate sheath cell; o, outer sheath cell; pd, peg cuticle; pbb, proximal basal body of proximal dendritic segment; po, terminal pore; r, rootlets; scu, style cuticle; ss, sensillar sinus; tb, tubular body. This figure was adapted from [1].

3. Sensory responses to deterrents

At least one sensory cell is particularly sensitive to substances that cause a deterrent response in some larval Lepidoptera known as the deterrent neuron [8].

Neurophysiological responses from one or more taste cells within the sensillum can be recorded using an electrophysiological tip recording method [7].

Deterrent receptors in caterpillars were thought to have evolved as a proliferation of receptor types. They have an extensive action spectrum sensitive to a large variety of secondary plant compounds, ultimately resulting in appropriate behavioral outcomes that are associated with specific sensory inputs [8]. In 1992, Schoonhoven et al., hypothesized that the deterrent receptor evolved from ancestral nerve cells that retained their sensitivity to noxious plant compounds [9]. It was thought that other chemoreceptor cell types, such as sugar-sensitive cells, developed a relative insensitivity to noxious chemicals. Deterrent cells were thought to respond to compounds not previously experienced in their recent evolution [10]. If the insect transitioned to a new host-plant, a loss of sensitivity by a deterrent receptor could occur [10]. If the ingested deterrent compound, or its metabolic products, are taken up in the blood, they could potentially travel to the chemosensory cells causing a desensitization of response [11]. Over the course of evolution, the deterrent cell in the crucifer specialist, *Pieris brassicae*, became insensitive to sinigrin, probably because of this insect's very close host-plant association with the Cruciferae [12–14]. Another cell in *P. brassicae* is sensitive to glucosinolates, presumably mediates host-recognition, and likely signals acceptance rather than rejection [13].

4. Insect-plant interactions: sensory basis of feeding

The sense of taste plays a key role in the behavior of insects. Insects often rely on gustatory cues from plants to detect and find their food sources. These cues are typically nonvolatile chemicals that are either liquids or solids and can be simple or complex. They can be detected via contact chemoreceptors located on various body parts [15, 16]. Other compounds may be partially volatile [16, 17]. Examples of such compounds include DEET (N,N-diethyl-m-toluamide) [18, 19], ammonia, water, polyamines, and certain acids, pheromones, and fatty acids. Insects, in general, are selective to some extent with respect to the selection of their food choices. Monophagous insects feed on one or a few closely related plant species, whereas oligophagous insects feed on a larger number of hosts, usually confined within a certain plant family. Polyphagous insects consume many plants representing a wide taxonomic range. Insects never feed on all plant groups [20], however.

Tastants have often been grouped into taste qualities: sweet, sour, bitter, and salty [21]. Umami (savory) was added later [22]. While insects can respond to these five canonical taste qualities, taste quality perception in insects may be different than in humans. Sweet, often associated with sugars [23, 24] and sugar alcohols [23, 25–28] are attractive to Lepidoptera, as well as other insects, as are some artificial sweeteners (e.g., acesulfame K) [29]. Bitter, i.e., deterrent tastants, are represented by compounds such as caffeine, denatonium, and quinine. They may be toxic [30–33] and have diverse chemical structures [34]. Sour tastants are associated with certain acids, including acetic acid, citric acid, hydrochloric acid, and lactic acid [35–38]. Salty tastants are associated with sodium and other mineral ions, such as NaCl and KCl [39–41]. Lastly, umami tastants are associated with some amino acids [24, 42–45].

Two theories exist to explain how chemical constituents of plants provide stimuli that determine food-plant preferences. Brues first suggested that insects' "botanical

instinct” was based on responses to chemical and physical stimuli originating from plants [46]. Later, Dethier [47] and Fraenkel [48] stated that nutritionally unimportant “token stimuli” or attractants and repellents were primarily responsible for regulating the feeding preferences of phytophagous insects.

Many plant feeders are very specific in their food habits. They are usually restricted to a single order, family, genus, species, or even subspecies of plants. This specificity can be supported by one of two different factors, or possibly their combination: (i) insects will tend to specialize on plants that meet their dietary needs (i.e., protein, carbohydrates, fat, minerals, sterols, and vitamins) and (ii) if dietary composition is very similar for all insects, the guiding factor will be the presence or absence of additional compounds (i.e., “secondary” plant substances); the presence of nutrients would be less important. The “dual discrimination” theory proposes that insects respond to secondary compounds (token stimuli for recognition of host-plant species), as well as nutrients (for recognition of plants of the exact physiological condition nutrient content [49]). The primary “sapid” nutrients in plants act as important taste indicators of a suitable food, in addition to the recognition of secondary plant substances [50]. Host-plant selection by specialist feeders is thought to be largely influenced by the presence of token stimuli, whereas for generalist species, the presence of deterrents plays a major role [51].

Host-plant recognition and utilization, as well as avoidance or rejection of non-host plants, are generally inherited and cannot be changed by experience [52]. The primary role of secondary plant substances in insect-host-plant relationships is that they form the “fingerprint” (specific signal pattern) or biochemical profile, by which the insect identifies the plant [53]. If the plant biochemistry, as perceived by the insect, fits the expected innate image of “host-plant” to the insect, the plant will be consumed or selected as a location for egg-laying [54].

For an insect to feed, it must (a) recognize and orient to the plant; (b) begin feeding (biting or piercing); (c) maintain feeding, and (d) stop feeding, prior to dispersal. Terms applied to define classes of stimuli should encompass both physical and chemical stimuli. An “attractant” is a stimulus to which the insect responds by moving toward the food source. “Arrestants” cause the insect to stop moving toward the food source. Initiation and maintenance of feeding are separable phenomena. “Feeding incitant” is a stimulus initiating biting or piercing of the plant tissue. Once biting has started, maintenance of feeding is dependent on the presence or absence of feeding stimulants or deterrents [55]. Food selection behavior can be compared to a “key-lock” system, where the key represents a complex sensory pattern [56]. A precise behavioral response will be triggered if the pattern sufficiently corresponds with an innate standard. When the incoming sensory information differs too much from the desired pattern, the food is rejected. Host selection comprises of a series of steps (i.e., keys). Each step unlocks only one behavioral step. The lack of detail in one key will be compensated for by details in another sensory pattern (**Figure 3**) [57, 58].

The gustatory and olfactory systems of lepidopterous larvae distinguish the presence of various chemicals. Sensilla associated with these senses are located and distributed on their antennae, mouthparts, and legs. The styloconic sensilla, located on the mouthparts, are in continuous contact with plant sap during feeding. Four types of gustatory receptors have been classified into four cell types: those sensitive to nutrients, salts, phagostimulating alleochemicals, and deterrents (**Figures 4 and 5**) [59, 60].

The sensitivity of chemoreceptors also vary with age, time of day, feeding history, effect of food deprivation, adaptation rate, individual insect, and temperature

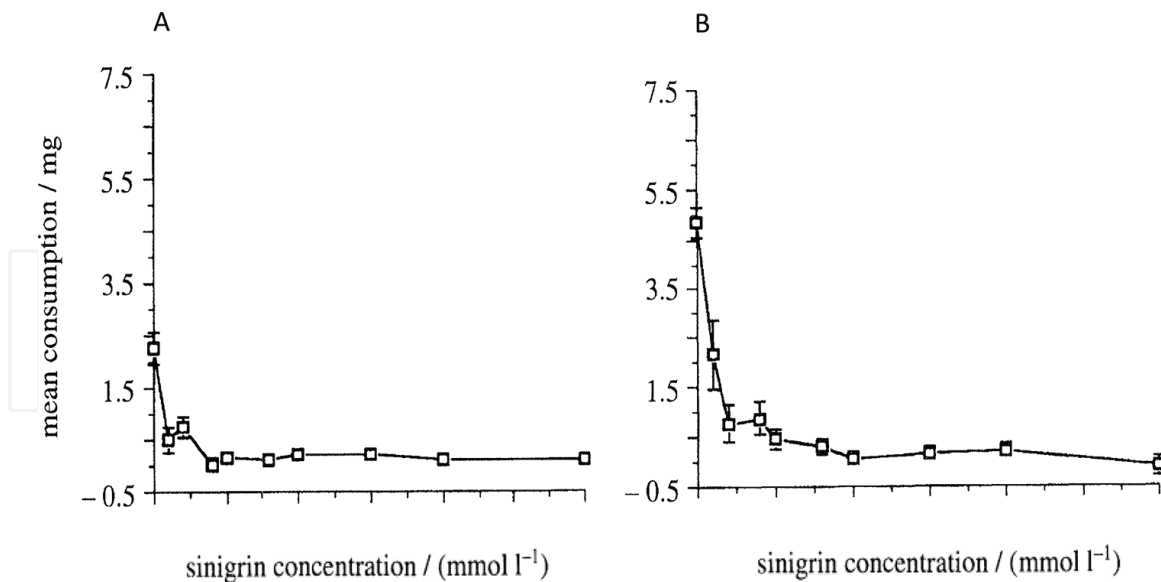


Figure 3.

A. Mean consumption by fifth instar *Mamestra configurata* exposed to a diet containing increasing concentrations of sinigrin. B. Mean consumption by fifth instar *Trichoplusia ni* exposed to a diet containing increasing concentrations of sinigrin. This figure was adapted from [58].

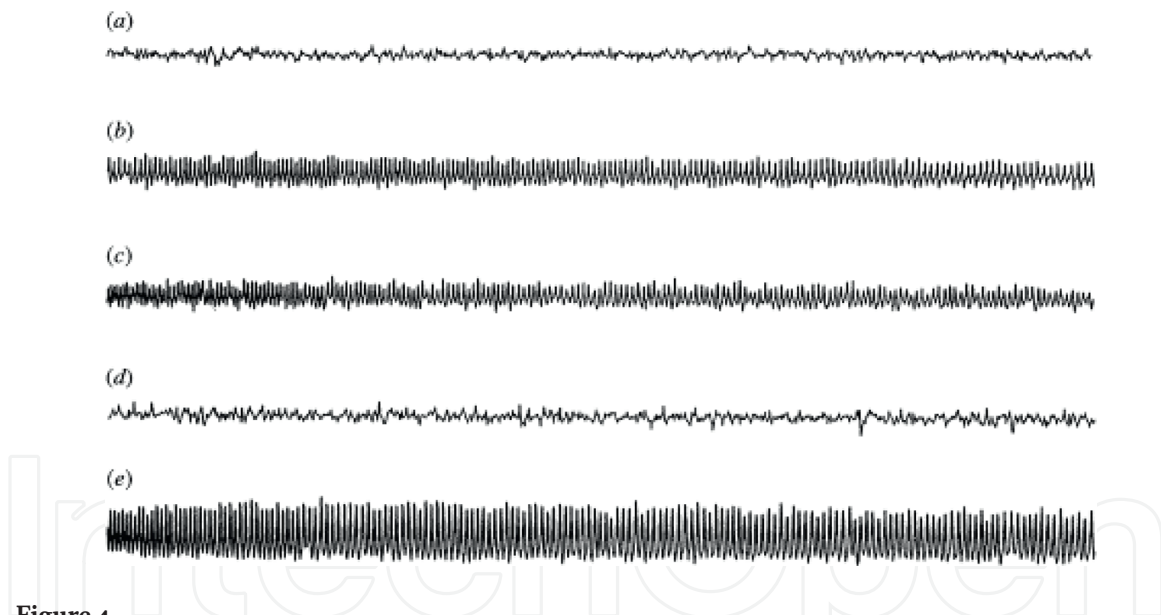


Figure 4.

Representative electrophysiological responses from the lateral and medial styloconic sensilla of fifth instar *Mamestra configurata* in response to: (a) 50 mM potassium chloride; (b) 2 mM sinigrin (glucosinolate); and from (c) 60 mM sucrose from lateral sensilla; (d) 50 mM potassium chloride, and (e) inositol from medial sensilla. Potassium chloride (50 mM) served as the electrolyte. Note the strong firing response to inositol in (e), whereas potassium chloride evoked a very minimal response (a). This figure was adapted from [60].

[57, 59]. Städler and Hanson demonstrated in *Manduca sexta* larvae, that three of the four chemoreceptive cells, only in lateral styloconic sensilla, possessed a short-range (0–0.5 mm) olfactory capability to perceive vapors [61]. This would allow the receptors to monitor food without being in actual physical contact with it. The three mechanosensory galeal trichoid sensilla may provide information about the proximity of the food source, permitting the lateral sensillum to gauge the concentration of plant vapors accurately [61].

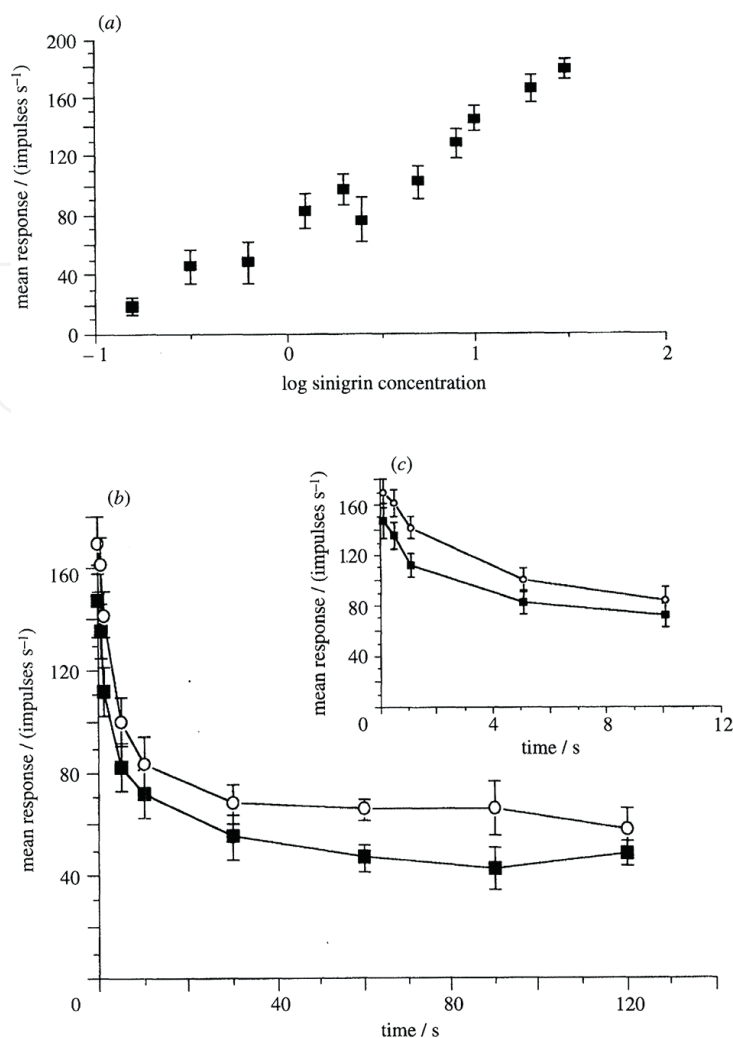


Figure 5. (a) Dose-response curve showing the sinigrin-sensitive cell in the lateral styloconic sensillum of *Mamestra configurata* when stimulated with various concentrations (mM) of sinigrin. Each point represents 10-23 larvae (cells). Error bars represent standard error of the means. (b) Adaptation curves for the sinigrin-sensitive cell in the lateral styloconic sensillum of *M. configurata* during stimulation with 8 mM (filled squares) and 20 mM (open circles) sinigrin. Each point represents means for 4-6 larvae (cells). Error bars represent standard error of the means. (c) The inset shows the first 10.1 secs. of the adaptation response for both cells. This figure was adapted from [60].

5. Secondary plant compounds and the role of sinigrin as a feeding stimulant or deterrent

There are four major classes of secondary plant compounds: nitrogen-containing (alkaloids, amines, amino acids, cyanogenic glycosides, and glucosinolates), terpenoids (monoterpenes, sesquiterpenes, diterpenes, saponins, limonoids, cucurbitacins, cardenolides, carotenoids), phenolics (simple phenols, flavonoids including tannins, quinones), and polyacetates (polyacetylenes). These are distributed widely in vascular plants, including Solanaceae, Scrophulariaceae, Cucurbitaceae, Gymnospermae, etc. Secondary plant compounds are found in concentrations varying from, e.g., 0.0002-→40% concentration dry weight [62].

Secondary plant compounds serve as positive compound signals when an insect species becomes adapted to particular plants and uses these cues to recognize their

hosts. Glucosinolates, found in the family Brassicaceae, the mustard family of flowering plants (order Brassicales), composed of 338 genera and 3700 species, appear to be limited to families of dicotyledonous angiosperms occurring in the order Capparales including the families Cruciferae, Capparaceae, Tovariaceae, Resedaceae, and Moringaceae [62]. They are present in every part of the oilseed rape plant [63] and are unlikely to serve a role in the basic metabolism of plants. Food specificity of insects is thought to be based solely on the presence or absence of these compounds [51]. Glucosinolates, or mustard oil glucosides, are derived from amino acids and contain sulfur, as well as nitrogen atoms. They can either be acyclic (e.g., sinigrin) or aromatic (e.g., sinalbin) [62].

Sinigrin (allyl- or 2-propenyl glucosinolate) is a principal crucifer token stimulus and is a widespread glucosinolate in many species of Cruciferae, as well as in other plant families. Glucosinolates are broken down by a glucosinolate-degrading enzyme (myrosinase) when plant tissues are eaten or damaged, thereby releasing toxic hydrolysis products. These products may include isothiocyanates, nitriles, thiocyanates, and oxazolidinethiones [63, 64]. Myrosinase is present in idioblasts (specialized cells in parenchymatous tissue of the green parts of crucifer plants, whereas glucosinolates are stored in vacuoles of leaf cells [64].

The role of mustard oil glucosides acting as feeding attractants, incitants, and stimulants have been studied extensively. Insects, not adapted to a particular plant species, may be repelled or deterred by the plant. For noncruciferous feeding insects, glucosinolates have been implicated as feeding deterrents. Verschaffelt demonstrated the role of a mustard oil glucoside in food-plant selection in two lepidopterous species, namely *Pieris brassicae* and *Pieris rapae* [12]. Experiments showed that these insects could be stimulated to feed on normally rejected plants by treating the plant tissue with juices extracted from crucifers. When solutions of pure sinigrin were applied to unacceptable plants, they rendered them palatable. This was further exhibited with the diamond-back moth (*Plutella maculipennis*) when a solution of either sinigrin or sinalbin (p-hydroxybenzyl glucosinolate) was applied to the leaves of nonhost plants stimulating feeding [65]. Feeding did not occur, however, when leaves were treated with the mustard oil, allyl isothiocyanate, a product of enzymatic degradation from sinigrin. The stimulatory effect of sinigrin and sinalbin was demonstrated in larval *Pieris maculipennis* feeding on a synthetic diet [66], as was the case when the addition of sinigrin strongly promoted feeding in the mustard beetle, *Phaedon cochleariae* on a synthetic diet. [67]. A similar result was observed by other researchers with synthetic diet for larval *P. brassicae* [68–71]. Isothiocyanates, such as allyl isothiocyanate, are effective in attracting larvae of the European cabbage butterfly, *P. rapae* [72, 73].

Glucosinolates were found to be both deterrent and toxic to the noncrucifer-feeding lepidopterous caterpillar, *Papilio polyxenes*, which normally feeds on Umbelliferae [74]. Breakdown products may be responsible for the potency of sinigrin, as well as other glucosinolates as feeding deterrents [75]. Allyl isothiocyanate is known to be a powerful tissue irritant [64] and may be responsible for sinigrin toxicity to some species due to its release in the gut. Sinigrin may represent an innocuous form of storage in the plant, possibly as a means of avoiding autotoxicity [76]. Recently, some crucifer feeders have been shown to be deterred by some glucosinolates. Work on *Mamestra configurata* and the flea beetle, *Phyllotreta cruciferae* [77] (using the glucosinolate, sinalbin) and *Mamestra brassicae* [78], *M. configurata*, and *Trichoplusia ni* (using sinigrin [58]), clearly demonstrated deterrence in these crucifer-feeding insects.

6. Conclusions

Insects constantly monitor and respond to changes in their internal and external environments to maintain themselves under the most favorable conditions for survival. In the case of lepidopterous larvae, gustatory sensilla (i.e., lateral and medial styloconic sensilla) located on each maxilla can detect phytochemicals present in plants. They act as the first level of environmental perception and play important roles in host–plant selection, as they are in constant contact with plant sap liberated during feeding. The plant material enters each of these sensilla through an apical pore and interacts with four gustatory neurons and their receptors. Receptors bound to the dendrites transduce the chemical stimulus into a code of action potentials reflecting the quality and quantity of the complex plant chemistry. Subsequently, these nerve impulses are sent to the brain of the insect. The responses of these receptors to phytochemicals are key in determining which plants are deemed palatable and which should be rejected. Deterrent substances, such as e.g., some glucosinolates and alkaloids, are important in influencing the food selection of many insects, as they may be potentially toxic. Having a better understanding of the sensory mechanisms by which insects detect plant phytochemicals will help in finding novel biocontrol techniques against insect pests, especially highly polyphagous ones capable of defoliating forests or destroying crops.

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