

INSECT DEFENCES

Taste alteration and endoparasites

Taste sensation and food selection by animals can change adaptively in response to experience, for example to redress specific nutrient deficiencies¹. We show here, in two species of caterpillar, that infection by lethal parasites alters the taste of specific phytochemicals for the larvae. Given that these compounds are toxic to the parasites and are found in plants eaten by the caterpillars, their changed taste may encourage parasitized caterpillars to increase consumption of plants that provide a biochemical defence against the invaders.

Caterpillars of the tiger moths (Lepidoptera Arctiidae) *Grammia geneura* and *Estigmene acraea* are dietary generalists that occupy a grassland and savanna habitat in southern Arizona. Both are susceptible to several species of parasite (insect parasitoids)² that typically wound their host mortally. The caterpillars defend themselves by sequestering pyrrolizidine alkaloids, which are toxic to a range of predators and parasitoids^{3,4}, from favoured food plants⁵ such as *Senecio longilobus*.

The caterpillars can detect pyrrolizidine alkaloids even at extremely low concentration by virtue of specialist receptor cells, which stimulate feeding behaviour^{6,7}. *Grammia geneura* also sequesters iridoid glycosides, which induce rapid firing of sucrose-receptor cells and promote feeding on the iridoid-containing plant *Plantago insularis*⁸. This plant is known to confer protection against predators^{9,10}.

To quantify these gustatory-cell responses and determine whether they are linked to parasitism, we collected *G. geneura* and *E. acraea* from the field and tested how the response of their gustatory cells to these plant compounds and to selected feeding deterrents was affected by the presence of parasites (for methods, see supplementary information).

We found that the taste cells of parasitized *G. geneura* caterpillars increased their firing rates in response to the pyrrolizidine alkaloid

seneciophylline *N*-oxide and the iridoid catalpol, but reduced their firing rate in response to the deterrent caffeine, as compared with unparasitized caterpillars; there were no differences in the response to a sucrose control (Fig. 1a) (one-way analyses of variance (ANOVAs): seneciophylline *N*-oxide, $F_{44,1} = 19.448$, $P < 0.0001$; catalpol, $F_{44,1} = 8.1$, $P = 0.007$; caffeine, $F_{44,1} = 4.398$, $P = 0.0424$; sucrose, $F_{44,1} = 0.0045$, $P = 0.947$).

Of 20 *E. acraea* caterpillars tested from Gardner Canyon, 12 were parasitized, and of 57 tested from Box Canyon, 46 were parasitized. Parasitized larvae showed a greater response to the pyrrolizidine alkaloid (two-way ANOVA: seneciophylline *N*-oxide, $F_{75,1} = 11.745$, $P < 0.0001$; population, $F_{75,1} = 0.0354$, $P = 0.851$; *N*-oxide \times population, $F_{75,1} = 0.868$, $P = 0.41$) (Fig. 1b). However, the responses to the deterrent protocatechuic acid were reduced (two-way ANOVA: deterrent, $F_{75,1} = 14.62$, $P = 0.003$; population, $F_{75,1} = 1.29$, $P = 0.259$; deterrent \times population, $F_{75,1} = 0.359$, $P = 0.551$), and responses to sucrose were inconsistently different (two-way ANOVA: sucrose, $F_{75,1} = 4.438$, $P = 0.039$; population, $F_{75,1} = 0.651$, $P = 0.422$; sucrose \times population, $F_{75,1} = 5.296$, $P = 0.024$) (Fig. 1b).

Previous work has indicated that increased gustatory responsiveness in caterpillars to pyrrolizidine alkaloids and iridoid glycosides may cause them to increase their consumption of host plants containing these compounds^{10–12}. The reduced responsiveness to deterrent compounds demonstrated here may increase the likelihood that the caterpillar will feed on normally unpalatable plants, which could also provide chemical defence. Other species of generalist arctiid caterpillars are known to sequester opportunistically a wide range of toxins from plants, including ones foreign to their natural habitats¹³.

The opposite directions of sensory change for feeding stimulants and deterrents, and the absence of a consistent change in response to the phagostimulatory nutrient sucrose in relation to parasitism, dispel the possibility that we were recording a generalized change in sensory neurons. In *G. geneura*, the sucrose sensitivity lies on the same gustatory neuron as iridoid sensitivity⁸, indicating that the change does not affect the whole cell, but rather the particular receptor protein or its second messengers.

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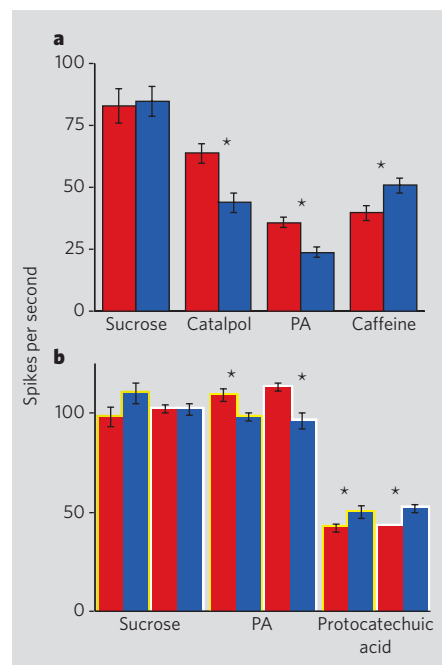


Figure 1 Gustatory responses of parasitized and unparasitized *Grammia geneura* and *Estigmene acraea* caterpillars. **a**, Depolarizations occurring in the first second of stimulation are shown for: a phagostimulant-specific gustatory cell from *G. geneura*, in response to a sucrose control and to the iridoid catalpol; a gustatory cell specific for the pyrrolizidine alkaloid (PA) seneciophylline *N*-oxide; and a gustatory cell specific for the deterrent caffeine; mean and s.e.m. are shown; asterisk indicates significant difference of $P < 0.01$. Parasitized larvae (red bars), $n = 23$; unparasitized larvae (blue bars), $n = 21$. **b**, As in **a**, but in *E. acraea* and using protocatechuic acid as deterrent. Gardner Canyon population (yellow outline): parasitized larvae, $n = 12$; unparasitized larvae, $n = 8$; Box Canyon population (white outline): parasitized larvae, $n = 46$; unparasitized larvae, $n = 11$.

- Simpson, S. J., James, S., Simmonds, M. S. J. & Blaney, W. M. *Appetite* **17**, 141–154 (1991).
- Stireman, J. O. & Singer, M. S. *Ecology* **84**, 296–310 (2003).
- Nishida, R. *Annu. Rev. Entomol.* **47**, 57–92 (2002).
- Bezzerides, A. et al. *Proc. Natl Acad. Sci. USA* **101**, 9029–9032 (2004).
- Hartmann, T. et al. *J. Chem. Ecol.* **30**, 229–254 (2004).
- Bernays, E. A., Chapman, R. F. & Hartmann, T. *J. Comp. Physiol.* **188**, 715–723 (2002).
- Bernays, E. A., Chapman, R. F. & Hartmann, T. *Physiol. Entomol.* **27**, 312–321 (2002).
- Bernays, E. A., Chapman, R. F. & Singer, M. S. *J. Comp. Physiol.* **186**, 13–19 (2000).
- Bowers, M. D. in *Caterpillars: Ecological and Evolutionary Constraints on Foraging* (eds Stamp, N. E. & Casey, T. M.) 331–371 (Chapman & Hall, New York, 1993).
- Singer, M. S. & Stireman, J. O. *Oikos* **100**, 554–562 (2003).
- Singer, M. S., Carriere, Y., Theuring, C. & Hartmann, T. *Am. Nat.* **164**, 423–429 (2004).
- Singer, M. S., Rodrigues, D., Stireman, J. O. & Carriere, Y. *Ecology* **85**, 2747–2753 (2004).
- Rothschild, M. *Biol. J. Linn. Soc.* **12**, 305–326 (1979).

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