

Review

The ecology of nutrient sensation and perception in insects

Fabian A. Ruedenauer ^{1,*} Maria Alejandra Parreño,¹ Ilona C. Grunwald Kadow,² Johannes Spaethe,³ and Sara D. Leonhardt¹

Insects are equipped with neurological, physiological, and behavioral tools to locate potential food sources and assess their nutritional quality based on volatile and chemotactile cues. We summarize current knowledge on insect taste perception and the different modalities of reception and perception. We suggest that the neurophysiological mechanisms of reception and perception are closely linked to the species-specific ecology of different insects. Understanding these links consequently requires a multidisciplinary approach. We also highlight existing knowledge gaps, especially in terms of the exact ligands of receptors, and provide evidence for a perceptual hierarchy suggesting that insects have adapted their reception and perception to preferentially perceive nutrient stimuli that are important for their fitness.

The importance of taste

To maintain their metabolism, insects must find and select food of appropriate **nutritional quality** (see [Glossary](#)) to maximize survival and fitness [1]. Assessing food nutritional quality is a challenging task because most food sources are complex mixtures of many different nutrients and other substances. Moreover, nutrition not only affects fitness but also influences behavior and intra- and interspecific interactions such as coordination of migration, foraging, and reproduction ([Figure 1](#)) [2]. Poor nutrition can lead to severe fitness consequences, including decreased reproductive success and survival [1,3]. Food assessment, selection, and consumption typically depend on different species-specific physiological, behavioral, and ecological factors ([Figure 1](#)) [4].

Olfactory information, such as that provided by volatile organic compounds (VOCs), often enables food localization from a greater distance (**olfaction**). However, **contact chemoreception**, frequently referred to as **taste**, is necessary to obtain information about largely non-volatile nutrients.

Taste is typically conveyed through a plethora of different substances that contribute to a bouquet of different tastes which may interact with each other [5]. Making sense of this chemical complexity and filtering out relevant nutritional information is challenging. Insects have evolved a variety of receptive and perceptive mechanisms that respond to various internal (e.g., hunger) and external (e.g., the chemical composition of food) cues ([Figure 1](#)). These mechanisms enable the **sensation** and **perception** of relevant stimuli. The integration of information on nutritional quality, the presence of potentially harmful substances, and current physiological state leads to a decision on food consumption ([Figures 1 and 2](#)).

Stretch **receptors** in the foregut are the first step in controlling hunger, and do not rely on external information [6]. Interestingly, hunger reinforces neuronal signals for some nutritional cues [7,8], while it can reduce inhibitory signals such as those induced by bitter substances [9]. Starved or sick individuals can be less selective in their food choice and more readily accept detrimental

Highlights

A substantial body of evidence suggests that the environment and their metabolic state influence the perception of nutrients by insects.

Insects can provide insights into the basic mechanisms of sensory processing and nutrient signaling, which may have broader implications for understanding how other organisms, including humans, perceive and respond to their environment. In addition, by understanding how insects perceive and respond to different nutrients, researchers can develop more effective strategies to control pest populations and improve crop yields.

Most studies are limited to few model species, such as *Drosophila*, thus preventing a broader and universally applicable view on the topic.

We develop a perceptual hierarchy hypothesis which suggests that the perception of food by insects is oriented towards nutrients that are particularly beneficial or detrimental. The hypothesis integrates neurobiological, physiological, and ecological aspects of insect nutrient perception.

¹Plant–Insect Interactions, Research Department Life Science Systems, TUM School of Life Sciences, Technical University of Munich (TUM), Freising, Germany

²Institute of Physiology II, University of Bonn, University Clinic Bonn (UKB), Bonn, Germany

³Department of Behavioral Physiology and Sociobiology, Biocenter, University of Würzburg, Am Hubland, Würzburg, Germany

*Correspondence: fabian.ruedenauer@tum.de (F.A. Ruedenauer).



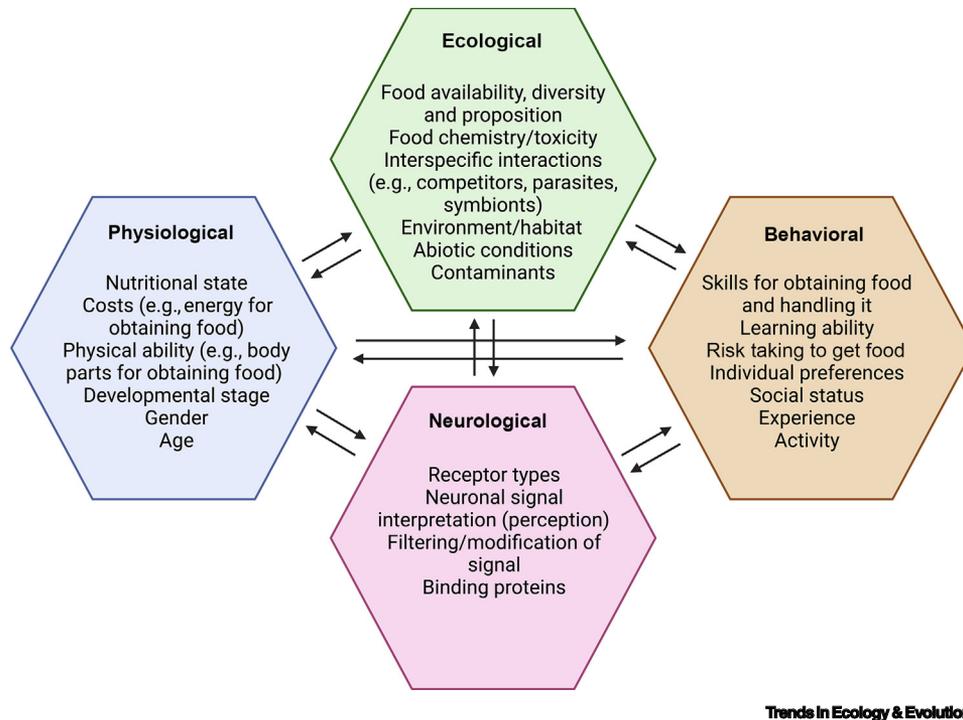


Figure 1. Ecological, physiological, neurological, and behavioral factors influencing the nutrient intake of animals. Although physiological and neurological factors are mostly genetically or temporally determined, and are therefore relatively stable among individuals of the same species, behavioral and ecological factors can differ strongly between individuals at different locations and with individual experience and context. All four categories likely interact with each other. For example, age (physiology) usually leads to a higher level of experience (behavior), and the identification of food chemistry (ecology) depends on the receptor types (neurology) possessed by a species. This figure was created using BioRender (<https://biorender.com/>).

substances [8,10]. This process seems to be regulated via neuromodulation [8,11], and may help insects to properly assess the cost–benefit ratio of food intake. Post-consumption information on nutrient profiles is mediated by internal nutrient receptors (that do not contact the food directly, unlike other internal receptors such as those in the pharynx [12] that are located in the brain, hemolymph, fat body, or gut. These resemble the types of receptors that are in direct contact with food [13,14]. In fact, even with dysfunctional external receptors, internal receptors have been shown to be sufficient for feeding modulation [15,16].

This review explores the link between different aspects of feeding and their importance for nutrient perception, mainly in adult insects (Figure 1). We identify knowledge gaps and highlight how combining knowledge from different disciplines, such as physiology and ecology, may improve our understanding of taste modalities across insect species. Our focus is on external mechanisms of nutrient perception which occur before food consumption. We compare findings in insect groups and species other than *Drosophila* which has been extensively studied [17–22], but all receptor and gene names used are based on *Drosophila* nomenclature, unless otherwise specified.

Physiological aspects of nutrient perception

Contact chemoreceptors in insects: types and diversity

Chemosensory receptors fall into three main groups – olfactory receptors (ORs), gustatory receptors (GRs), and ionotropic receptors (IRs) – but can also be other types of ion channels or even

Glossary

Chemoreceptor gene: a gene coding for a chemoreceptor.

Contact chemoreception: the reception of non-volatile substances via direct contact of a sensory organ with the substance.

Gustation: the action of tasting.

Nutritional quality: originally the composition of nutrients in a food item; in the literature the term is often used to describe the nutritional value of food items for an animal.

Olfaction: the reception of volatile substances/odors.

Perception: individual interpretation of sensory input.

Perceptual hierarchy: the hypothesis that stimuli become more salient when they are more important for the health, survival, and/or reproductive fitness of an animal (in a specific current state/situation).

Receptor: protein (complex) responsive to external ligand(s).

Receptor neuron: neuron transmitting information from the receptor to the next neuronal level.

Sensation: process of a molecule (ligand) binding to a receptor and triggering a nerve impulse in sensory neurons registered in the brain.

Sensillum: hair-like structure on sensory organs containing chemosensory receptors.

Taste: the ability to recognize different flavors via contact chemoreception.

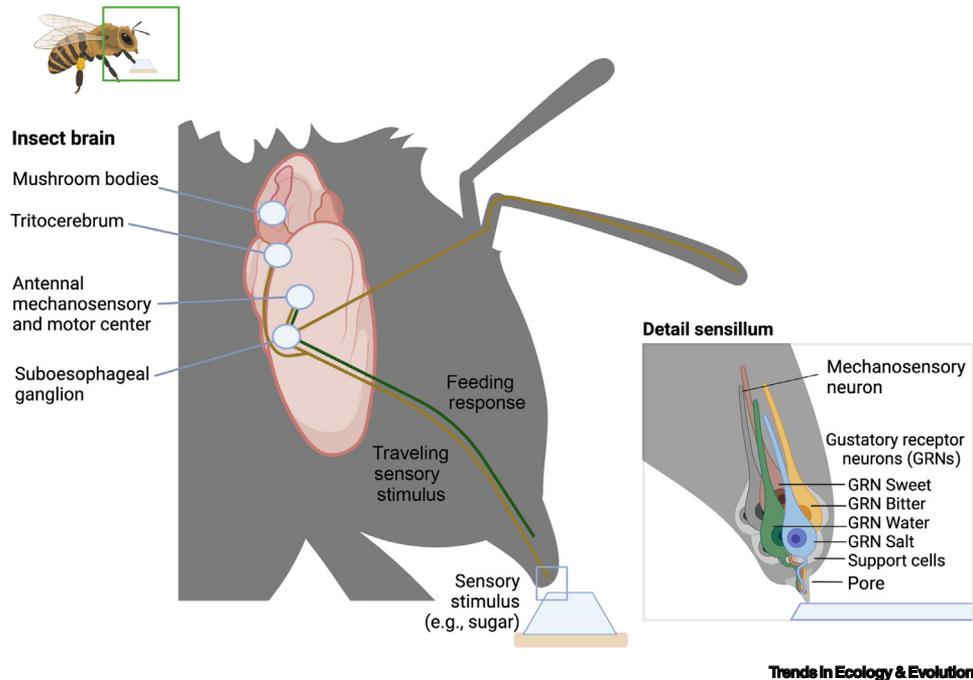


Figure 2. Schematic drawing of the pathway of a sweet stimulus (e.g., sugar) signal in a hypothetical insect. Gustatory sensilla in the proboscis and in the antennae of insects contain gustatory receptor neurons (GRNs), which mostly coappear with a mechanosensory neuron. After being in contact with a sweet stimulus, the neurons send the information into the subesophageal zone (SEZ) and the tritocerebrum (TC). From the SEZ the signal is forwarded via the antennal mechanosensory and motor center (AMMC) to higher brain centers such as the mushroom bodies (MBs), or feed back to the SEZ where it can elicit a feeding response. Brown lines represent incoming sensory information, and green lines represent outgoing signals to the proboscis, leading to a feeding response. The zoom on the proboscis (blue box) provides a detailed (disproportionate) view of a sensillum with different types of gustatory receptor neurons and a mechanosensory neuron. This figure was created using BioRender (<https://biorender.com/>).

opsins (Table 1). Although several taste receptors have been identified, a specific ligand repertoire has only been identified for sugar receptors (SRs) [23], primarily in *Drosophilidae* (Table S1 in the supplemental information online). For instance, GR5a was the first and one of the few GRs with an identified ligand, namely trehalose [24].

Species-specific chemoreceptor repertoires: a matter of ecology and evolution

ORs likely evolved from a branch of GRs [33], thus accounting for the higher structural diversity of GRs owing to their longer evolutionary history. IRs evolved independently from the other two receptor classes [34]. In general, **chemoreceptor genes** seem to diversify relatively quickly, and ORs diversify even faster than GRs – as seen in *Bombus* spp. (bumble bee) that has a large variety of chemoreceptors that differ among species [35]. The evolution of receptors likely played an important role in occupying new nutritional niches (Figure 1). For example, after the genus *Bombyx* (silk moths) separated from other lepidopteran genera, its bitter receptor repertoire evolved faster than other chemosensory receptors, suggesting a prominent role of bitter substances in its new ecological niche [36]. In fact, *Bombyx mori* (domestic silk moth) has 76 identified GR genes of which 51 code for bitter receptors [37,38], most likely owing to the large number of plant secondary metabolites it encounters in its host plants. *Helicoverpa armigera* (cotton bollworm) even comprises a repertoire of 180 bitter GRs, probably owing to its broad polyphagous diet [38]. Therefore, bitter receptor diversity seems to be crucial for accurately evaluating the defensive capabilities of host plants to avoid those with defense profiles that significantly lower offspring survival rates.

Table 1. Overview of the different chemoreceptor types of insects, including the structure and ligands of the different receptor groups

Receptor type	Structure	Ligands
Olfactory receptors (ORs)	Seven transmembrane domains; similar to G protein-coupled receptors but the N-terminus is intracellular and the C-terminus is extracellular [25]	Mostly volatile odor compounds; can also take part in gustatory sensation [19]
Gustatory receptors (GRs)	See ORs	Mainly contact chemoreceptors; can also take part in olfaction [17]
Ionotropic receptors (IRs)	Only three transmembrane domains [26]	Take part in both olfaction and gustation [26], and additionally function as temperature [27] or moisture [28] sensors
Ion channels and others	Typically four transmembrane domains, but some have two (e.g., Pickpocket (PPK) [29]) or six (e.g., Transient receptor potential (TRP) [30])	Mostly important coreceptors for both types of chemosensation types [31]; for example, opsins reinforce signals [32]

Similarly, the number of SRs in some insects appears to correlate with the diversity of sugars in their diets. For example, *Drosophila melanogaster*, which typically feeds on various fruits, has seven SRs, whereas bees and wasps, which collect nectar, have only two or three (Table S2 in the supplemental information online). Two of these (GR5a and GR64a) are necessary for sugar detection in general [39], but do not allow distinction between different sugars. Such a distinction is facilitated by diversification of SRs, as seen in *D. melanogaster* [40]. Fruit, the main food of *Drosophila*, contains a variety of different sugars [41], whereas nectar primarily consists of only three sugars – glucose, fructose, and sucrose [42]. Bees and wasps mainly rely on other food resources such as pollen (bees and a few wasp species) and insect prey (the majority of wasps) for egg production and offspring provisioning, making perception of overall sugar concentration sufficient. By contrast, most fruit fly species, which rely entirely on fruit for egg production and offspring provisioning, likely need to differentiate between different types of sugars when selecting among fruits, since these sugars also influence the yeast community on fruit, their major source of protein.

Contact chemoreceptive organs in insects: types and sensitivity

The insect gustatory system is more diverse than in mammals and is spread across several contact chemoreceptive organs, such as antennae, mouthparts, and tarsi [43], which typically harbor gustatory sensilla (Figure 2). Gustatory sensilla differ in size and shape among insect species and form either long taste hairs or shorter taste pegs [44]. Both have apertures (terminal pores) at their tip allowing gustatory molecules to enter the lymph-filled inner surface [45,46] where they interact with chemosensory proteins [32,44] or odorant-binding proteins [32,47]. Afterwards, they bind to receptors on the surface of the dendrites of gustatory **receptor neurons** (GRNs). Each gustatory **sensillum** comprises two or four GRNs which convey the signals to the brain (Figure 2). Most gustatory sensilla also contain a mechanosensory neuron that may aid in assessing the texture and viscosity of food, which is important for both mammal [48] and insect [49] food **gustation**.

Gustatory sensitivity and discrimination depend on the number of gustatory sensilla and the receptor types of their GRNs. Individual differences in gustatory sensitivity within a species may thus relate to differences in the number and density of different gustatory sensilla (e.g., differences between sexes [50]). Moreover, sensilla type and distribution can differ strongly between different body parts [51]. For example, in *Drosophila*, sensilla expressing Gr22c are mainly found on the legs, whereas sensilla expressing Gr59b are exclusively found on the labial palp

[51]. In consequence, whether a food item is consumed or not also partly depends on which organ is used for probing the food.

Taste perception in the insect brain and onset of feeding

Less is known about taste perception compared to sensation and the underlying receptors. In principle, after being excited by receptors, the GRNs transfer signals to the central nervous system where they are integrated with other information from different organs and finally form a percept (Figure 2). In *Drosophila* and *Phormia regina* (black blowfly), the neurons first project to different regions of the brain where the signal is then processed [31,52–54] (Figure 2). The brain region to which a signal is projected depends on the contact chemoreceptive organ and the receptor type [32,55].

Following perception, the gustatory information is translated into action, which is achieved through gustatory-responding neurons – neurons that receive direct information from the GRNs. Some of the few second-order gustatory-responding neurons identified so far are sweet gustatory projection neurons. They originate in the SEZ and terminate in the antennal mechanosensory and motor center (AMMC, Figure 2) [56]. These neurons are both necessary and sufficient to elicit a proboscis extension response (PER) in *D. melanogaster* – an extension of the proboscis in response to sugar [56]. From the AMMC, information can be transmitted either to higher brain centers or back to the SEZ where it may activate, for example, motor neurons (connected to the proboscis) to initiate feeding [56] (Table S1). However, higher-order processing of contact chemoreceptive signals is still not well understood (cf [57,58]) and has many knowledge gaps (Table S1).

Chemosensory perception of different nutrient groups

Like other animals, insects require both sufficient amounts and appropriate ratios of several macro- and micronutrients. Nutrients often serve as ligands of taste receptors, which is a prerequisite for their direct reception and subsequent perception (Figure 1). However, our understanding of the perception of specific nutrients is often limited, particularly for insects other than *Drosophila* (Table S1).

Sugar sensation and perception

Carbohydrates and sugars are the main energy sources. When consumed in higher amounts than needed, sugars can be stored as fat [59]. However, overconsumption for longer time-periods can lead to negative effects such as diabetes [60] and/or obesity [61,62]. Therefore, sugar sensing is essential for insects to regulate their sugar consumption. Sweet sensing is the most investigated taste modality in insects, likely because SRs were the first contact chemoreceptors discovered. Different insect species comprise between two and eight SRs, and there is no clear phylogenetic pattern of receptor expression (Tables S1 and S2). IRs also seem to be involved in sugar sensation, likely in inhibiting signals to prevent overconsumption (Figure 3) [13].

Similarly, sugar perception has been more thoroughly investigated than perception of other nutrients. Sugar signals are projected by ventral unpaired median (VUM) neurons, which also modulate proboscis extension in response to metabolic sugar needs. Specifically, response thresholds decrease with increasing sugar requirements [63]. Neurotransmitters and hormones also modulate sugar sensitivity and intake. For example, increased dopamine levels increase the sugar sensitivity of starved flies [63], and diuretic hormone 44 (DH44) increases sugar consumption [64]. As a result, hungry flies likely consume lower-quality food owing to increased levels of these neurotransmitters and hormones.

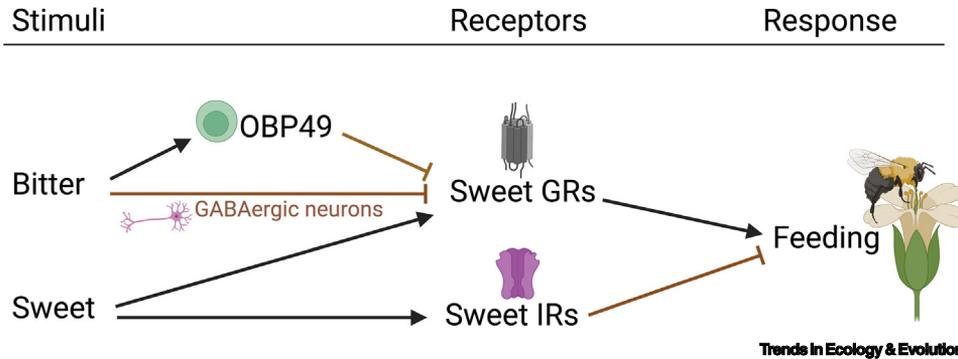


Figure 3. Schematic showing how bitter and sweet stimuli work opposingly via sweet receptors in feeding response regulation in insects. Bitter stimuli can inhibit sweet gustatory receptors (GRs), either directly via γ -aminobutyric acid (GABA)-ergic neurons or indirectly via Olfactory binding protein 49 (OBP49) and therefore inhibit the feeding response that is usually triggered via sweet GRs. Sweet stimuli can either trigger feeding via these GRs or inhibit feeding via ionotropic receptors (IRs). This figure was created using BioRender (<https://biorender.com>).

Protein/amino acid (AA) sensation and perception

Proteins and AAs are crucial to maintain a variety of body functions including growth, cell repair, and hormone regulation. In consequence, insufficient protein intake can lead to tissue degeneration or loss of body functions [65]. However, protein intake also represents an interesting dilemma in nutritional ecology [66], summarized as follows: high intake of protein, particularly of free AAs [67], typically increases reproductive success but can decrease lifespan. However, specific AAs such as methionine increase reproductive success in *Drosophila* without negative effects on lifespan [68]. This differential effect of specific AAs on lifespan may explain why, in some insects, specific AAs such as aspartic acid either act as phagostimulants or as antifeedants [69–71] regulated by neurotransmitters. Given the substantial effect of protein on survival and fitness, insects in general clearly benefit from being able to assess the protein/AA content of food. Notably, most protein molecules are likely too large to fit into chemoreceptors, but they may excite receptors with their terminal ends [72]. Moreover, the concentration of protein in food may correlate with the concentration of free AAs, as shown for pollen [73]. Insects may thus use the quantity of free AAs and polyamines as a proxy to assess the protein content of food. Interestingly, most insects require the same ten essential AAs [74], but strongly differ in AA reception and perception, likely depending on the foraging ecology and resource use of a species. For example, *Locusta migratoria* (migratory locust), an exclusive herbivore, can detect at least four AAs [75], whereas *Periplaneta americana* (American cockroach), which forages on highly variable resources, responds to almost all 23 AAs offered in behavioral experiments [76].

In some insects, GRs seem to be involved in AA sensation. In honey bees, for example, *AmGR10* was found to respond to a variety of different AAs [77]. In *Drosophila* and possibly other insects, IRs may also play a prominent role in AA and amine sensation (Table 1). For example, in *D. melanogaster*, AAs sensation is mediated by IR76b acting as a coreceptor with other IRs [71].

Polyamines (organic substances composed of more than two amino groups) represent another important group of proteinaceous compounds, not only as nutrients but also as environmental and social cues (e.g., cadaverin is a signal of oviposition sites for carrion-breeding insects [78]). A deficit in polyamines can result in neurodegenerative disease, fast aging, and decreased fertility (Figure 1). In consequence, polyamine content should also be assessed to regulate polyamine intake. Long-range detection of different polyamines requires a different IR (IR41a) than chemotactile reception (GR66a located in labellar taste hairs) in addition to two other IRs that

are necessary for both [79]. This example demonstrates that detailed and even context-dependent nutrient sensation can be achieved by activating a suite of different receptors and coreceptors.

Fat/fatty acid (FA) sensation and perception

Fat is a crucial nutrient for energy storage in insects. Similarly to protein, fat under- or overconsumption can be detrimental. Some FAs (e.g., linoleic and linolenic acid) are essential for insects and therefore need to be consumed in sufficient amounts and appropriate ratios [80]. In turn, excess concentrations of FAs in the hemolymph can lead to cell membrane damage [81] and subsequently reduced survival or reproduction, as shown in bumble bees [3] and honeybees [82]. In consequence, insects should be able to assess the fat content of food to some degree, either in detail or at least by assessing overall lipid amounts depending on species-specific ecological niche requirements (Figure 1). In fact, bumble bees were shown to detect differences in pollen FA concentrations and different FAs using chemotactile reception via antennae, including relatively short FA molecules such as capric and lauric acid [3]. This differs from mammals, which can only detect longer-chained FAs [83]. Fat receptors were recently found in *D. melanogaster* (i.e., IR56d, IR25a, and IR76b) [19,84] (Table S1). Notably, both sweet and FA signals activate sweet-sensing GRNs, but in different ways. Transfer of the FA signal additionally activates IR25a and IR76b [85], whereas sweet stimuli do not activate these IRs. This reveals other means by which insects can increase the number of molecules detected by combining an already existing receptor repertoire.

Interestingly, FA preferences differ substantially, even between closely related insect species. For example, the fruit fly *Drosophila sechellia* is attracted to high concentrations of FAs, likely due to its specialization for fruits of *Morinda citrifolia* (Indian mulberry) which are rich in FAs [86]. By contrast, *D. melanogaster* is repelled by high but attracted by low concentrations of FAs [87], which may be due to its preference for typically low-fat food resources. These findings further highlight the interaction between nutrient sensitivity, sensory fine-tuning, and nutritional needs as a consequence of species-specific ecological niche requirements.

Micronutrient sensation and perception

In addition to macronutrients (i.e., sugar, protein and fat), micronutrients such as minerals (salts) and vitamins are essential for animal health, even though much less is known about their requirements and effects in insects. Micronutrients serve manifold functions. They are important elements of enzymes and hormones, contribute to cell growth, and support immune responses [88]. Deficiencies in micronutrients can lead to severe health consequences, even though they are generally needed in relatively small amounts [88]. Hence, regulation of micronutrient uptake is as important as for macronutrients. Given their importance, surprisingly little is known about micronutrient reception and perception, except for the perception of several minerals in a few insect species [89,90]. In *Drosophila*, different types of receptors sense different minerals depending on their concentration. For example, the ion channel PPK23 responds exclusively to high levels of calcium and induces avoidance [91], while several IRs (among them IR76b) are required to detect low levels of calcium [91]. In consequence, micronutrient sensation seems to be mediated via concentration-dependent activation of some receptors and inhibition of others. Unfortunately, little is known about species-specific differences in micronutrient sensation in insects.

Bitter tastes and toxic substances

Bitter tastes usually indicate detrimental or even toxic substances and are therefore typically avoided by insects, which may explain why plants often use bitter substances as defense against herbivores [92]. Bitter substances therefore are not necessarily nutrients but comprise a variety of

substances. Their perception as bitter generally depends on the context, concentration, and species [31]. Unlike in humans [93], no specialized bitter taste receptors have so far been described in insects. Instead, bitter substances often inhibit sweet tasting neurons [94], which likely represents an adaptation to food comprising both sweet and toxic substances. Bitter tasting substances therefore usually inhibit feeding, in particular when encountered at high concentrations. For example, in *Drosophila* they can indirectly suppress sweet receptor signals via OBP49a [94] or directly via connected γ -aminobutyric acid (GABA)-ergic interneurons [95] (Figure 3).

Perceptual nutritional hierarchy: making sense of complexity

The examples mentioned in the preceding text for the sensation of various nutrients by insects reveal not only many knowledge gaps but also a striking complexity and diversity of the underlying mechanisms. For example, the sensation of micronutrients, sweet, fat, and bitter is mediated via concentration-dependent activation of some receptors, but inhibition of others [72]. Different pathways for different concentrations of the same gustatory ligand therefore seem to be relatively common [96]. This underlines the importance of assessing nutrient concentrations for insects and explains their ability to adjust their receptive and perceptive repertoire to precisely regulate the intake of specific nutrients [1,4]. However, the accuracy of nutrient perception strongly varies among nutrients, context, and insect species, suggesting that accurate perception may be restricted to some key substances which have either especially beneficial or detrimental effects. Based on this finding we hypothesize a **perceptual hierarchy** which enables insects to reduce time and energy for food quality assessment (Figure 1). Such a perceptual hierarchy might be adapted to the current physiological state of the animal. Nutrients that are currently most needed would be primarily perceived, for example by increasing the sensitivity of receptors or by amplifying signals, as has been shown specifically for locusts [7] and strongly implied for other insects [8,97,98]. In addition, there are some hints that not only beneficial but, at least for some species, also detrimental substances would be high in this perceptual hierarchy, for example FAs for *B. terrestris* [3] or bitter substances in *B. mori* ([37]; discussed in the section on Species-specific chemoreceptor repertoires: a matter of ecology and evolution). There is some evidence that a perceptual hierarchy might be especially important for food with a complex mixture of nutritional and non-nutritional compounds and thus a plethora of potential chemotactile cues [1]. For example, honey bees, that are typically very tuned towards detecting sugar, do not seem to detect sugar in pollen [99]. In addition, *B. terrestris* workers prioritize perception of FAs in pollen and appear to ignore other chemotactile cues, such as AAs or sterols [3], despite being able to perceive them when they are presented individually [100]. Interestingly, variation in pollen FA concentrations was also found to have the strongest effect on bee survival and reproductive fitness [3]. This suggests that foraging insects may focus on chemotactile cues that are ecologically most relevant to them, such as very important/limited or detrimental substances. Such perceptual prioritization of specific cues likely relies on specific neuronal tools such as a higher number/sensitivity of receptors or reinforcement/overwriting of signals.

Concluding remarks

This review emphasizes the interconnections between insect physiology, behavior, and the ecology of nutrient reception and perception. To further advance the field, future research should aim to fill the many knowledge gaps (see [Outstanding questions](#)), particularly regarding taste perception for less well studied nutrients (e.g., micronutrients) and for insects other than typical model species. Fully understanding the evolution and variation in taste modalities in insects will likely also require more collaboration across different disciplines of biology that study nutrition from different angles (Figure 1).

Outstanding questions

Can findings regarding nutrient perception in *Drosophila* be transferred to other insect species?

Can less well studied nutrients (e.g., minerals) be perceived by a high number of insects?

Which receptors respond to which specific ligands?

To what extent is the perceptual repertoire of an insect influenced by its (nutritional) ecology?

Which ecological factors are influencing this perceptual repertoire?

In particular: can the perceptual hierarchy hypothesis be confirmed?

We also provide support for a perceptual hierarchy hypothesis suggesting that the perception of important nutrients is prioritized and often achieved at high accuracy. Given the variety of receptors and underlying mechanisms mediating perception observed across species and modalities studied so far, it is highly likely that prioritization could be adjusted to the current nutritional needs of an insect by changing perception thresholds or switching to alternative receptors, potentially allowing flexibility in foraging while minimizing neurophysiological costs.

Finally, environmental factors such as food availability, diversity, composition, competitors, and climatic conditions affect food consumption in insects and may also alter taste perception. Anthropogenic substances such as pollutants and pesticides, as well as rising temperatures, may additionally affect receptive and perceptive abilities. However, it is not clear how these factors affect taste perception or whether insects can adjust their receptive and perceptive repertoire to changing environmental conditions induced by anthropogenic activities or climate change. Hence, understanding this interaction between environmental factors and taste perception in insects will require more joint action of physiologists, ethologists, and ecologists.

Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2023.05.006>.

References

- Simpson, S.J. and Raubenheimer, D. (2012) *The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity*, Princeton University Press
- Lihoreau, M. et al. (2018) Social nutrition: an emerging field in insect science. *Curr. Opin. Insect Sci.* 28, 73–80
- Ruedenauer, F.A. et al. (2020) Best be(e) on low fat: linking nutrient perception, regulation and fitness. *Ecol. Lett.* 23, 545–554
- Behmer, S.T. (2009) Insect herbivore nutrient regulation. *Annu. Rev. Entomol.* 54, 165–187
- Martin, C. and Issanchou, S. (2019) Nutrient sensing: what can we learn from different tastes about the nutrient contents in today's foods? *Food Qual. Prefer.* 71, 185–196
- Gelperin, A. (1967) Stretch receptors in the foregut of the blowfly. *Science* 157, 208–210
- Simpson, S.J. et al. (1991) Variation in chemosensitivity and the control of dietary selection behaviour in the locust. *Appetite* 17, 141–154
- Sengupta, P. (2013) The belly rules the nose: feeding state-dependent modulation of peripheral chemosensory responses. *Curr. Opin. Neurobiol.* 23, 68–75
- Inagaki, H.K. et al. (2014) Independent, reciprocal neuromodulatory control of sweet and bitter taste sensitivity during starvation in *Drosophila*. *Neuron* 84, 806–820
- Zhang, D.-W. et al. (2019) Insect behavior and physiological adaptation mechanisms under starvation stress. *Front. Physiol.* 10, 163
- Wu, Q. et al. (2005) Regulation of aversion to noxious food by *Drosophila* neuropeptide Y and insulin-like systems. *Nat. Neurosci.* 8, 1350–1355
- Pontes, G. et al. (2014) Bitter stimuli modulate the feeding decision of a blood-sucking insect via two sensory inputs. *J. Exp. Biol.* 217, 3708–3717
- Joseph, R.M. et al. (2017) A receptor and neuron that activate a circuit limiting sucrose consumption. *eLife* 6, e24992
- Miyamoto, T. and Amrein, H. (2014) Diverse roles for the *Drosophila* fructose sensor Gr43a. *Fly* 8, 19–25
- Dus, M. et al. (2011) Taste-independent detection of the caloric content of sugar in *Drosophila*. *PNAS* 108, 11644–11649
- Pool, A.-H. and Scott, K. (2014) Feeding regulation in *Drosophila*. *Curr. Opin. Neurobiol.* 29, 57–63
- Hallam, E.A. et al. (2006) Insect odor and taste receptors. *Annu. Rev. Entomol.* 51, 113–135
- Rytz, R. et al. (2013) Ionotropic receptors (IRs): chemosensory ionotropic glutamate receptors in *Drosophila* and beyond. *Insect Biochem. Mol.* 43, 888–897
- Chen, Y.-C.D. and Dahanukar, A. (2019) Recent advances in the genetic basis of taste detection in *Drosophila*. *Cell. Mol. Life Sci.* 77, 1087–1101
- Wang, G.-H. and Wang, L.-M. (2019) Recent advances in the neural regulation of feeding behavior in adult *Drosophila*. *J. Zhejiang Univ. Sci. B* 20, 541–549
- Vosshall, L.B. and Stocker, R.F. (2007) Molecular architecture of smell and taste in *Drosophila*. *Annu. Rev. Neurosci.* 30, 505–533
- Joseph, R.M. and Carlson, J.R. (2015) *Drosophila* chemoreceptors: a molecular interface between the chemical world and the brain. *Trends Genet.* 31, 683–695
- Chen, W.-W. et al. (2019) Identification of a sugar gustatory receptor and its effect on fecundity of the brown planthopper *Nilaparvata lugens*. *Insect Sci.* 26, 441–452
- Dahanukar, A. et al. (2001) A Gr receptor is required for response to the sugar trehalose in taste neurons of *Drosophila*. *Nat. Neurosci.* 4, 1182–1186
- Butterwick, J.A. et al. (2018) Cryo-EM structure of the insect olfactory receptor Orco. *Nature* 560, 447–452
- Croset, V. et al. (2010) Ancient protostome origin of chemosensory ionotropic glutamate receptors and the evolution of insect taste and olfaction. *PLoS Genet.* 6, e1001064
- Ni, L. et al. (2016) The ionotropic receptors IR21a and IR25a mediate cool sensing in *Drosophila*. *eLife* 5, e13254
- Knecht, Z.A. et al. (2017) Ionotropic receptor-dependent moist and dry cells control hygrosensation in *Drosophila*. *eLife* 6, e26654
- Cameron, P. et al. (2010) The molecular basis for water taste in *Drosophila*. *Nature* 465, 91–95
- Kim, S.H. et al. (2010) *Drosophila* TRPA1 channel mediates chemical avoidance in gustatory receptor neurons. *PNAS* 107, 8440–8445

31. Freeman, E.G. and Dahanukar, A. (2015) Molecular neurobiology of *Drosophila* taste. *Curr. Opin. Neurobiol.* 34, 140–148
32. Montell, C. (2021) *Drosophila* sensory receptors – a set of molecular Swiss Army knives. *Genetics* 217, 1–34
33. Robertson, H.M. *et al.* (2003) Molecular evolution of the insect chemoreceptor gene superfamily in *Drosophila melanogaster*. *PNAS* 100, 14537–14542
34. Robertson, H.M. (2019) Molecular evolution of the major arthropod chemoreceptor gene families. *Annu. Rev. Entomol.* 64, 227–242
35. Sun, C. *et al.* (2020) Genus-wide characterization of bumblebee genomes provides insights into their evolution and variation in ecological and behavioral traits. *Mol. Biol. Evol.* 38, 486–501
36. Guo, H. *et al.* (2017) Expression map of a complete set of gustatory receptor genes in chemosensory organs of *Bombyx mori*. *Insect Biochem. Mol.* 82, 74–82
37. Wanner, K.W. and Robertson, H.M. (2008) The gustatory receptor family in the silkworm moth *Bombyx mori* is characterized by a large expansion of a single lineage of putative bitter receptors. *Insect Mol. Biol.* 17, 621–629
38. Xu, W. *et al.* (2016) Expansion of a bitter taste receptor family in a polyphagous insect herbivore. *Sci. Rep.* 6, 23666
39. Dahanukar, A. *et al.* (2007) Two Gr genes underlie sugar reception in *Drosophila*. *Neuron* 56, 503–516
40. Kent, L.B. and Robertson, H.M. (2009) Evolution of the sugar receptors in insects. *BMC Evol. Biol.* 9, 41
41. Wrolstad, R.E. and Shallenberger, R.S. (1981) Free sugars and sorbitol in fruits – a compilation from the literature. *J. Assoc. Off. Anal. Chem.* 64, 91–103
42. Nicolson, S.W. and Thornburg, R.W. (2007) Nectar chemistry. In *Nectaries and Nectar* (Nicolson, S.W. *et al.*, eds), pp. 215–264, Springer
43. de Brito Sanchez, M.G. (2011) Taste perception in honey bees. *Chem. Senses* 36, 675–692
44. Amrein, H. and Thome, N. (2005) Gustatory perception and behavior in *Drosophila melanogaster*. *Curr. Biol.* 15, R673–R684
45. Morita, H. (1992) Transduction process and impulse initiation in insect contact chemoreceptor. *Zool. Sci.* 9, 1–16
46. Xu, W. (2020) How do moth and butterfly taste? Molecular basis of gustatory receptors in Lepidoptera. *Insect Sci.* 27, 1148–1157
47. Brito, N.F. *et al.* (2016) A look inside odorant-binding proteins in insect chemoreception. *J. Insect Physiol.* 95, 51–65
48. Singh, R.N. (1997) Neurobiology of the gustatory systems of *Drosophila* and some terrestrial insects. *Microsc. Res. Tech.* 39, 547–563
49. Zhang, Yali V. *et al.* (2016) The basis of food texture sensation in *Drosophila*. *Neuron* 91, 863–877
50. Marion-Poll, F.C. *et al.* (1992) Sexual dimorphism of tarsal receptors and sensory equipment of the ovipositor in the European corn borer, *Ostrinia nubilalis*. *Cell Tissue Res.* 267, 507–518
51. Dunipace, L. *et al.* (2001) Spatially restricted expression of candidate taste receptors in the *Drosophila* gustatory system. *Curr. Biol.* 11, 822–835
52. Edgecomb, R.S. and Murdock, L.L. (1992) Central projections of axons from taste hairs on the labellum and tarsi of the blowfly, *Phormia regina* Meigen. *J. Comp. Neurol.* 315, 431–444
53. Nayak, S.V. and Singh, R.N. (1985) Primary sensory projections from the labella to the brain of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). *Int. J. Insect. Morphol.* 14, 115–129
54. Yetman, S. and Pollack, G.S. (1986) Central projections of labellar taste hairs in the blowfly, *Phormia regina* Meigen. *Cell Tissue Res.* 245, 555–561
55. Isono, K. and Morita, H. (2010) Molecular and cellular designs of insect taste receptor system. *Front. Cell. Neurosci.* 4, 20
56. Kain, P. and Dahanukar, A. (2015) Secondary taste neurons that convey sweet taste and starvation in the *Drosophila* brain. *Neuron* 85, 819–832
57. Gordon, M.D. and Scott, K. (2009) Motor control in a *Drosophila* taste circuit. *Neuron* 61, 373–384
58. Scott, K. (2018) Gustatory processing in *Drosophila melanogaster*. *Annu. Rev. Entomol.* 63, 15–30
59. Timberlake, T.P. *et al.* (2019) Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585–1596
60. Branch, A. *et al.* (2017) Genetic and neurobiological analyses of the noradrenergic-like system in vulnerability to sugar overconsumption using a *Drosophila* model. *Sci. Rep.* 7, 17642
61. May, C.E. *et al.* (2019) High dietary sugar reshapes sweet taste to promote feeding behavior in *Drosophila melanogaster*. *Cell Rep.* 27, 1675–1685
62. Abrat, O.B. *et al.* (2018) High amylose starch consumption induces obesity in *Drosophila melanogaster* and metformin partially prevents accumulation of storage lipids and shortens lifespan of the insects. *Comp. Biochem. Phys. A* 215, 55–62
63. Marella, S. *et al.* (2012) Dopaminergic modulation of sucrose acceptance behavior in *Drosophila*. *Neuron* 73, 941–950
64. Dus, M. *et al.* (2015) Nutrient sensor in the brain directs the action of the brain-gut axis in *Drosophila*. *Neuron* 87, 139–151
65. Al Shareefi, E. and Cotter, S.C. (2018) The nutritional ecology of maturation in a carnivorous insect. *Behav. Ecol.* 30, 256–266
66. Lee, K.P. *et al.* (2008) Lifespan and reproduction in *Drosophila*: new insights from nutritional geometry. *PNAS* 105, 2498–2503
67. Arganda, S. *et al.* (2017) Parsing the life-shortening effects of dietary protein: effects of individual amino acids. *Proc. Biol. Sci.* 284, 20162052
68. Grandison, R.C. *et al.* (2009) Amino-acid imbalance explains extension of lifespan by dietary restriction in *Drosophila*. *Nature* 462, 1061–1065
69. Croset, V. *et al.* (2016) A molecular and neuronal basis for amino acid sensing in the *Drosophila* larva. *Sci. Rep.* 6, 34871
70. Kudow, N. *et al.* (2017) Preference for and learning of amino acids in larval *Drosophila*. *Biol. Open* 6, 365–369
71. Ganguly, A. *et al.* (2017) A molecular and cellular context-dependent role for Ir76b in detection of amino acid taste. *Cell Rep.* 18, 737–750
72. Chapman, R.F. (2003) Contact chemoreception in feeding by phytophagous insects. *Annu. Rev. Entomol.* 48, 455–484
73. Ruedenauer, F.A. *et al.* (2019) Pollinator or pedagogue: which factors determine the evolution of pollen nutrients? *Oecologia* 191, 349–358
74. Kraus, S. *et al.* (2019) Insect diet. In *Encyclopedia of Animal Cognition and Behavior* (Vonk, J. and Shackelford, T., eds), pp. 3471–3479, Springer International
75. Blaney, W.M. (1974) Electrophysiological responses of the terminal sensilla on the maxillary palps of *Locusta migratoria* (L.) to some electrolytes and non-electrolytes. *J. Exp. Biol.* 60, 275–293
76. Sugarman, D. and Jakinovich, W. (1986) Behavioural gustatory responses of adult cockroaches, *Periplaneta americana* D and L amino acids. *J. Insect Physiol.* 32, 35–41
77. Lim, S. *et al.* (2019) Characterization and its implication of a novel taste receptor detecting nutrients in the honey bee, *Apis mellifera*. *Sci. Rep.* 9, 11620
78. Archer, M.S. and Elgar, M.A. (2003) Effects of decomposition on carcass attendance in a guild of carrion-breeding flies. *Med. Vet. Entomol.* 17, 263–271
79. Hussain, A. *et al.* (2016) Ionotropic chemosensory receptors mediate the taste and smell of polyamines. *PLoS Biol.* 14, e1002454
80. Cohen, A.C. (2003) *Insect Diets: Science and Technology*, CRC Press
81. Canavoso, L.E. *et al.* (2001) Fat metabolism in insects. *Annu. Rev. Nutr.* 21, 23–46
82. Arien, Y. *et al.* (2020) Effect of diet lipids and omega-6:3 ratio on honey bee brood development, adult survival and body composition. *J. Insect Physiol.* 124, 104074
83. Laugerette, F. *et al.* (2007) Do we taste fat? *Biochimie* 89, 265–269
84. Brown, E.B. *et al.* (2021) Ir56d-dependent fatty acid responses in *Drosophila* uncover taste discrimination between different classes of fatty acids. *eLife* 10, e67878
85. Ahn, J.-E. *et al.* (2017) Molecular basis of fatty acid taste in *Drosophila*. *eLife* 6, e30115
86. Matsuo, T. *et al.* (2007) Odorant-binding proteins OBP57d and OBP57e affect taste perception and host-plant preference in *Drosophila sechellia*. *PLoS Biol.* 5, e118

87. Masek, P. and Keene, A.C. (2013) *Drosophila* fatty acid taste signals through the PLC pathway in sugar-sensing neurons. *PLoS Genet.* 9, e1003710
88. Higdon, J. and Drake, V.J. (2011) *Evidence-Based Approach to Vitamins and Minerals: Health Benefits and Intake Recommendations*, Thieme
89. Pontes, G. *et al.* (2022) Molecular and functional basis of high-salt avoidance in a blood-sucking insect. *iScience* 25, 104502
90. Baik, L.S. and Carlson, J.R. (2020) The mosquito taste system and disease control. *PNAS* 117, 32848–32856
91. Lee, Y. *et al.* (2018) Calcium taste avoidance in *Drosophila*. *Neuron* 97, 67–74
92. War, A.R. *et al.* (2012) Mechanisms of plant defense against insect herbivores. *Plant Signal. Behav.* 7, 1306–1320
93. Maehashi, K. and Huang, L. (2009) Bitter peptides and bitter taste receptors. *Cell. Mol. Life Sci.* 66, 1661–1671
94. Jeong, Y.T. *et al.* (2013) An odorant-binding protein required for suppression of sweet taste by bitter chemicals. *Neuron* 79, 725–737
95. Chu, B. *et al.* (2014) Presynaptic gain control drives sweet and bitter taste integration in *Drosophila*. *Curr. Biol.* 24, 1978–1984
96. Jaeger, A.H. *et al.* (2018) A complex peripheral code for salt taste in *Drosophila*. *eLife* 7, e37167
97. Jourjine, N. (2017) Hunger and thirst interact to regulate ingestive behavior in flies and mammals. *BioEssays* 39, 1600261
98. Steck, K. *et al.* (2018) Internal amino acid state modulates yeast taste neurons to support protein homeostasis in *Drosophila*. *eLife* 7, e31625
99. Nicholls, E. and Hempel de Ibarra, N. (2017) Assessment of pollen rewards by foraging bees. *Funct. Ecol.* 31, 76–87
100. Ruedenauer, F.A. *et al.* (2019) Bumblebees are able to perceive amino acids via chemotactile antennal stimulation. *J. Comp. Physiol. A.* 205, 321–331