

amygdala [7], whereas joyful, pleasant music, conversely, does recruit it [8]. More generally, these findings suggest that there is a more complex relationship between perceived roughness, experienced fear, and the role of the amygdala. Kumar *et al.* [9] showed that the amygdala does respond to the valence of unpleasant sounds, but also encodes acoustical features, and that effective connectivity between it and the auditory cortex is reciprocally modulated such that the representation of salient information is jointly processed by this circuit. The reverse correlation findings of Arnal *et al.* [1] indicate that, among the sounds they have used, the amygdala responds best to those containing roughness, but this need not indicate that the auditory cortex — and by extension cognitive top-down mechanisms — play no role in modulating the response. Indeed, the coding of vocal affect, such as anger or fear, involves a distributed circuit [10] encompassing amygdala and voice-sensitive auditory cortical areas [11], as well as insula and prefrontal areas that encode more abstract cognitive representations of emotion.

The findings by Arnal *et al.* [1] in turn lead to a series of new questions likely to motivate further research in different domains. For instance: are screams of

fear the only vocalizations characterized by increased energy in the 50–200 Hz temporal modulation rate, or would angry vocalizations, for example, also show this feature? To what extent are such rapid temporal modulations, reported here in adult screams of fear, also exploited by infant cries — a sound category of particular survival value? And are these fast modulations specifically human or are they also exploited by other species to make their vocalizations more attention-grabbing, along with other well-known cues such as amplitude rise time and fast changes in fundamental frequency [12]? What are the neural top-down mechanisms that enable roughness to be perceived either as a danger signal requiring immediate action, or a sign of emotional intensity, to be enjoyed at a concert?

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Behavioral Ecology: Manipulative Mutualism

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A new study reveals that an apparent mutualism between lycaenid caterpillars and their attendant ants may not be all it seems, as the caterpillars produce secretions that modify the brains and behavior of their attendant ants.

Herbivores have a problem. The plants they eat are immobile and this, together with their low nutrient content, requires herbivores to spend a lot of time in one place until they get their daily calorie

intake. This makes herbivores predictable and easy pickings for predators. To counteract predation, natural selection has led to two principal modes of defense for herbivores: camouflage and defensive

capabilities that deter predators. The caterpillar larvae of butterflies and moths (Family Lepidoptera) are almost entirely herbivorous and display many examples of both types of anti-herbivore strategy.



Figure 1. Bodyguards and sugar taps.

Pristomyrmex punctatus ants tapping the caterpillar *Narathura japonica* for sugar rewards in return for the protection they offer. In addition the ants receive compounds that affect key biogenic amines in their brains enforcing their cooperation. Photo by Masaru Hojo.

Some can blend into the surrounding leaves, making it difficult for predators to spot them, while others advertise their presence with striking warning coloration, because they possess chemical or physical defenses — spines or hairs that make eating them decidedly unpleasant. Many herbivorous insects, including some caterpillars, have another way to defend and that is to enlist the help of those most pugnacious of insects, the ants [1]. This has long been considered a textbook example of a mutualism — the ant receiving sugar rewards in return for providing the caterpillars a standing guard. A new study published recently in *Current Biology* by Hojo *et al.* [2] now shows that the deal may not be as sweet as generally assumed. In fact, the sugar reward caterpillars provide in return for the protective service of ants contains manipulative drugs that alter the behavior of the ant bodyguards (Figure 1). The drugs keep the pugnacious ants on a shorter leash and make them more aggressive — to the benefit, it would seem, of the hungry caterpillar.

Ants rule the world! Despite accounting for less than 2% of all insect species, ants make up as much as half of insect biomass [3]. For a long time, this was a puzzle, as it wasn't clear what was fueling the massive ant societies, often

comprising hundreds of thousands and even millions of individuals [4]. By using stable isotope ratio studies, researchers discovered that many genera of ants are in fact cryptic herbivores [5]. They feed on plant material, but do so indirectly via many species of plant feeding insects, which consume plants and then excrete sugars. The ants tap these sugars and in return provide an essential service to the herbivorous insects by acting as standing bodyguards 24 hours a day. The benefits of such bodyguards are apparent from experiments that showed that plant-feeding insects suffer very high levels of mortality when ants are removed [6]. This dual benefit had all the hallmarks of a classic mutualism.

Now, a twist to this narrative emerges that may in fact require re-evaluation of other apparent mutualisms. In their new study, Hojo, Pierce and Tsuji [2] studied a well known ant-herbivore mutualism between Lycaenid caterpillars and their attendant ants. There are in fact two types of associations between these caterpillars and ants, one as impressive as the other. One mode, not the focus of the study by Hojo *et al.* [2], is an example of parasitism, where the caterpillars chemically mimic the smell of the ants and gain entry to consume the resources of the colony and even the ant

larvae. This is a very rare example of herbivores evolving to be predators [7]. These caterpillars are essentially cuckoos, with adaptations on par with anything we find in the avian world [8]. The other relationship, focused on by Hojo *et al.* [2], has long been considered a mutualism. There are a number of different species pairs engaged in this type of mutualism. Hojo *et al.* [2] studied the caterpillar *Narathura japonica*, which feeds on Oak trees (*Quercus glauca*) in Japan and provides ants (*Pristomyrmex punctatus*) with secreted substances in return for protective services.

It is well known that myrmecophilous (ant-loving) lycaenid caterpillars have a dorsal nectary organ which, as its name suggests, produces a sugar and amino acid containing substance for ants [9]. This nectary organ is flanked by tentacle organs on the eighth abdominal segment. The tentacle organs are thought to secrete volatile chemicals that attract and alert ants either when the caterpillar is alarmed or when the nectary organ is depleted. Previous work on this species pair had shown that ants having fed on nectar were more likely to be attendant ants in the future, even if the nectary organs were experimentally occluded [10]. This hinted at the tantalizing possibility that perhaps compounds within the nectary organs were not merely nutritious rewards but could manipulate ant behavior.

The team set up a simple behavioral experiment to test the role of the nectary organs. Ants placed together with a caterpillar with a functioning nectary organ moved significantly less than ants that either had no interaction with a caterpillar or only interacted with a caterpillar where the nectary organs were occluded with nail polish. This experiment implied that nectary organs of caterpillars functioned to enlist a 'standing guard' [2]. Furthermore, the bodyguard ants became more pugnacious with more exposure to whatever substances were produced by the nectary organs. When the caterpillars everted their tentacle organs (which contain a volatile to signal the caterpillar is alarmed) then those ants that had access to nectary organs responded aggressively, whereas in the other treatment (occluded nectary

organs) the ants did not respond aggressively.

Not only were the behaviors of the attendant ants changed but also dopamine levels in their brains, which increased significantly in ants that attended caterpillars with functioning nectary organs. Other biogenic amines (serotonin, octopamine and tyramine) were not affected. Exactly how the secretions from the nectary organs could elicit such changes in an important neuromodulator and neurotransmitter remains unknown. The quantity of secretions from the nectary organs is very small, making a complete chemical characterization difficult. In addition, the researchers only measured four biogenic amines, but other changes in the brains of attendant ants might be taking place. Hopefully, future work such as whole brain metabolomics or RNA-seq experiments on individual brains will provide further insights.

But the importance of this paper is not just for the details it provides on the proximate mechanisms of behavioral manipulation [11]. The importance is also that apparently mutualistic caterpillars manipulate ant behavior at all. It is well known that parasites can adaptively manipulate the behavior of their hosts. This is the concept of the extended phenotype [12], where changes in host behavior benefit parasite fitness. In the

study by Hojo *et al.* [2], it seems that attending bodyguard ants are less likely to wander from their charge and more likely to be aggressive, which should benefit the caterpillar. This ‘mutualism’ thus has all the hallmarks of adaptive manipulation of host behavior by a parasite!

It would appear that caterpillars enforce the cooperation they require. This is likely to be due to the fact that the ant colony may not need its caterpillar ‘sugar tap’ as much as the sugar tap needs its fierce bodyguards. As other sources of sugar present themselves, the danger for the caterpillar is that the ants shift away from their protective role, leaving the caterpillar vulnerable to predation. And so, perhaps by way of an insurance mechanism, the hungry caterpillar has evolved to keep their ant bodyguards on a short leash using manipulative drugs. This study will hopefully encourage different researchers to examine other apparent manipulations for signs of similar manipulative behaviors.

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Plant Intracellular Transport: Tracing Functions of the Retrograde Kinesin

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Adding to its varied repertoire of functions in cell morphogenesis and cell division, a molecular motor protein of the kinesin-14 class has recently been implicated in rapid retrograde transport along cellular tracks in moss.

Like traffic in general, cellular trafficking also relies on dedicated tracks and vehicles that facilitate the transport of cargo. In all eukaryotes, transport tracks

are made of the cytoskeleton — polar microtubules and actin filaments. Aided by versatile molecular motors, the list of cellular mechanisms requiring the

cytoskeleton is nearly infinite, and includes diverse functions in cell division, cell polarization and growth as well as in subcellular transport. In most eukaryotes,