# Aircraft Detectors, Trap Triggers and Combination Locks

## Functional Diversity of Insect Mechanosensory Hairs

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Sensory systems of animals are receivers of signals, which serve specific functions in the interaction amongst animals and with their environment. The diversity of niches and habitats that different animals occupy is also reflected in the diversity of sensory systems that have evolved in these animals. These sensory systems help an animal to find food and shelter, escape predators, reproduce, etc.

In order to understand fully the properties of any biological system, for example a sensory system, one must ask, how does the system work? (the proximate question) and what is it good for? (the ultimate question). To answer these two questions, classical zoological disciplines have to be combined with modern physico-chemical techniques. And the two answers together would give a satisfying biological answer. This combined approach is exemplified here on a very simple mechanoreceptor in insects.

Mechanosensory hairs consist of two functionally important components: 1) a hair shaft made of cuticle, which is connected to the surrounding cuticle by a membrane and 2) a sensory neuron which translates the primary stimulus (hair movement) into the language of the nervous system (electrical action potentials) (*Figure* 1). The stiffness of the connecting membrane determines the mechanical sensitivity of the hair, the channel properties of the sensory neuron determine the specificity and the geometric shape of the neuron determines its action speed. This simple system has been further modified in ways to fulfil the specific needs of different animals. Some examples are discussed below.

| Animals interacting | Ecological 'Role' | Relevant receptor Property |
|---|---|---|
| Caterpillars – wasps | Prey | Sensitivity |
| Ants – springtail | Predator | Speed |
| Caterpillars – ants | Symbiosis partner | Specificity |

***Table 1. Depending on the role an animal plays in an ecosystem, different receptor properties are of importance.***

The roles that animals play in an ecological context are usually either as prey, predator or symbiont. For animals which are potential prey for other animals, the key to survival is to detect the predator as soon as possible (determined by the *sensitivity* of the sensory system), for a predator it is important to be faster than the prey (determined by the *speed* of the sensory system) and for symbiotic interactions it is important to detect the symbiotic partner (determined by the *specificity* of the sensory system). Real-life examples of cases where the above criteria have been fulfilled are given in *Table* 1.

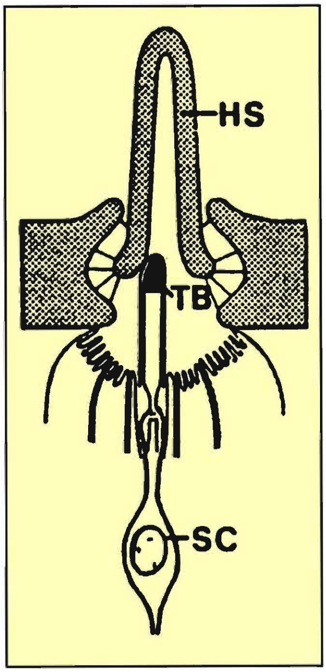


***Figure 1 : Schematic drawing of a mechanosensory hair in insects. HS = cuticular hair shaft, SC = sensory cell, TB = tubular body (intracellular differentiation in the sensory neuron and site of transduction of mechanical stimulus into electrical signals).***

## Aircraft Detectors

The life of a caterpillar is dangerous. Caterpillars make a great meal for numerous predators, amongst which social wasps are perhaps the most successful hunters. A wasp colony with about 300 members can catch as many as 2000 caterpillars in a day. In response to such an enormous predator pressure, caterpillars employ various means to escape from the wasps. For example, they camouflage themselves as twigs or bird droppings (*Figure* 2 and cover of this issue). However, this imitation is convincing only if the caterpillar does not move. Indeed, caterpillars freeze in motion as soon as they detect a hunting wasp. Even though caterpillars are poorly equipped with receptor systems, they have developed a very efficient 'wasp-approach-warning system'. Sensory hairs located on the three thoracic segments (*Figure* 3) are specifically responsive to the vibrations in the air that an approaching wasp produces with its wings. If such a stimulus is strong enough it stimulates the caterpillar to simply

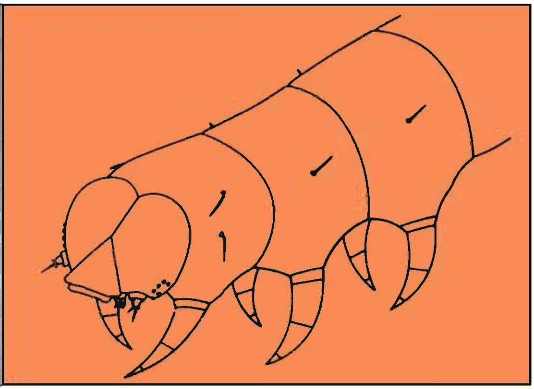


*Figure 2 (left). Early caterpillar stage of the European alder moth Apatele alni. In color and shape it mimics a bird dropping.*

*Figure 3 (right). Drawing of the front part of a caterpillar of the cabbage moth Barathra brassicae. Located always in the same position among hundreds of stiff hairs (not shown here) are 8 hairs highly moveable by the slightest wind.*

freeze in its place (the 'freeze' reaction of the caterpillar). One can mimic the vibrations produced by the beating of the wings in the air by using a loudspeaker. By controlling the frequency of vibrations emitted by the loudspeaker one can determine the range of vibratory frequencies for which the 'freeze' reaction can be elicited. The behavioral threshold curve for the freeze reaction is U-shaped with a broad sensitivity maximum between 100 Hz and 600 Hz (*Figure* 4). This range covers the frequency of wing beats of all larger social wasps.

The sensory cell of each sensory hair produces one action potential per wing-beat as soon as the vibrations produced by the wings reach the threshold frequency. Details like stimulus intensity (which would be an indication of how close the wasp is

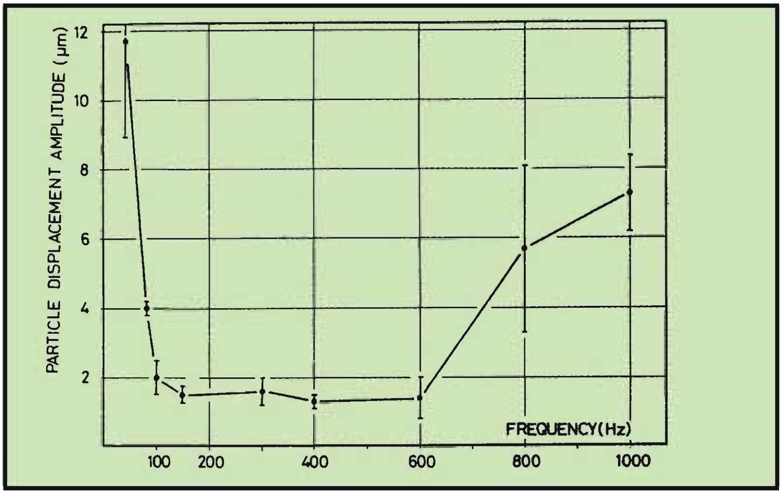


*Figure 4: Spectral threshold curve for the freeze reaction of Barathra brassicae caterpillars. X-axis: frequency of the air oscillation, Y-axis: amplitude of the air oscillation (particle displacement amplitude) necessary to elicit the freeze reaction of the caterpillar.*

to the caterpillar) or direction of the wasp relative to the caterpillar are not coded in the temporal pattern of the electrical activity of the sensory cell. The sensory system acts therefore as a simple detector which does not measure any details of the stimulus. The only function of this 'aircraft-detector system' is to signal the presence of a predatory wasp as early as possible. The earliest the caterpillar can detect the wasp is when the flying predator is at a distance of 70 cm from it (*Figure* 5). Notably, this is the distance from which the wasps dart down onto prey they have discovered. Thus the 'arms-race' between wasps and caterpillars has resulted in a balance between the limits of the sensori-motor abilities of both hunter and prey.

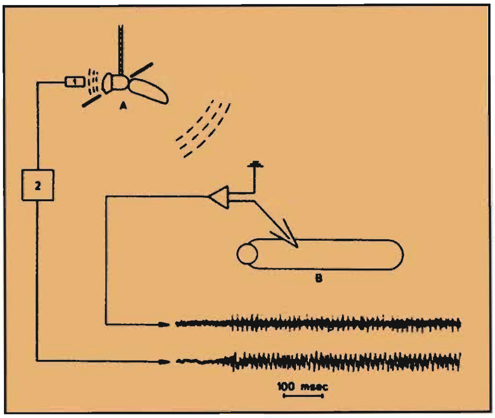


***Figure 5. Simultaneous recording of the wind (lower trace) produced by a tethered flying wasp (A) and the electrical impulses of the sensory cell (upper trace) of a caterpillar (B).***

Social wasps have a wide spectrum of prey and thus have alternatives to unsuccessful caterpillar-hunts. However, there are specialized wasps which parasitise caterpillars (these wasps are often species specific and obligatory parasites) which depend on their ability to approach the caterpillars undetected and deposit their eggs on the host-body. Considering the great sensitivity of the caterpillars for air-vibrations produced by wasp wings, it is not surprising that most of these solitary wasps are either extremely small (and thus their wing vibrations are below the stimulatory threshold for the caterpillar) or do not fly but hunt on foot.

## Trap Triggers

Among the ants we find herbivores as well as carnivores. Some specialized ants hunt extremely fast prey, e.g. springtails (collemboles) which catapult themselves out of danger within a few milli-seconds. In order to catch such fast prey the predator has to be faster.

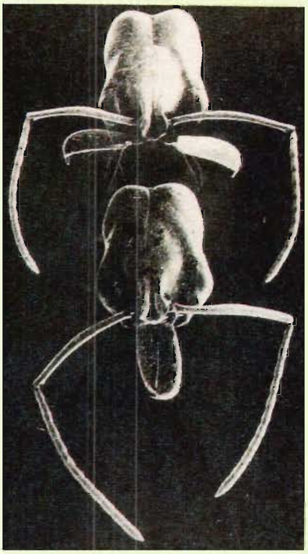
The neotropical ant *Odontomachus bauri* has mandibles, which close as soon as a collembole touches one of the four hair recep-

## Suggested Reading

[1] J Tautz and H Markl, Caterpillars detect flying wasps by hairs sensitive to airborne vibration, *Behav. Ecol. Sociobiol.*, 4, 101–110, 1978.

[2] J Tautz and K Fiedler, Mechanoreceptive properties of caterpillar hairs involved in mediation of butterfly-ant symbioses, *Naturwissenschaften*, 79, 561–563, 1992.

[3] W Gronenberg, J Tautz and B Hölldobler, Fast trap-jaws and giant neurons in the ant *Odontomachus*, *Science*, 262, 561-563, 1993.



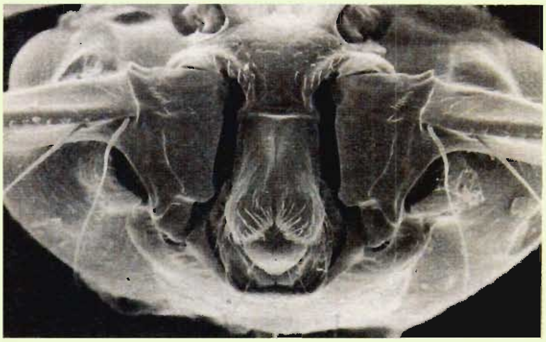
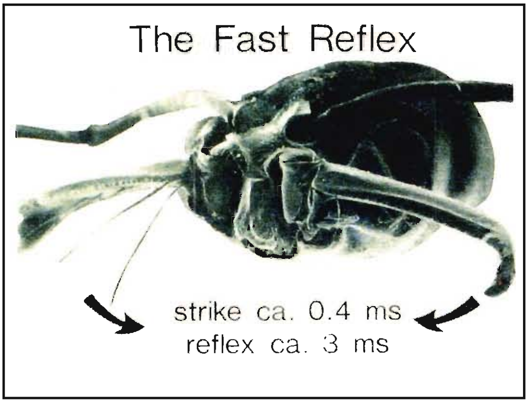


*Figure 6a (left). Dorsal view of the head of the neotropical ant Odontomachus bauri with mandibles opened and closed. Figure 6b (right) Frontal view of the mouth region of Odontomachus bauri looking onto the bases of the wide opened mandibles and the two long sensory hairs located on each mandible. (Photos by W Gronenberg).*

tors on the mandible (*Figure* 6a, b). A detailed analysis of the mandible-movement using high-speed film-recordings and of the mandible closing reflex using electro-physiological techniques revealed two 'world records': the complete closing of the mandibles from the time the hair receptor is touched, takes about 3 milli-seconds. The strike movement lasts less than 0.4 milli-seconds (*Figure* 7). Such a high speed can only be achieved by processes which save time maximally in each step from touching the hairs on the mandibles to the closure of the mandibles. The dendrites of the neurons in the central nervous system of the ant are extremely thick and are among the largest found in any animal (*Figure* 8). Such a morphology guarantees a very fast transmission of the action potentials produced as a response to a contact with the prey. Further time saving is achieved by the presence of electrical synapses between sensory cells, motor neurons and the muscles.

*Figure 7: The head of Odontomachus bauri with mandibles wide open. Touching one of the 4 sensory hairs on the mandibles leads to an extremely rapid closure of the mandibles. (Figure by W Gronenberg).*



## Combination Locks

Certain ant species and caterpillars of lycaenid butterflies are engaged in a symbiotic interaction. The ants guard the caterpillars against predatory beetles, spiders etc., and the caterpillars in turn offer the ants a nutritious secretion from a special unpaired gland located on the back of the caterpillar (*Figure* 9a, b, c). This gland, the dorsal nectar organ (DNO) is surrounded by mechanosensory hairs of different shapes (*Figure* 10). The DNO is closed most of the time. In order to open it up and release a droplet of the secretion the ants have to touch these hairs around the DNO in a certain temporal pattern. This tactile pattern must be applied with high precision by the ants and must be coded reliably by the sensory cells. Spiders or beetles simply walking over these hairs do not elicit the DNO-opening. Small ants (like *Lasius* spp., *Figure* 9b) are as successful in eliciting the opening of the DNO as large ones (like *Oecophylla* spp., *Figure* 9c). At first glance this is astonishing as such different-sized ants apply different pressures onto the sensory hairs and different pressures would result in different temporal patterns of the action potentials produced by the sensory cells.

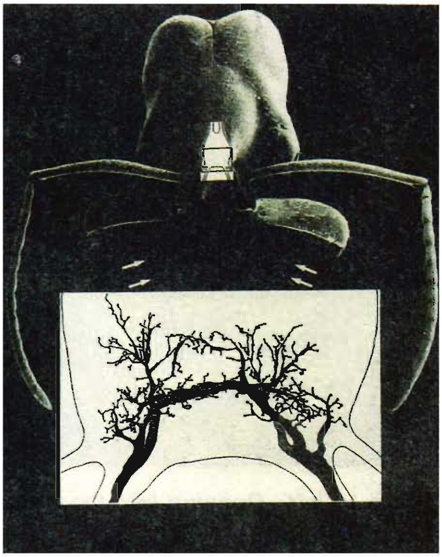


*Figure 8. Each of the four trigger hairs on the mandibles is innervated by one sensory neuron. The central projections into the sub-oesophageal ganglion of the ant (shown schematically) are among the largest known in the animal kingdom.(Figure by W Gronenberg)*

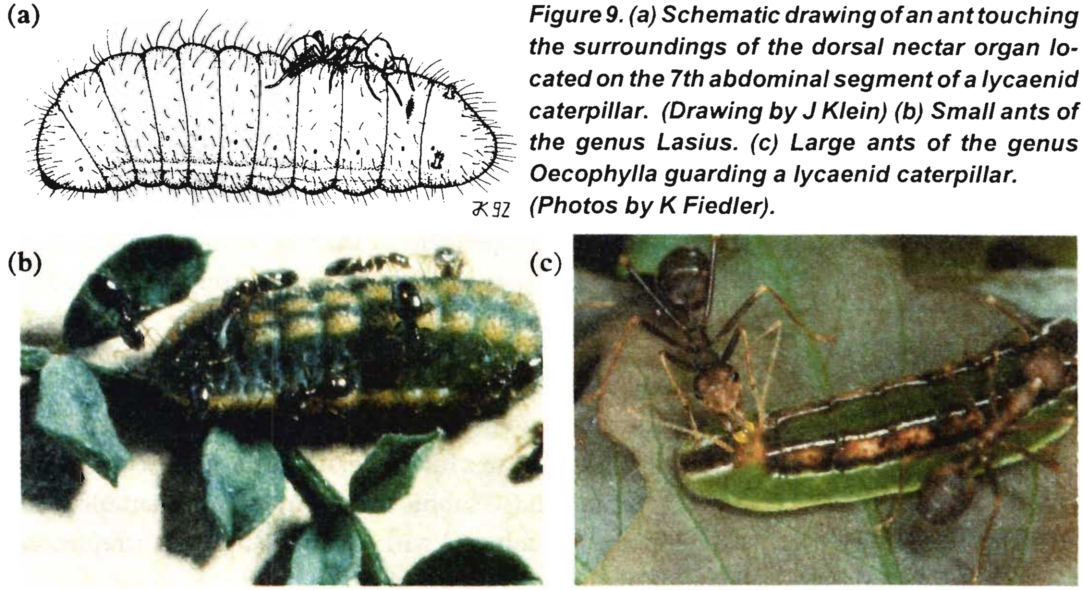
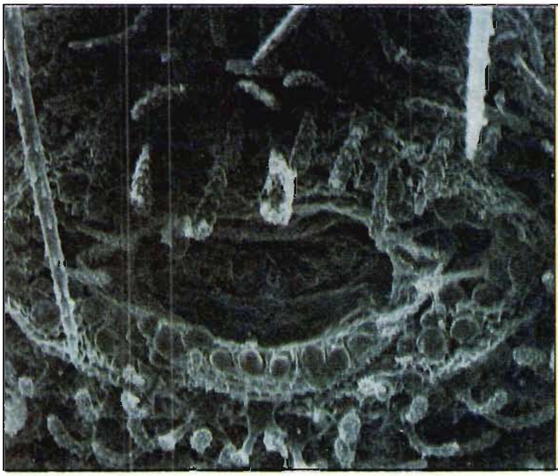


*Figure 9. (a) Schematic drawing of an ant touching the surroundings of the dorsal nectar organ located on the 7th abdominal segment of a lycaenid caterpillar. (Drawing by J Klein) (b) Small ants of the genus Lasius. (c) Large ants of the genus Oecophylla guarding a lycaenid caterpillar. (Photos by K Fiedler).*



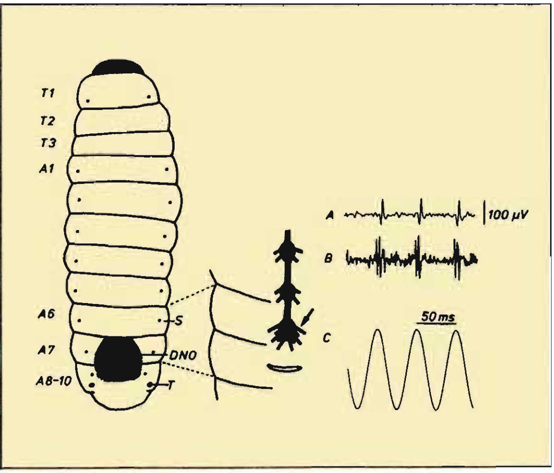


*Figure 10(left). Opening into the dorsal nectar organ surrounded by mechano-sensory hairs of different shapes.*

*Figure 11(right). Caterpillar of a lycaenid butterfly (Polyommatus icarus) with DNO and the field of mechano-sensory hairs around it (dotted area). Recording of the electrical activity of the sensory neurons from an afferent nerve (center) reveals just one action potential (A) per tactile stimulus irrespective of its strength (C), or two (B), if two hairs are touched at once.*

Thus the same tactile stimuli could lead to different patterns of electrical excitation in the central nervous system of the caterpillars and thus result in ambiguous signals. However, the time code produced by the sensory cells must be unambiguous and must reflect reliably the tactile stimulus pattern exerted by the ants. The solution to this problem is found throughout evolution in the modification of the physiology of these specialized sensory cells: each contact with the hair receptors leads to only one action potential irrespective of the intensity or pressure of the contact (i.e independent of the size of the ant – *Figure* 11). Thus the tactile contact pattern is precisely conserved and transmitted to the central nervous system of the caterpillar.

The number of fascinating examples of the astonishing solutions nature offers to relevant problems is endless. We only have a chance to get close to a full understanding of these phenomena if we combine most sophisticated frontline technologies in studying the 'machinery' with classical and still irreplaceable good old naturalistic approaches.

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