One of the Crowd

The Amazing Biology of the Desert Locust

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The Amazing Biology of the Desert Locust

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Further information

Sample references: A behavioural analysis of phase change in the desert locust. Simpson *et al Biol Rev* (1999) 74 461-480. Spatial scales of desert locus gregarization. Collett et al. *PNAS* (1998) 95 13052-13055. Exploitation of gut bacteria in the locust. Dillon *et al Nature* (2000) 403 851. Processing of gustatory information by spiking local interneurones in the locust. Newland, P.L. *J Neurophysiol.* (2000) 82 3149-3159.

Simpson S J *et al.* (2001) Gregarious behaviour in desert locusts is evoked by touching their back legs. *PNAS* 98 3895-3897.

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//www.bbsrc.ac.uk/life

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Source of animals

Locusts used in experiments are bred and reared under carefully controlled conditions to maintain their health and welfare.

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Summer 2001

Research and the locust

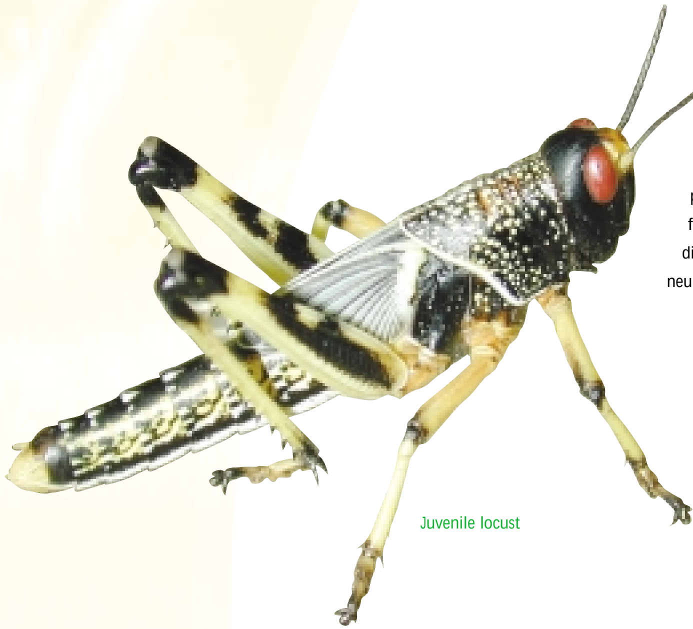
This booklet gives some examples that show how genotype, biochemistry, physiology and environmental factors interact to influence the behaviour of locusts.

The desert locust *(Shistocerca gregaria)* is an amazing animal. Notorious as a swarming pest with a voracious appetite, that can devastate crops in around 60 countries of the world, the desert locust typically spends most of its life, of up to about 5 months, as a shy and solitary individual that carefully balances its nutritional intake to match its body's needs. This booklet outlines some of the biological processes by which locusts survive in some of the world's most hostile environments.

Scientists study locusts for four main reasons:

- to understand the underlying mechanisms of locust-specific behaviours such as the transition from non-swarming to swarming forms, and how locusts communicate with each other;
- to identify targets for improved control of locusts, for example, by preventing or dispersing swarms and to identify better ways of predicting swarms so that controls can be introduced earlier and so be more effective;
- to use the nervous system of the locust as a model to understand the basic cellular and physiological processes that drive behaviour in insects, and other more complex animals including mammals;
- and to use the locust gut microbiota (microorganisms living in the gut) as a model for the study of animal-microbe interactions in general, and microbial transformation of plant secondary compounds in insect guts in particular.

A clearer picture is emerging of how locusts gain information about their environment, and about how they use and respond to it. This is becoming possible because of the integration of findings from several distinct scientific disciplines - animal behaviour, biochemistry, neurophysiology and computer modelling.

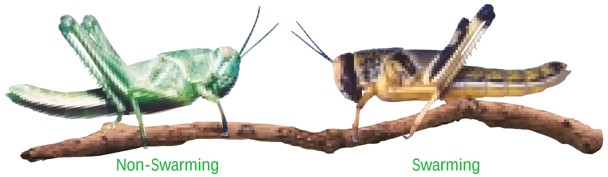


Juvenile locust

Swarm formation

Phase change

In their non-swarming (solitarious) phase, locusts are shy animals that will actively avoid each other if possible. But if they are crowded together for only an hour or two they switch to gregarious behaviour and begin actively to aggregate. This change in behaviour, called gregarisation, can be triggered in the laboratory by crowding locusts together. In the wild it most typically happens when individuals crowd together to compete for dwindling food supplies after a period of abundance during which locust numbers had risen (see page 5).



Non-Swarming juvenile locust

Swarming juvenile locust

As well as a change in behaviour, the switch from solitarious to gregarious phase also results in a change in the appearance of immature locusts. During their development, immature, wingless locust nymphs undergo several moults. Gregarious locusts moult 5 times; and solitarious ones moult 6 times. Gregarisation results in a change at the next moult from the green solitarious form to the multi-coloured gregarious form.

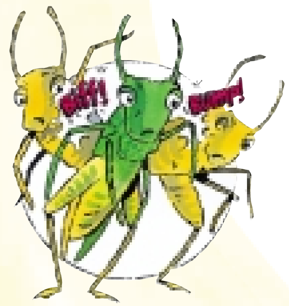
The multi-coloured pattern of the gregarious form makes it difficult for predators to identify individuals in the swarm, and probably also has a “warning” role. In contrast, the green colouration of the solitarious form serves to conceal the locust in vegetation. Research in Mauritania, by scientists of the University of Oxford, shows that lizards learn to avoid the multi-coloured form when made sick after eating a locust with a gut full of toxic plant material, but they cannot learn to avoid green-form locusts even if made just as sick by eating one with a gut full of toxic plant. It also seems that locusts begin to feed preferentially on poisonous plants when they begin to gregarise.

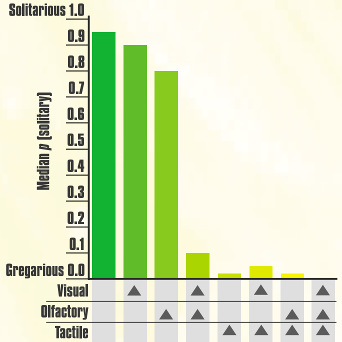
Just as forced crowding triggers gregarious behaviour in previously isolated individuals, so removal from a crowd triggers an individual to switch to solitarious behaviour, although this is a two phase change and so not a simple reversal.

The rate of change in behaviour from one form to the other depends on the length of exposure to either the solitary or crowded state.

Locust swarms can comprise billions of individuals and can cover several hundred square kilometres. Swarms can travel up to 130km or more in a day.

In experiments, solitarious locusts are housed individually in cages under controlled conditions in which they neither see nor smell other individuals.





The effect of a 4-hour period of stimulation on the phase state of solitarious locust nymphs. Locusts were subjected to the sight of other locusts, the smell of other locusts or being buffeted with small balls of papier mâché (to simulate contact with others). A value of 1.0 for Median p (solitary) indicates that the nymphs were behaving solitariously (hence unaffected by the treatment), while a value of 0.0 would indicate a complete shift to the gregarious state. Note how tactile stimuli were the most powerful gregarising influence, and that visual and odour stimuli together but not singly were also effective.

The power of touch

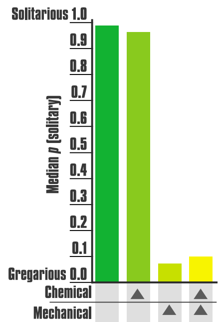
Experiments at the University of Oxford have been designed to identify whether it is the sight, smell or contact with others - or a combination of these - that causes the phase change.

Results show that touch alone is the major stimulus - and it does not even have to be the touch of another locust, buffeting with small balls of papier mâché is sufficient to trigger gregarising behaviour. Touch is the only sense that is effective on its own.

Sight of other locusts is ineffective on its own, as is the smell of other locusts. However sight and smell together also cause solitarious locusts to become gregarious. Smell is important in keeping gregarised locusts together (see pages 8-9).

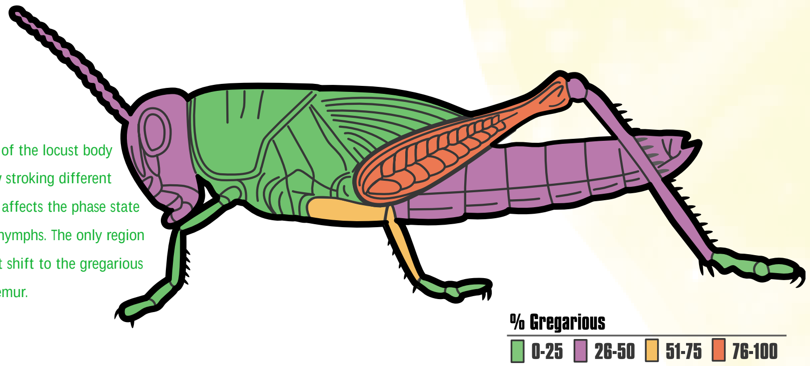
To rule out the possibility that the observed gregarising effect of bombardment with papier mâché balls might be due to inadvertent transfer of chemicals on the balls, scientists compared the effects of showering locusts with millet seeds and coating their roosting sites with extracts from locusts’ cuticle (“skin”). Only the former was effective in triggering gregarious behaviour, exposure to the chemical extracts had no effect.

The importance of touch could help to explain the observed phenomenon that solitarious individuals caught in a short violent rain storm can briefly become gregarious in their behaviour, presumably as a result of buffeting by the rain drops. In this case, as exposure to the gregarising stimulus is short, the animals quickly revert to solitarious behaviour.



Teasing apart the relative effects of contact chemical stimuli and touch. Locust nymphs were stimulated with chemical extracts of the cuticle of other locusts and/or by showering with millet seeds. Note how the latter but not the former caused solitarious locusts to gregarise.

The power of touch.
A colour-coded map of the locust body surface showing how stroking different regions with a brush affects the phase state of solitarious locust nymphs. The only region to cause a significant shift to the gregarious state was the hind femur.

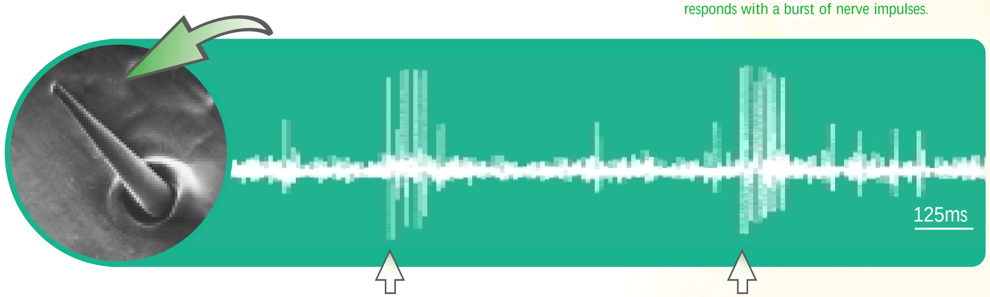


In the real world, of course, touch, sight and smell all act together. However touch is clearly the key trigger of swarming behaviour as locusts jostle and bump into each other.

Locusts have touch-sensitive receptors all over their bodies, but it turns out that it is those on the hind legs that are important in gregarisation.

Researchers at the University of Oxford stroked solitarious locusts for five seconds each minute for four hours on one of eleven body regions. Only stroking of the hind leg (femur) caused significant gregarisation.

Tactile stimulation is detected by a nerve cell at the base of each of the thousands of touch-sensitive receptors on the locusts' body, (see pages 10-11). When the hair-like receptor is deflected it activates the nerve cell which responds with a burst of nerve impulses.



The experimental procedures:

At the University of Oxford, the behaviour of locusts is observed and recorded using specially designed perspex chambers in which individual locusts can experience different stimuli. For example, an individual may be able to see others behind a transparent partition, but neither smell nor touch them. In another experiment individuals are buffeted by small balls of papier mâché, to simulate contact with others. In experiments, 4-hour periods of stimulation are given to locust nymphs.

The role of vegetation distribution

The environment influences locust behaviour either by congregating solitarious locusts that would otherwise avoid each other or by dispersing groups that would otherwise remain aggregated.

An obvious reason why solitarious locusts would be forced to come together, despite preferring to be alone, is to find food (see page 2). So the distribution and abundance of food in the environment is likely to drive phase change.

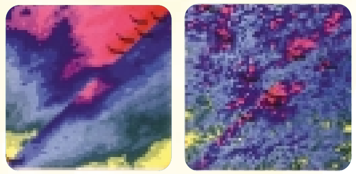
Scientists at the University of Oxford designed experiments in which solitarious locusts were placed into an arena with either a single clump of food or several smaller clumps. Locusts gregarised after 4 hours with a single food clump but remained solitarious when there were several clumps. In other words, when they could eat and keep apart from each other they stayed solitarious, but when they encountered each other around a single food source they became gregarious.

The Oxford scientists have constructed computer simulation models in which virtual locusts are programmed to behave like real locusts and allowed to interact within simulated worlds. Three key environmental variables are manipulated and their interactions explored. These are:

- The number of locusts
- The abundance of food
- The distribution of food patches

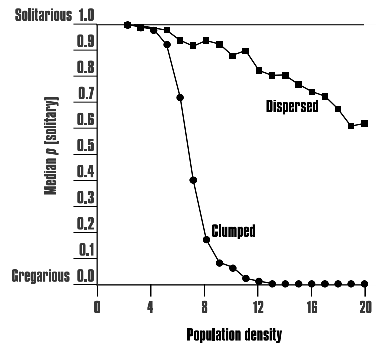
When food is clumped, only a small increase in the number of locusts triggers gregarious behaviour. In field trials, parents in conditions of clumped vegetation gave rise to hatchlings that were more gregariously behaved.

Results from laboratory experiments showing the effect of food distribution on gregarisation have been replicated under field conditions in Morocco (illustration) and Mauritania.



Resource concentrated   Resource dispersed

Computer simulations of environments in which food resource (pink) is concentrated or dispersed. When food is scattered, individuals can remain solitarious even at high levels of population.



The importance of resource distribution. Results of a simulation exploring the effect of the distribution of feeding sites and locust numbers on the likelihood that a local population of solitarious locusts will gregarise. The same total amount of food was present but feeding sites were either dispersed or clumped in their distribution. It is apparent that when food is clumped, only a small increase in locust numbers will cause the population to switch into the gregarious state and potentially seed a swarm.

Understanding the importance of fine-scale distribution of vegetation should improve our ability to predict locust swarms, for example, by combining data from geographic information systems with models of locust behaviour.

Maternal pheromones

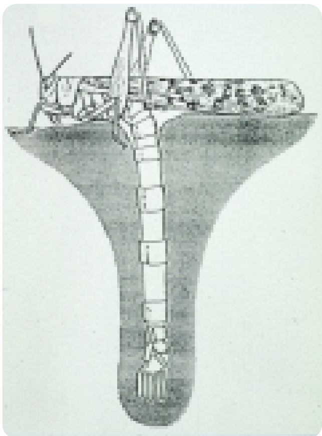
Research at the University of Oxford has shown how phase change from solitarious to gregarious behaviour can be transferred across generations. Adult females can influence the phase-state of their developing offspring. There is also a less pronounced paternal influence.

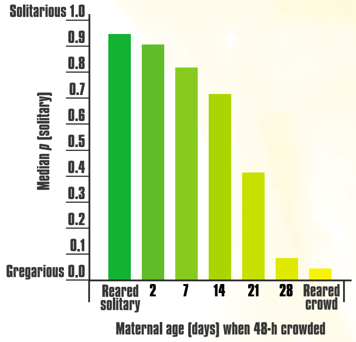
The scientists found that a solitarious mother causes her hatchlings to emerge from the egg in the gregarious state if she was recently crowded. The extent to which she gregarises her hatchlings was found to depend on how recently she has been crowded. If she is crowded at the time when she lays her eggs then she gregarises her developing hatchlings completely, but she gregarises them to a lesser degree the longer ago she was crowded.

A solitarious mother will also cause her hatchlings to emerge in the gregarious state if she mated with a gregarious male. This shows that she gains indirect evidence of population density from her mate during courtship and mating. How she does this is unknown.

Even crowding during the period between mating and egg-laying can induce a solitarious mother that had mated with a solitarious male to produce gregarious offspring. So the female can influence how her offspring develop at a very late stage in the reproductive cycle.

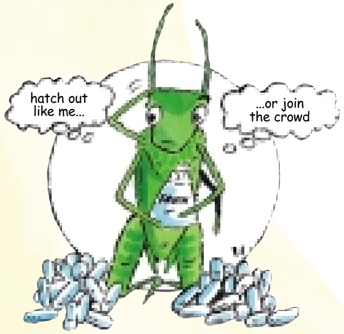
After mating, female locusts dig a hole in the ground and lay their eggs (typically 30-100) in a cylindrical pod. They surround the eggs with a frothy substance that is secreted by their accessory reproductive glands. This froth helps to protect the eggs by serving as a "plug". It also prevents them from drying out.



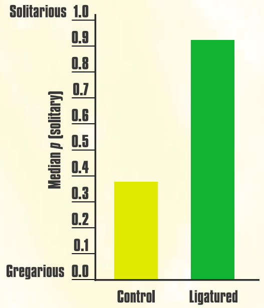


Mother knows best.
Graph showing the effect of how recently the mother was crowded on the phase state of her newly emerged offspring. A value of 1.0 for Median p (solitary) indicates that the offspring were behaving solitariously, while a value of 0.0 would indicate complete gregariousness.

In effect, the mother uses her own experience of crowding, and that of her mate, to predict the likelihood that her offspring will find themselves in a crowd and predisposes their behaviour accordingly. She gives her young a headstart in phase state.



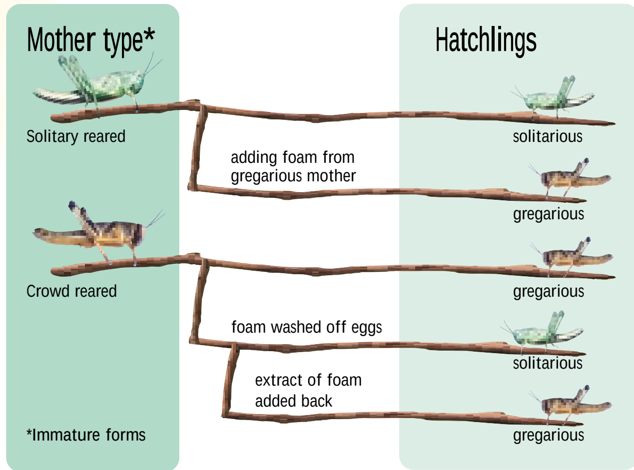
Researchers at Oxford investigated whether or not the froth or foam contains any pheromones - behaviour controlling chemicals - that influence whether the eggs hatch into solitarious or gregarious individuals. They found that while there is no evidence of a "solitarising" agent in the eggs of solitarious females, there is an agent in the foam produced by crowd-reared females that triggers eggs to hatch into gregarious individuals.



Tying off the accessory glands in a gregarious female (right) causes her eggs to hatch as solitarious rather than gregarious individuals (left).

The key evidence is:

- adding egg foam from a gregarious mother will gregarise the young from eggs laid by a solitarious mother
- washing the foam off gregarious eggs causes them to develop into solitarious young.



Analysis is underway to identify the active chemical agents in the foam. These may offer possibilities for patents and the development of novel control agents in the battle against locust swarms.

Keeping the swarm together

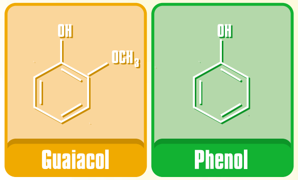
Once locusts have become gregarious and started to aggregate, it is important that the swarm stays together. Isolated, multi-coloured gregarious forms would be easily caught by natural predators such as spiders, birds and lizards.

Smell seems to be a key stimulus in keeping swarms together.

Researchers at the University of Bath have found that among the volatile chemicals given off by locust faeces are two, guaiacol and phenol, that have been implicated in a blend of chemicals that helps keep swarming locusts together - a cohesion pheromone.

The scientists explored the possible involvement of bacteria in the locust's gut in the production of guaiacol and phenol. They used a special sterile isolator system (see opposite) to establish a colony of germ-free locusts (i.e. locusts with no bacteria in their guts) which could then be compared with conventionally reared locusts.

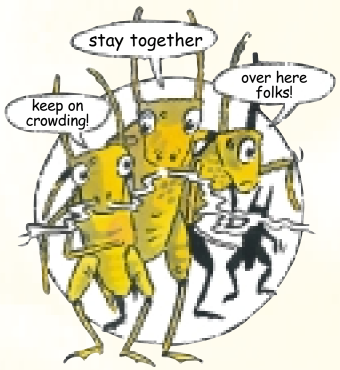
Pheromonal compounds

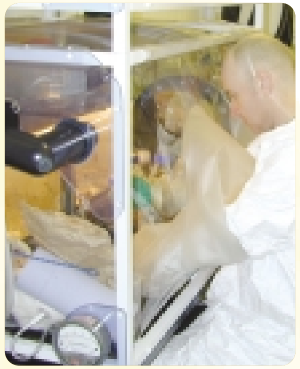


The dominant physiologically active compounds released from faecal pellets of 5th instar and adult locusts.

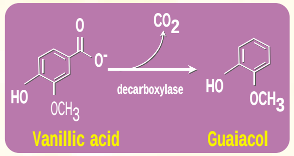
Gas chromatography is used to separate and identify the volatile compounds in extracts from locust faeces.

A scanning electron micrograph showing a mixture of bacteria, dominated by *P. agglomerans* on the surface of the hindgut of a locust.





The sterile isolator used to rear germ-free locusts. The animals are fed irradiated freeze-dried grass and bran.



Guaiacol is probably produced by decarboxylation of vanillic acid. Soil bacteria are known to use enzymes such as decarboxylases to break down lignin in plants.

The research at Bath found that faecal pellets from germ-free locusts smell different from those produced by locusts with a gut bacterial flora. The germ-free pellets smell like fresh hay, while normal faecal pellets smell like beer that has "gone off". Analysis shows that the difference in smell is due to the absence of guaiacol and low levels of phenol in volatiles released from the germ-free faecal pellets. Guaiacol and phenol in volatiles from faecal pellets of locusts have been associated with a single bacterial species *Pantoea agglomerans*, indicating a bacterial origin for guaiacol. Moreover, three species of locust gut bacteria (including *P. agglomerans*) produce guaiacol directly from germ-free faecal pellets in culture.

The most likely precursor for guaiacol synthesis is vanillic acid (4-hydroxy-3-methoxybenzoic acid) which is found in the faeces of germ-free and normal locusts. Three species of gut bacteria will produce guaiacol in culture when provided with vanillic acid. Furthermore, faeces from normal insects fed cellulose filter paper, impregnated with vanillic acid, gave large amounts of guaiacol (see table).

Volatile phenolic compounds released from locust faecal pellets

Treatment	Guaiacol ($\mu g\ g^{-1}\ 24h^{-1}$)	Phenol ($\mu g\ g^{-1}\ 24h^{-1}$)
Germ-free:		
5th instar	ND	0.5
Mature Adult	ND	0.3
Monoassociated:		
5th instar	6.4	4.3
Young adult (7 day)	1.0	2.0
Adult (14 day)	4.9	8.7
Mature adult	17.1	18.9
Conventional:		
5th instar, (wheat seedling diet)	44.5	10.7
5th instar, (irradiated grass diet)	4.9	13.1
Mature adult (wheat seedling diet)	10.6	12.3
5th instar, (filter paper + vanillic acid diet)	67.6	8.8
5th instar, (filter paper diet only)	13.9	4.5
Mature adult, (filter paper + vanillic acid diet)	38.5	1.4
Mature adult, (filter paper diet only)	2.6	0.7

ND - not detected. Compounds estimated per g dry weight of faecal pellets.

Locusts have adapted to use as pheromonal components chemicals derived from their digestive waste products by the action of bacteria taken in with the food. Synthesis of the major compound, guaiacol, starts in the hindgut and continues in the faeces from where it is released. Bacteria in dry faecal pellets will resume synthesis upon addition of water. A high concentration of guaiacol from hydrated faeces is an apt aggregation stimulus, as it signals optimal conditions (viz. presence of water) for plant growth and egg development that are both essential to the survival of the desert locust. This adaptation by an insect to exploit a common metabolite produced by indigenous gut bacteria has wide implications for our appreciation of the role of the gut microbiota in insects.

Taste, touch and decision-making

Taste is an important sense for all animals. Like humans, locusts can readily distinguish between what tastes good and what tastes bad.

The sense of taste in insects relies on contact chemoreception where a chemical is detected by the many taste receptors that cover the surface of their bodies. As befits their reputation as voracious feeders, locusts use taste to sense their environment, and the information they gain from this determines their behaviour.

Locusts use their sense of taste:
(a) to select food, on the basis of its chemical composition and their nutritional status
(b) to select egg laying sites, on the basis of the chemical composition of the soil
(c) to detect and move away from noxious chemicals.

This involves the locust in detecting a stimulus, converting this information into a series of nerve impulses which are transmitted to the central nervous system, and acting (deciding) on the information.

Taste and touch detection and conversion

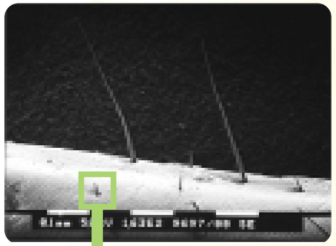
Locusts have sensors, called contact chemoreceptors, all over their bodies. These respond to both taste and touch. They are small "hair-like" structures, less than 0.1mm long, that occur in large numbers. Over 1,000 are found on each leg, and many thousands are present on the mouthparts.

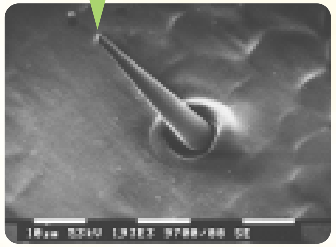
The chemoreceptors are articulated and can be moved by contact. At the tip is a small pore through which the locust detects chemicals. Inside the shaft of the hair are several sensory cells that detect chemicals. At the base of the receptor is another nerve cell that responds to touch.

Scientists at the Universities of Southampton and Oxford are using microelectrodes to record the electrical activity of locust nerve cells as they respond to different stimuli. Results show that, for example, deflecting the shaft of the receptor activates the sensory nerve cell that responds to touch to produce a burst of nerve impulses (see page 4). These nerve cells are sensitive to the direction of deflection and the velocity of the movement.

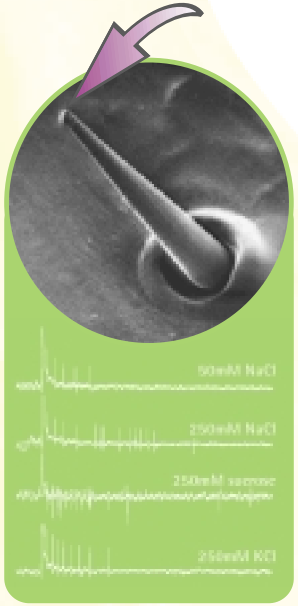
The mouthparts of a locust.

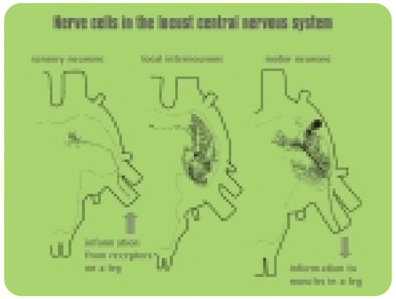
Scanning electron micrograph of tactile hairs and taste receptors on the hind leg of a locust.





High-powered micrograph of a taste receptor.





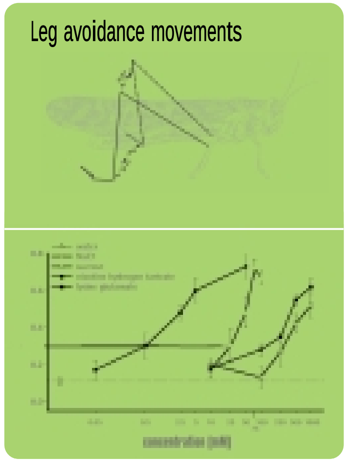
Chemicals applied to the tips of the chemoreceptors activate the nerve cells sensitive to chemicals. The pattern of nerve activity depends on the chemical. No one nerve cell detects only one chemical, but instead, the identity of a chemical is encoded in a pattern of activation of all chemosensory cells in the receptor. The greater the concentration of the chemical, the greater the nerve impulse frequency.

Decision-making

At the University of Southampton, researchers have analysed the behavioural responses of locusts to salts, proteins, carbohydrates and feeding deterrents applied to chemoreceptors on a leg. The responses elicited by these chemicals are avoidance movements, in which the locust rapidly moves a limb away from the stimulus.

They found that the probability of eliciting an avoidance response is dose-dependent with increasing concentration of a chemical, and that chemical identity determines the concentration "threshold" at which different chemicals became an effective stimulus. In experiments, all chemicals had the potential to evoke avoidance movements.

This means that for locusts, any chemical has the potential to be aversive and may be rejected by the animal if it is present at sufficient concentration.



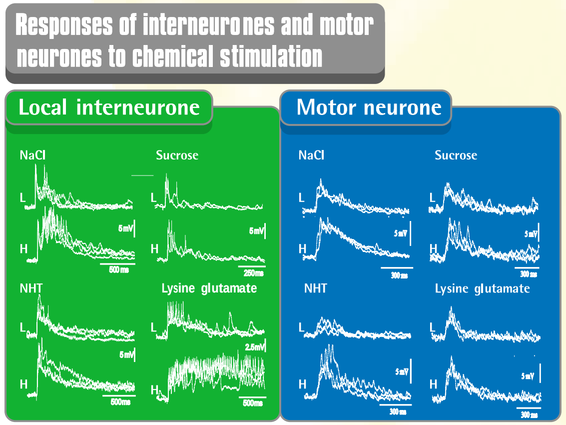
To understand how locusts accept or reject food, and avoid noxious chemicals, we need to know how the sensory codes are represented and transformed in the central nervous system.

Sensory cells from receptors on a leg convey information in their patterns of nerve impulses from the taste receptors to the central nervous system where it is collated by sets of interneurones with elaborate morphology that are entirely restricted to the central nervous system. These interneurones process the signals and pass on their codes to motor neurones that convey information back to a leg and activate sets of muscles.

Scientists at Southampton tested the responses of interneurones and motor neurones to salts, amino acids, carbohydrates and feeding deterrents applied to the chemoreceptors on a leg.

They find that all interneurones and motor neurones tested, respond to all test chemicals - nutrient and non-nutrient, and that the frequency of action potentials and duration of response are greater for higher concentrations of each chemical.

This suggests that chemosensory signals pass through the nervous system with little transformation. This means that information determined from the initial detection process (which is modulated by nutritional state - see below) is crucial to the final behaviour. The central nervous system converts the neural code into an action pattern determined by the initial concentration of a chemical. It adds context to the signals so that an avoidance movement is evoked only at times that are appropriate.

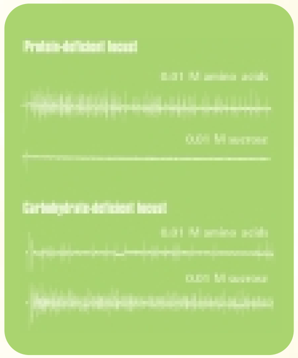


NHT – feeding deterrent   L - low concentration   H - high concentration

Scientists at the University of Oxford have found that locusts can make extraordinarily sophisticated nutritional decisions. The animals tightly regulate their intake of protein, carbohydrate and salt to an optimal "intake target" when challenged to do so in a range of experiments. For example, they will:

- eat five times as much of a food that is diluted five-fold with indigestible cellulose, to maintain nutrient intake
- select among foods according to (a) the nutritional composition and (b) the relative frequency of those foods in the environment, to attain the "intake target" amount of protein, carbohydrate and salt
- adjust their patterns of food selection according to their current nutritional state, compensating for previous nutrient deficits and excesses
- balance their intake of nutrients against the ingestion of toxins and other harmful compounds in food.

Taste in locusts is organised along a range of neural responses from suitable to aversive, in much the same way as in humans. Even high concentrations of single nutrients evoke large neural responses that cue avoidance.



Eating the right things: nutritional wisdom in locusts

Electrophysiological recordings from taste hairs on the maxillary palps of locusts fed for 4 hours on a food lacking either protein or carbohydrate. A single hair was stimulated with both 0.01 M amino acids (components of proteins) and 0.01 M sucrose (carbohydrate). Each trace shows the electrophysiological response over the first second of stimulation. Note how the taste receptors of the protein-deficient (but carbohydrate replete) locust were highly responsive to amino acids but did not respond to sucrose, whereas the reverse was the case for the carbohydrate-deprived, protein-replete locust. Hence locusts are most responsive to, and thus selectively feed upon, foods containing the nutrients they need. This mechanism provides a uniquely simple yet powerful means to direct feeding behaviour.

The amazing desert locust

The desert locust, *Shistocerca gregaria*, is one of about a dozen species of grasshoppers known as locusts which unlike other grasshoppers are able to change their behaviour in response to population density and to form swarms that can migrate over large distances.

Between plagues, desert locusts typically exist in an area that occupies a band across Africa south of the Sahara and in to India. The shy solitarious (non-swarming) adults tend to avoid each other except to mate, and fly mainly at night. At unpredictable intervals locust plagues occur, with swarms moving into neighbouring areas of Africa, Asia and Europe, and occasionally beyond. The gregarious (swarming) forms fly by day in swarms that can extend over hundreds of square kilometres and can contain hundreds of millions of insects per square kilometre.

Like most animals of its size, a locust eats roughly its own weight in food each day. This is true of both solitarious and gregarious forms. Swarms can consume hundreds of thousands of tonnes of vegetation per day.

In recent decades, locust swarms have been reported in many countries, including Mali, Mauritania, Kazakhstan, Uzbekistan, Russia and China.

One of the Crowd
The Amazing Biology of the Desert Locust