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REVIEW

Chemosensory detection of glucosinolates as token stimuli for specialist insects on brassicaceous plants: discovery and impact

Chen-Zhu Wang[1,2] · **Joop J. A. van Loon**[3]

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Abstract
In this paper, we take a historical perspective by going back to Verschaffelt's landmark study published in 1910, in which he found that glucosinolates were used as token stimuli by larvae of *Pieris* butterflies, specialist feeders on plants in the family Brassicaceae. This classic discovery provided key evidence for Fraenkel (Science 129:1466–1470, 1959) to elaborate on the function of secondary plant substances and for Ehrlich and Raven (Evolution 18:586–608, 1964) to put forward the hypothesis of insect–plant coevolution. The discovery by Schoonhoven (Kon Nederl Akad Wetensch Amsterdam Proc Ser C70:556–568, 1967) of taste neurons highly sensitive to glucosinolates in *Pieris brassicae* was an important milestone in elucidating the chemosensory basis of host-plant specialization. The molecular basis of glucosinolate sensitivity was elucidated recently (Yang et al., PLoS Genet 17, 2021) paving the way to unravel the evolution of gustatory receptors tuned to glucosinolates that are crucial for host-plant selection of *Pieris* butterflies. We propose a hypothetical model for the evolution of labeled-line neurons tuned to token stimuli.

Keywords Glucosinolates · Token stimuli · *Pieris* · Taste cells · Gustatory receptors

Introduction

Phytophagous insects can be separated into three categories depending on their host-plant ranges. Polyphagous insects feed on more than one family of chemotaxonomically unrelated plants, oligophagous insects feed on plants in several genera but in the same family or families sharing secondary plant substances, and monophagous insects feed on a single plant species or plants in the same genus (Bernays and Chapman 1994). Polyphagous insects are also called generalists, while oligophagous and monophagous insects are collectively called specialists. What factors determine the diet breadth of phytophagous insects is a key question in the field of insect–plant relationships since the beginning of insect–plant research (Schoonhoven et al. 2005).

The discovery of token stimuli in insect–plant research

In 1910, Verschaffelt published an article in the Proceedings of the Royal Academy of Amsterdam entitled "What determines the choice of food for certain herbivores" (Verschaffelt 1910). In a series of feeding experiments, he found that glucosinolates promoted feeding by the larvae of *Pieris brassicae* L. and *Pieris rapae* L. (Lepidoptera: Pieridae), and that the distribution of glucosinolates could account for their host-plant range. *Apios tuberosa* is not used as a host plant by either *P. brassicae* or *P. rapae* larvae. When the juice obtained from the leaves of the brassicaceous (*syn.* cruciferous) plant (*Bunias orientalis*) was smeared on *A. tuberosa*, this was immediately consumed by the larvae. When the juice of *B. orientalis* was added to cornstarch or filter paper, these were also consumed by *Pieris* larvae. This study has

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Chen-Zhu Wang
czwang@ioz.ac.cn

Joop J. A. van Loon
joop.vanloon@wur.nl

[1] State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China

[2] Chinese Academy of Sciences Center for Excellence in Biotic Interactions, University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China

[3] Laboratory of Entomology, Wageningen University and Research, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

been recognized as the first to discover the chemical basis of specialized insect–plant relationships. Later, using *Plutella maculipennis* (nowadays named *P. xylostella* L.*)*, another specialist on brassicaceous plants, Thorsteinson re-examined Verschaffelt's research and expanded it experimentally and conceptually, and the results of Verschaffelt were fully confirmed (Thorsteinson 1955). Glucosinolates are secondary substances unique to the Brassicaceae and a small number of species in chemotaxonomically related plant families (*e.g.,* Tropaeolaceae) that are hydrolyzed by the enzyme myrosinase to various breakdown products arising during feeding damage to plant tissues (Rask et al. 2000), such as nitriles and isothiocyanates. Such secondary plant substances, without a nutritional function, are mainly responsible for host-plant recognition by phytophagous insects and were called "token stimuli" (Dethier 1941, 1954; Lipke and Fraenkel 1956).

Key evidence for the coevolution of insects and plants

Verschaffelt's results did not receive much attention at the time. Only half a century later, the role of secondary plant substances in insect–plant relationships was again emphasized. After years of studying insect nutrition, Fraenkel (1959) came to the conclusion that the nutritional requirements of all insects were basically very similar, and the presence of all required nutrients in plants was common, so why were so many insects restricted in the plants they would eat? Examination of the literature, including Dethier (1941), led him to the insight that secondary substances in different plants were responsible for the chemical signatures characteristic for plant families and species and thereby might provide a clue to the evolution of host-plant selection behavior (Fraenkel 1959). He took insects particularly on Brassicaceae (Cruciferae), Umbelliferae, Leguminosae, Solanaceae, Moraceae, and Gramineae as examples, and clearly explained the role of secondary plant substances in these plants, such as glucosinolates, alkaloids, and terpenoids, as repellents (deterrents) or attractants (stimulants). Over the course of evolution, these compounds emerged as defense mechanisms in plants against phytophagous insects and against other organisms. Insects, in turn, have developed defense mechanisms against the toxic effects of these substances, allowing them to process these molecules in many different ways. In some cases, this plant defense–insect counter-defense evolution gave rise to monophagous and oligophagous insects that are attracted or stimulated by these substances and will not feed or lay eggs in their absence, as in the case of glucosinolates—*Pieris* and *Plutella*, whereas polyphagous insects feed on plants that do not contain strong repellents or deterrents to them. This plant adaptation–insect counter-adaptation cascade, also termed 'chemical arms-race', has been put forward to explain the great diversity of secondary substances in plants and their significance in insect–host-plant relationships (Fraenkel 1959, 1981). After intense debate and the growing knowledge on plant chemistry and insect–host-plant selection behavior, the importance of secondary plant substances, next to plant nutrients, in host-plant acceptance by insects was firmly established (Kennedy 1958; Thorsteinson 1960).

A few years after Fraenkel's paper, Ehrlich and Raven (1964) came to a conclusion similar to Fraenkel's, based on literature on butterfly–host-plant interactions, building among others on Verschaffelt (1910), Dethier (1941, 1954, and 1959) and Fraenkel (1959). That is, secondary plant substances play a dominant role in determining the pattern of plant utilization by insects (Ehrlich and Raven 1964). Based on this, they coined the term "coevolution" as a hypothesis for how insect–plant interactions evolved, that is, plants produce a variety of secondary substances through accidental gene mutations and genetic recombination, some genetic variants are less consumed by insects, so that the plants experience reduced fitness loss due to insect attack, giving rise to an adaptive zone. As counter-adaptation, insect populations may diversify, promoting speciation events. Such adaptive interactions result in host-plant specialization of insects and the impressive diversity of ecological relationships between plants and insects. Such a stepwise 'arms-race' evolution has been widely accepted by the academic community, greatly promoting research progress in the field of insect–plant relationships, and triggering a large number of studies on species interactions, adaptation and differentiation. However, the role of secondary plant substances as token stimuli has in all cases been inferred from behavioral observations, except for only two cases: the butterfly *Papilio xuthus* in response to the oviposition stimulant synephrine and for *Pieris rapae* in response to the glucosinolate token stimulus sinigrin; for these two species, the sensory mechanisms at both the electrophysiological and molecular levels have been identified.

The taste perception of glucosinolates in *Pieris*

The study of insect–plant interactions has benefited from multidisciplinary approaches at all times. In 1955, Hodgson and his colleagues developed an electrophysiological technique called 'tip recording', which allowed to register the electrophysiological activity of neurons in the taste sensilla of insects (Hodgson et al. 1955). For phytophagous insects, this technique was first used in studies on Colorado potato beetles (*Leptinotarsa decemlineata* Say), silkworms (*Bombyx mori* L.), and the large cabbage white butterfly (*P. brassicae*) to study their chemosensory physiology (Ishikawa 1966; Schoonhoven 1967; Stürckow 1959). Schoonhoven (1967) was the first to identify gustatory receptor neurons in

Pieris larvae highly sensitive to glucosinolates. The two neurons located in the pair of sensilla styloconica on the maxillary galea in *P. brassicae* larvae responded to glucosinolates, the characteristic of brassicaceous plants. Their response spectra overlap but are not identical, and the sensory threshold concentration of the response to glucosinolates is in the range of the behavioral threshold of the larvae. Such chemoreceptor neurons can be designated as "labeled lines", that is, along the lines (axons), information is transmitted to the brain that is quantitatively correlated with the strength of the behavioral response. In this case, the host acceptance behavior can be explained by the chemosensory perception of a number of chemically similar token stimuli by several specialized chemoreceptors.

To understand the molecular basis of recognition of glucosinolates, the next question was which gustatory receptors are expressed on the taste neurons tuned to glucosinolates. However, the molecular mechanisms of glucosinolate perception remained an enigma during 54 years. The first study addressing the molecular basis of glucosinolates sensing in an insect was published by Yang et al. (2021). The latter authors screened two highly expressed ‘bitter’-sensitive gustatory receptor genes, *PrapGr28* and *PrapGr15*, from the taste organs of female adults of *Pieris rapae* using transcriptome sequencing and fluorescent quantitative PCR detection, and hypothesized that they might be involved in the perception of glucosinolates (Yang et al. 2021). Further experiments on *Xenopus* oocytes and two-electrode voltage-clamp studies showed that only the oocytes expressing *PrapGr28* were sensitive to the glucosinolate sinigrin. To verify this result, they heterogeneously expressed *PrapGr28* in the Gr5a gustatory receptor neurons of *Drosophila* L-type sensilla, successfully conferring their sensitivity to sinigrin. Finally, they used RNAi to reduce the expression of *PrapGr28* and found that the electrophysiological response of the taste sensilla of the foreleg tarsi of adults to sinigrin was significantly reduced, confirming that PrapGr28 is the gustatory receptor tuned to sinigrin in *P. rapae* (Yang et al. 2021). Glucosinolates occur in three chemically distinct types, *i.e.*, aliphatic (*e.g.,* sinigrin), aromatic, and indolic, based on the side chain of these molecules. Thus far, the molecular receptors for sensing other aliphatic, aromatic, and indolic glucosinolates remain unknown.

Prevalence of glucosinolates as token stimuli for specialist insects on crucifers

Glucosinolates and their breakdown products have been shown to deter and repel generalist insects (Louda and Mole 1991; Renwick 2002), and various specialist insects on Brassicaceae use glucosinolates as token stimuli to promote feeding in addition to *Pieris* species and *P. xylostella* mentioned earlier, for example, the aphid *Brevicoryne brassicae* (Wensler 1962), the weevil *Ceutorhynchus inaffectatus* (Larsen et al. 1992), various chrysomelid beetles (*Phyllotreta cruciferae*, *P. nemorum*, *P. undulata*, *P. tetrastigma*, *P. armoraciae*, *P. tetrastigma,* and *Phaedon cochleariae*) (Hicks 1974; Nielsen 1978a, b; Nielsen et al. 1979; Reifenrath and Müller 2008), or to promote oviposition, *e.g.*, *P. rapae* and *P. brassicae* (Renwick et al. 1992; Van Loon et al. 1992), the fly *Delia radicum* (Nair and McEwen 1976; Städler 1978), the sawfly *Athalia rosae* (Barker et al. 2006). Apparently, the specialist insects on Brassicaceae seem to employ a simple “lock and key” model, triggering stereotypical host acceptance behaviors through a few token stimuli (Hopkins et al. 2009). Currently, there are only a few documented insect–plant interactions outside of the Brassicaceae for which secondary plant substances have unequivocally been identified as token stimuli at both behavioral and physiological levels, *e.g.*, *Chrysolina brunsvicensis*–*Hypericum* (Rees 1969), *Diabrotica* spp.–*Cucurbita* spp. (Metcalf et al. 1980; Mullins et al. 1994), *Papilio polyxenes*–*Daucus carota* (Feeny et al. 1988; Roessingh et al. 1991), *Papilio xuthus*–*Citrus unshiu* (Ohsugi et al. 1991; Ozaki et al. 2011), *Manduca sexta*–*Solanum* spp. (del Campo et al. 2001), and *Tyria jacobaeae*–*Senecio jacobaea* (Bernays et al. 2004). However, the molecular aspects have only been studied in two cases (Ozaki et al. 2011; Yang et al. 2021).

Evolution of taste neurons coding for token stimuli

The behavioral response of insects to potential food plants consists of a reaction chain during which multiple sensory inputs are utilized, including optical, mechanosensory, olfactory and gustatory cues. There is ample evidence that in the final step in the chain gustatory cues are of overriding importance and provide the highest degree of specificity in the form of plant family-, genus-, or species-specific secondary chemicals (Chapman 2003; Schoonhoven et al. 2005). Stimulatory and inhibitory inputs are transmitted to the central nervous system and may be processed in an additive manner such that the decision-making can be visualized as a balance: if the positive inputs outweigh the negative inputs, the insect feeds or lays eggs, if the negative inputs prevail, the insect rejects the food (Dethier and Crnjar 1982; Schoonhoven and Blom 1988).

The gustatory receptor neurons in the taste sensilla of generalist insects are generally divided into two types (Chapman 2003): the first type is called the ‘common stimulus’ neuron, which senses nutritive compounds such as sugars and amino acids that stimulate the insects to feed or lay eggs; the second type is called ‘deterrent’ neuron, sensing secondary plant substances that prevent insects from feeding or laying eggs. In addition to the above two, in specialist insects a third type of neuron has evolved, which senses token stimuli that are specific secondary plant substances

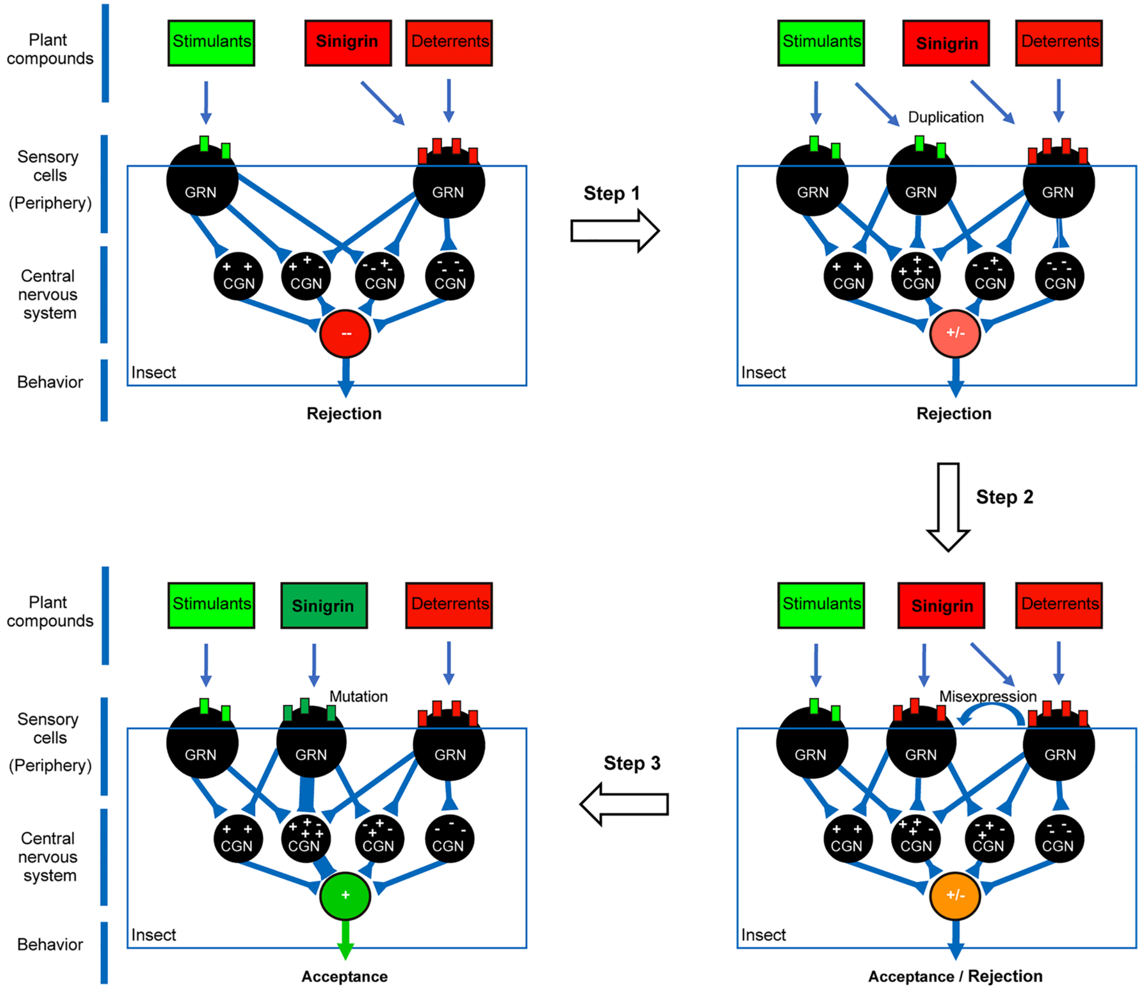

Fig. 1 Schematic representation of a hypothetical molecular genetic scenario for evolution of a token stimulus gustatory receptor neuron acting as a "labeled line". Top left: ancestral situation with 'common stimulus' gustatory receptor neurons (GRN) expressing receptor proteins (Grs, depicted as green rectangles) and deterrent neurons expressing "bitter" receptor proteins (red rectangles) responding to deterrent secondary plant substances including the glucosinolate sinigrin. Synapses between GRNs and neurons in the central nervous system (CGN) involved in gustatory integration and processing either depolarize (excitation, indicated by '+') or hyperpolarize (inhibition, '–') to different degrees depending on the number of synapses of each type, reflected by the number of '+' and '–' symbols. At the next level of gustatory information processing (red circle), the intensity of stimulatory neural activity is lower than the intensity of inhibitory activity and the host plant is rejected for feeding or oviposition. This scenario corresponds to the chemosensory system of a generalist phytophagous insect species that avoids sinigrin-containing plants. Step 1 leads to duplication of 'common stimulus' neurons, thereby increasing the intensity of stimulatory neural activity to the brain CGNs, yet rejection ensues. In Step 2, certain "bitter" *Gr* genes are mis-expressed in the 'common stimulus' GRNs, causing a shift to increased intensity of excitatory inputs of CGNs and the probability of behavioral acceptance increased (orange circle). In Step 3, mutations in these *Gr*s occurred and variants were selected that specifically bind to host-plant taxon-specific secondary chemicals, thereby favoring host-plant specialization by allowing fast behavioral decision-making through labeled-line coding (thick green line): neural activity in this processing pathway triggers acceptance of the plant for feeding or oviposition (green circle). The neurons that evolved in this way to "token stimulus GRNs" retained sensitivity to a few secondary substances and lost *Gr*s to chemically unrelated compounds

that stimulate the insects to feed and lay eggs. In addition, in *Pieris* species, a specialized type of deterrent neuron has been discovered that is tuned to a group of steroidal deterrent compounds, cardenolides, found only in some genera of the Brassicaceae (Van Loon and Schoonhoven 1999).

In general, glucosinolates are feeding or oviposition deterrents for generalist insects and token stimuli for specialist insects on Brassicaceae (Hopkins et al. 2009). We hypothesize that token stimuli originally acted as deterrents to insects. Our reasoning is based on the molecular evidence that the few gustatory receptors tuned to token stimuli identified so far belong to 'bitter' gustatory receptors, which are expressed by deterrent neurons (Ozaki et al. 2011; Yang et al. 2021). The following molecular genetic scenario could be envisaged (Fig. 1): initially the token stimulus neurons originated from the duplication of 'common stimulus' neurons, relaying stimulatory information to the brain. Next, certain bitter *Gr* genes expressed in deterrent neurons were mis-expressed in the common stimulus cells, causing subtle changes in the balance of positive and negative inputs. Subsequently, these *Gr*s changed over time as a result of mutation and variants were selected that favor host-plant specialization, *e.g.,* because they allow fast behavioral decision-making through labeled-line coding (Bernays 2001). The neurons that evolved in this way retained sensitivity to a few secondary substances and lost *Gr*s to chemically unrelated compounds. If the deterrent plant molecules are toxic, the molecular changes at the dendritic membrane of gustatory receptor neurons need to be accompanied by adaptations that allow overcoming the toxicity through enzymatic degradation or other mechanisms rendering these toxicants harmless. However, as was pointed out by Bernays (1991), there seems to be no strong relationship between deterrency and toxicity, which supports the plausibility of the hypothetical scenario outlined here.

Conclusions

It is a well-established fact that glucosinolates are token stimuli for many specialist insects on brassicaceous plants. These insects are equipped with specialized gustatory receptor neurons that act as "labeled lines" to sense the presence of glucosinolates. An interesting question from the perspective of neural coding is how phytophagous insects with their limited number of such neurons sense and discriminate between different glucosinolate mixtures in plants. We are just beginning to understand the molecular interactions that occur on the dendrite membranes of gustatory receptor neurons in phytophagous insects. Undoubtedly, elucidating the coding mechanisms of token stimuli at the molecular level and the evolution of *Gr* genes will reveal fundamental principles of insect–plant coevolution.

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Author contributions C-ZW and JJAvL wrote the main manuscript text and CZW prepared figure 1. All authors reviewed the manuscript.

Declarations

Conflict of interest The authors declare no conflict of interest.

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