

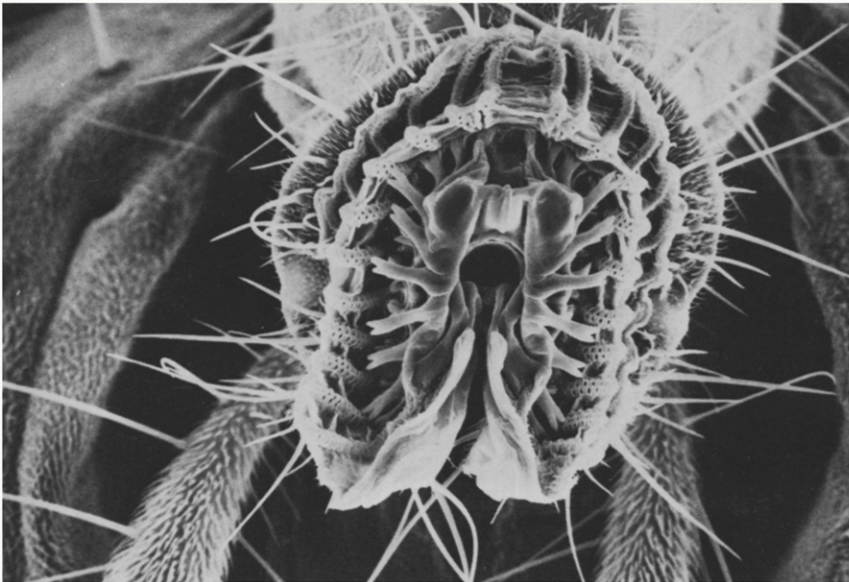
COMPREHENSIVE INSECT PHYSIOLOGY BIOCHEMISTRY AND PHARMACOLOGY

Executive Editors

G A KERKUT
L I GILBERT

Volume 4

REGULATION: DIGESTION,
NUTRITION, EXCRETION



PERGAMON PRESS

COMPREHENSIVE

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BIOCHEMISTRY AND
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Foreword

Aristotle was enchanted by the phenomenon of insect metamorphosis and the early microscopists such as Robert Hook, Marcello Malpighi, Anton van Leeuwenhoek, René de Réaumur and Pieter Lyonet were fascinated by the structure and function of the different parts of insects and made some of the first important contributions to our knowledge of insect physiology. More detailed functional studies were made by Borelli in his book “*De Motu Animalium*”, published in 1680, and his interpretation of insect walking patterns remained in our textbooks until 1955.

In general, the 18th and 19th century research workers were more concerned with the morphology and classification of insects, though physiologists such as Claude Bernard and naturalists such as John Lubbock and Henri Fabre were always interested in the functional analysis of insects.

One of the milestones in the study of insect physiology was the publication by Wigglesworth of his small book on insect physiology in 1934. This was stimulated by an appreciation of the way in which studies on the basic physiology of insects were necessary before one could understand and ultimately control the activity of insect pests of man and crops.

Wigglesworth initially studied medicine and then carried out research at the London School of Hygiene and Tropical Medicine. His innate gift for planning simple but fundamental experiments on *Rhodnius* led rapidly to an increase in our knowledge about moulting, the control of larval and adult stages, and provided the foundation for insect endocrinology. Furthermore he inspired a group of co-workers who later played a key role in the application of modern techniques to solve the problems of insect physiology and biochemistry.

Wigglesworth's “Insect Physiology” was followed by a more detailed and full-sized textbook, “Principles of Insect Physiology”, which was published in 1947 and is now in its 7th edition (1972).

The three-volume edition of “Physiology of Insecta”, a multi-authored work edited by Morris

Rockstein, was published in 1964 and a new edition in six volumes followed in 1973.

The study of insect biochemistry developed more slowly, partly because there was no special distinction between physiology and biochemistry; the investigator just used the methods available for his studies. David Keilin started his studies working on insects: “From 1919 onwards I had been actively engaged in the study of the anatomy of the respiratory system, respiratory adaptation and respiration of dipterous larvae and pupae. Among the vast amount of material I was investigating, special attention was given to the larvae of *Gasterophilus intestinalis*”. For these studies Keilin developed a method for the spectroscopic analysis of respiratory pigments of insect pupae under the microscope, which ultimately led to the discovery of the cytochromes.

The pteridines were discovered in insect pigments, and the one gene—one enzyme hypothesis of Beadle and Tatum, which was the cornerstone of molecular biology, was a result of biochemical and genetic analysis of *Drosophila*.

The rapid expansion of biochemistry after 1945 led to many more workers studying insect biochemistry and the first textbook on the subject by Darcy Gilmore was published in 1961. This was followed by the multi-authored “Biochemistry of Insects”, edited by Morris Rockstein, in 1978.

The first evidence that a steroid hormone acts at the level of the gene came from the studies of Clever and Karlson in the 1960s on the puffing by the polytene chromosomes of *Chironomus*.

Though insect physiologists and biochemists initially published their papers in journals such as *Biological Bulletin*, *Journal of Biological Chemistry*, *Biochemical Journal*, *Journal of Physiology*, *Journal of Experimental Zoology*, *Journal of Experimental Biology*, *Roux' Archiv für Entwicklungsmechanik*, and *Zeitschrift für vergleichende Physiologie*, the great expansion of insect physiology and biochemistry from 1945 onwards led to the establishment of journals and other periodicals specialising in insects, such as the *Journal of Insect Physiology*, *Insect Biochemistry*, *Annual Review of Entomology*, and *Advances in Insect Physiology*.

It is also fitting to mention the work of other pioneers in the study of insect physiology and biochemistry, such as Autrum, Bounhiol, Bodenstein, Butenandt, Chadwick, Dethier, Fraenkel, Fukuda, Joly, Lees, Karlson, Kopec, Piepho, Richards, Roeder, Berta Scharrer, Snodgrass and Williams; these and many others laid the foundations of the subject and all following research workers have stood on the shoulders of these giants.

In July 1980 a meeting was held at Pergamon Press in Oxford to discuss the possibility of publishing a series of volumes on insect physiology, biochemistry and pharmacology. The idea was to produce 12 volumes that would provide an up-to-date summary and orientation on the physiology, biochemistry, pharmacology, behaviour and control of insects that would be of value to research workers, teachers and students. The volumes should provide the reader with the classical background to the literature and include all the important basic material. In addition, special attention would be given to the literature from 1950 to the present day. Emphasis would be given to illustrations, graphs, EM pictures and tabular summaries of data.

We were asked to act as Executive Editors and by December 1980 we had produced a 27-page booklet giving details of the aims and objectives of the project, details of the proposed volumes and chapters, suggested plans within the chapters, abbreviations, preparation of diagrams and tables, and journal citations to ensure uniformity of presentation as far as possible. This booklet was sent to authors of the chapters and their comments invited. By the middle of 1981 most of the chapters had been assigned to authors and the project was under way. The details of the volumes and the chapters they contain are given on the following pages so that the reader can see the contents of each of the other volumes.

In addition, there is a final volume, Volume 13, which is the Index Volume. Although each volume will contain its own subject index, species index and author index, Volume 13 will contain the combined subject, species and author indexes for all 12 text volumes so that any material in these volumes can be rapidly located.

All references in the volumes are given with full titles of papers, journal, volume, and first and last

pages. The references to the authors in the text are given with their initials so that it is clear that the text refers to D. Smith and not, say, to A. Smith. There are more than 50,000 references to the literature, more than 10,000 species of insect referred to, and all should be readily found in the 12 different volumes.

There are 240 authors of the 200 chapters in the volumes and they have produced a series of very readable, up-to-date, and critical summaries of the literature. In addition, they have considered the problems associated with their subject, indicated the present state of the subject and suggested its developmental pathway over the next decade.

We are very grateful to our colleagues for the efficient way that they have met the challenge and the deadlines in spite of their many other commitments.

This series of volumes will be very useful to libraries, but an important case can be made that the books should be considered as research instruments. A set of volumes should also be available in the laboratory for constant reference. They will provide the research worker with an account of the literature and will always be instantly available for consultation. For this reason they should be considered as research equipment equally important as microscopes, oscilloscopes or spectrophotometers.

The volumes should save research workers many weeks of time each year in that not only will they provide an awareness of the literature and the background, and so save valuable research time, but the full index to authors, subject and species, and the full literature references, should also make it much easier to write reports and papers on their own new research work.

It is hoped that these volumes will do much to strengthen the case for insects as a source of research material, not only because insects are important medical and agricultural pests (over 200 million people at present have malaria: insects eat or destroy about 20% of planted food crops), but also because in many cases insects are the ideal unique research material for studying and solving fundamental biological problems.

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Preface to Volume 4

The previous volume (Volume 3) has dealt with some other aspects of regulation: the structure and physiology of the circulatory system; chemistry and physiology of the hemolymph; cellular elements in the hemolymph; nephrocytes and pericardial cells; structure and physiology of the respiratory system.

The biochemistry of digestion and metabolism is described in Volume 10 where there are chapters on intermediary metabolism; carbohydrate metabolism, lipid metabolism, lipid transport; amino acid and protein metabolism; nucleic acids.

The first seven chapters of this volume (Volume 4) are concerned with feeding and are: the regulation of feeding behaviour; feeding mechanisms; food consumption and utilization; structure of the digestive system; coordination of digestion; absorption; biochemistry of digestion (readers should note that there is a chapter on feeding behaviour in Volume 9).

Insect nutrition is described in terms of the substances that insects normally eat, and includes chemical analysis of foods, nutrient requirements of insects, insect growth factors, the role of symbiotes, and the use of artificial diets in bringing up insects under controlled and axenic conditions.

The structure and physiology of the excretory system is described together with chapters on nitrogenous excretion (uric acid, ammonia, urea, amino acids, tryptophan derivatives, pteridines) and water balance. There should have been a chapter on ionic osmoregulation but unfortunately the author was unable to complete the chapter on time.

The volume ends with chapters on thermoregulation and on the biochemistry of insect luminescence (the behavioural aspects of luminescence are described in courtship and mating behaviour in Volume 9).

Feeding and diet occupy much of the space in this volume and this is reasonable since insects consume an estimated 15–20% of all the world's planted crops. Many insects have a specialized larval feeding stage that usually occupies a different ecological niche to the adult and so does not compete for the adult's food stock.

The other chapters describe the means by which

insects maintain their water balance, nitrogen balance and temperature balance under a range of conditions. These involve regulation by hormonal and behavioural systems that are also described here.

The ability of insects to utilize a wide range of substances as food materials and to regulate their internal environment over a wide range of temperatures and humidity, are two of the key factors that have enabled insects to become the dominant ecological force that they have been from the Carboniferous Age (Figure 1) 250 million years ago, to the present day, when they are found from the Arctic to the Tropics; buried deep within the soil; teeming over the earth's surface; flying hundreds of feet up in the air: ubiquitous and victorious.

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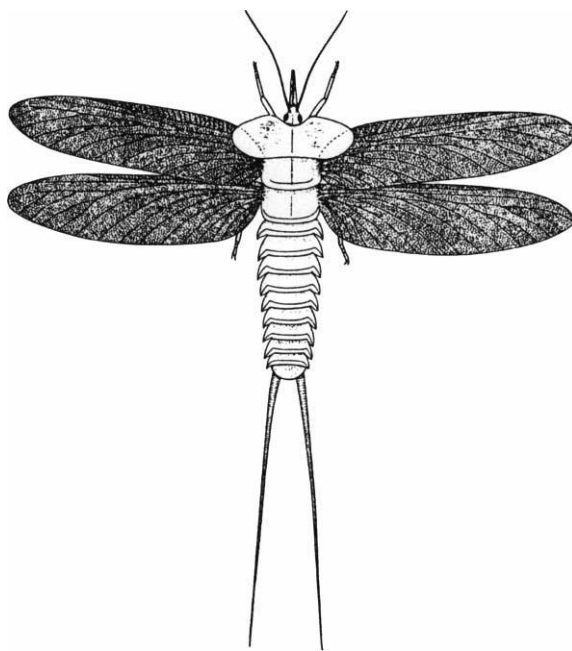


FIG. 1. Reconstruction of *Stenodictya lobata*, a representative of the Palaeodictyoptera found in the Carboniferous. (From *Basic Arthropod Stock* by A. G. Sharov, Pergamon Press, Oxford, 1966)

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1 Regulation of Feeding Behaviour

E. A. BERNAYS

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1 INITIATION OF INGESTION

Before ingestion begins insects must bring the head and mouthparts into a suitable position for feeding which enables them to monitor food quality critically. If the food is suitable, feeding follows. Although the steps in the behaviour pattern may occur rapidly and thus be difficult to distinguish, each step requires particular sensory inputs, often involving sensilla remote from the mouthparts, and the sequence may be interrupted by unsuitable stimulants at each stage.

A normal insect with continuous access to food does require some positive phagostimulation to initiate feeding.

The variety of ingestion mechanisms among insects is far greater than in any other class of animals, and as a result of this the preliminary aspects of feeding behaviour also vary between groups, the best-studied examples being among acridids and flies.

1.1 The early stages of feeding in chewing insects

The most detailed work has used locusts. Here

olfaction plays a major role in location of food, and tarsal chemoreceptors are involved in arresting movement prior to palpation. If the information from the large number of receptors at the tips of the labial and maxillary palps indicates that the food is acceptable, then the insect locates a suitable starting place. At this point additional information may be received by contact of outer labral receptors against the surface of the leaf. Only then does biting follow. The first bite is often very small but the leaf tissue is crushed and because of the hydrophilic nature of the inner surface of the mouthparts, fluid from within the leaf spreads over the various groups of chemoreceptors in the cibarial cavity. Work on these different aspects of the initiation of feeding is listed in Table 1.

The palpation which precedes biting in acridids is a rapid vibration of the maxillary and labial palps, which brings the sensilla at their tips into intermittent contact with the surface of the leaf. The information from up to 2000 sensilla determines whether or not head-lowering and biting follow. The terminal sensilla of the palps of *Locusta migratoria* respond to many different chemicals including sugars (Blaney, W. 1974) but Blaney, W. and Chapman, R. (1970) concluded that during the palpation phase of the initiation of feeding, they normally respond to long-chain components of the plant surface waxes.

Following the initial bite the sensilla on the inside of the clypeolabrum are stimulated by chemicals from the plant sap. These sensilla respond to a wide range of chemicals including phagostimulants and deterrents, the response varying in different species (for a full discussion see Bernays, E. and Chapman, R. 1978). In all orthopteroids very large numbers of

chemoreceptors are present in the cibarial cavity, mostly arranged in groups. See Chapman, R. (1982a) for a full reference list and a discussion of the significance of receptor numbers.

Ablation experiments suggest that all the major groups of chemoreceptors are involved in the regulation of ingestion, since in most cases their removal was shown to decrease amounts eaten (Haskell, P. and Mordue, A. 1969). However, studies involving cutting of nerves to these groups of sensilla showed that after an interval normal intake was often resumed (Louveaux, A. 1976). The insect can partly compensate for such loss of receptor input by changes in feeding behaviour. For instance, after palpectomy, greater use is made of the outer surface of the labrum in monitoring the food prior to ingestion (Sinoir, Y. 1969). A group of chemoreceptors near the tip of the labrum appear to be particularly important in monitoring the presence of feeding deterrents, and their ablation resulted in larger amounts of a previously unacceptable food being ingested. All the chemoreceptors tested neurophysiologically respond to many phagostimulants and deterrents and the system appears to be both complex and variable (Blaney, W. 1975, 1980). Very similar mouthparts and arrangements of sensilla in cockroaches and crickets suggest similar regulatory processes. Phagostimulation with liquids can result in ingestion without movement of the mouthparts. This indicates an ability to produce suction which could play a part in normal feeding by facilitating the spread of fluid over groups of chemoreceptors, or in the actual ingestion of very wet food.

Table 1: Table of references to work on acridid feeding behaviour, particularly the initiation of ingestion

Antennae	distance attraction	Kennedy, J. and Moorhouse, J. 1969
Tarsi	arrestment on food	Kendall, M. 1971
Palps	food monitoring and head lowering	Bernays, E. and Chapman, R. 1970 Blaney, W. and Chapman, R. 1970 Blaney, W. and Duckett, A. 1975 Mordue, A. 1974, 1979
	edge finding	
Labrum (outer)	test biting	Sinoir, Y. 1969
Cibarial receptors	feeding	Haskell, P. and Mordue, A. 1969 Haskell, P. and Schoonhoven, L. 1969 Cook, A. 1977a Sinoir, Y. 1970 Louveaux, A. 1976 Chapman, R. 1982b

Table 2: Numbers of chemoreceptors and receptor neurones on the mouthparts of some selected insects (from Chapman, R. 1982)

Insect	Sensilla	Neurones
<i>Locusta migratoria</i> 5th instar	2300	12,600
<i>Gryllus campestris</i> adult	6400	51,000
<i>Bombyx mori</i> larva	22	86
<i>Dysdercus koenigii</i>	20	80

The behavioural initiation of feeding has not been studied in detail in caterpillars, but it is assumed that it is broadly similar to that occurring in grasshoppers although the mouthparts and the number of sensilla are much reduced (Table 2) and the controlling chemoreceptor mechanisms simpler, being associated more with single chemicals. There are surprisingly simple correlations between impulse patterns from receptors and feeding activity, at least in the oligophagous *Pieris* spp. (Blom, F. 1978). Olfaction has been shown to play an important role in feeding (Dethier, V. 1937). Single chemosensilla or small groups of them occur on the antennae and mouthparts and their roles are described by Dethier, V. (1937), Ma, W. (1972) and Schoonhoven, L. (1968, 1973). As in acridids, phagostimulants are required to initiate and maintain feeding, but the process is achieved with relatively little sensory input: there are approximately 24 chemoreceptors on the mouthparts of caterpillars compared with nearly 2000 in a grasshopper of similar size (Chapman, R. 1982a).

Chewing insects other than phytophagous ones have been little studied.

1.2 Aspects of chemoreception

Chemoreception is of primary importance in initiating food intake. Phagostimulants are essential for feeding to start at all; while deterrents may inhibit feeding even in the presence of phagostimulants (see section 2.2). Certain chemicals may affect only some steps in the feeding sequence. In the larva of *Bombyx mori* β -sitosterol, isoquercitrin and morin induce biting but do not lead to ingestion when presented alone, and separate swallowing factors

were identified as cellulose, sugar, inositol, silica and potassium phosphate (Hamamura, Y. 1970). Maximum amounts of food are ingested only in the presence of both biting and swallowing factors. In acridids leaf surface chemicals, perceived by the palps, may stimulate biting but then play little part in continued feeding. However these categories cannot usually be distinguished, since many chemicals including sucrose stimulate all the chemoreceptor groups and thus elicit all the behavioural steps.

Acridid chemosensilla are responsive to a very wide range of chemicals and are not usually specialized for detecting particular compounds. Those which have been examined have neurones responding to all classes of chemical and may be termed generalists (Blaney, W. 1974, 1975). There are some compounds for which the deterrent threshold is extremely low, however, as with azadirachtin on palp and cibarial receptors of *Schistocerca gregaria* (Winstanley, C. and Blaney, W. 1978).

Lepidopteran larvae possess sensory neurones which are more or less specific for different types of chemicals such as water, glucose, fructose, salts and deterrents (Schoonhoven, L. 1973). In some cases a cell responding preferentially to particular phagostimulants may be present. The best-known example of such a cell is the glycoside receptor in *Pieris brassicae*, which responds particularly to glucosinolates from the cruciferous host plants. These compounds greatly enhance the amounts of a suboptimal diet (less than 0.2 M sucrose on filter paper) which is ingested (Schoonhoven, L. 1977) although they are only weakly stimulating when presented alone. Thus, the glucosinolates have been called incitants for *P. brassicae*, although it is possible that the effect is due to a synergistic action of the two chemicals at a central level.

Chemoreceptors start to adapt very quickly (see Morita, vol. 6) and some degree of adaptation will certainly have occurred before ingestion begins, but the discontinuous nature of the stimuli on different receptors when feeding on solid material probably minimizes adaptation, so that threshold levels are not reached. Its possible significance in determining meal length is discussed in section 3.

During the initiation of feeding on acceptable food "central excitation" is rapidly raised to a high level. The effect has been shown to be the result of

chemoreception (Dethier, V. *et al.*, 1965) and one of its functions may be to enhance the intensity of the feeding processes so that they will continue quickly and efficiently. Another function of a heightened excitatory state may be to increase the likelihood of relocating the food if contact with it is lost. To some extent it will also offset adaptation of the chemoreceptors, and its possible role in determining meal size is discussed in section 3.

Finally, the chemoreceptor input may influence the rate of feeding. Less acceptable foods are eaten more slowly, primarily due to pauses during the course of ingestion. Such pauses may be a direct effect of low palatability or of a reduced action of the chemoreceptor input in maintaining the excitatory state.

1.3 Fluid feeders

In order to ingest food the fly must first extend its proboscis. This generally occurs after phagostimulation of receptors remote from the mouthparts. Tarsal chemoreceptor hairs are normally involved at this stage. In *Phormia regina* there are about 250 chemoreceptors round the edge of the labellum which, if stimulated, also cause proboscis extension, but in the usual sequence of events their stimulation occurs after proboscis extension and results in spreading of the labellar lobes (Pollack, G. 1977). Details of the nature and specificity of tarsal and labellar chemoreceptors are summarized by Dethier, V. (1976). After spreading of the labellar lobes, an array of over 100 small chemoreceptor papillae (the interpseudotracheal papillae) can contact the substrate. Phagostimulation leads to the initiation and driving of sucking by the pharyngeal pump, while food quality is monitored by cibarial chemoreceptor sensilla, whose structure and distribution are described by Rice, M. (1973); Evans, D. and Barton Browne, L. (1960) review all the earlier work.

If the sensory input during ingestion declines below a certain threshold level, or if negative feedbacks lead to termination of the meal, the proboscis slowly retracts. If feeding deterrents are encountered, however, there may be fast retraction. The actions and control of the proboscis are described by Dethier, V. (1959), and van der Starre, H. and Ruigrok, T. (1980). The distribution and structure

of sensilla on the proboscis are reviewed by Dethier, V. (1976) and Chapman, R. (1982a) while the relationship between phagostimulant action on chemoreceptors and the consequent motor patterns has been demonstrated by Getting, P. (1971).

Stimulation of single chemoreceptors can elicit the appropriate behaviour patterns for each stage of feeding. For example, stimulation of one labellar receptor hair of *P. regina* with 0.4 M sucrose will result in proboscis extension. Stimulation of two receptors simultaneously with 0.06 M sucrose will have the same effect, while stimulation of the whole labellum with only 0.016 M sucrose is sufficient to cause extension (Arab, Y. 1959). Thus summation occurs and must normally be important. Also, stimulation of hairs on one side of the labellum causes extension to that side and the receptor fields may be represented centrally in spatially separate regions (Dethier, V. 1976).

If the fly is less "hungry" only a high frequency of impulses will cause feeding. The number or frequency of impulses required to produce proboscis extension for different deprivation states has received a lot of attention, and the work is fully reviewed by Barton Browne, L. (1975) and Dethier, V. (1976). Sensory adaptation occurs during feeding and it is more rapid with less stimulating materials. Within a second of stimulation with 1.0 M sucrose the impulse frequency is reduced by half, but reduction of impulse frequency for lower concentrations is much faster. At maximally stimulating concentrations, and in most natural situations, where the food source is chemically more complex, the role of adaptation in determining meal size is probably minimal (Thomson, A. and Holling, C. 1974) (and see section 3).

To some extent sensory adaptation may be offset by phagostimulants producing a state of arousal or a heightened "central excitatory state" which may last for over a minute and lower the behavioural threshold for responsiveness to less stimulating materials over this time (Dethier, V. *et al.*, 1965; Nelson, M. 1977). Proboscis extension following stimulation with water is more likely to occur if the same or other sensilla (for example on the tarsi) have been stimulated with sucrose. The effect lasts longer with increasing sucrose concentration. Thus, several chemosensory components play a role in the regulation of food intake by the fly.

The motor output causing sucking is a centrally generated rhythmic pattern, and mechanoreceptor inputs from the cibarium are necessary both to maintain continuity of rhythmicity of the motor output and to alter output as a function of load in various ways (see Dethier, V. 1976).

Within the blood-feeding insects there is a wide variety of feeding mechanisms and sensory receptor systems, each adapted to particular host characteristics. Details of mouthpart morphology are provided by Askew, R. (1971) and chemoreceptor groups reviewed by Chapman, R. (1982a). After host location there is a basic sequence of events during feeding which are common to most blood feeders: probing, piercing and penetrating the host surface, locating blood, ingesting blood and passing it into part or parts of the gut. Details of the behavioural sequences and their chemosensory control in a number of groups have been reviewed by Friend, W. and Smith, J. (1977) and Langley, P. (1976). A temperature gradient or differential is the major stimulus required to elicit probing in all blood feeders studied to date. Other factors which are known to affect probing and piercing include CO₂, visual, mechanical and chemical stimuli. Dietary composition, including the nature and concentrations of nucleotides, sugars and electrolytes, osmotic pressure and pH may determine whether ingestion and gorging occur. Receptors responding to temperature, water vapour and CO₂ have been described in various species (see Chapman, R. 1982a). Nucleotides are the major phagostimulants in the blood feeders, and receptors responding to them have been demonstrated in the tsetse fly *Glossina morsitans* (e.g. Mitchell, B. 1976), and assumed present in others.

In aphids and other hemipteroids there is also a distinct behavioural sequence leading to the initiation of feeding. For example, Klingauf, F. *et al.* (1971) showed that surface extracts of leaves induced probing attempts in *Acyrtosiphon pisum*, and Dagmar, J. (1979) showed that simple compounds occurring on leaf surfaces can cause more probing in *Aphis fabae*. Fier, D. and Beck, S. (1963) describe orientation and testing of the seed surface by *Oncopeltus fasciatus*. This insect distinctly places the area of labial receptors onto the surface of the seed before stylet penetration, and ethanolic extracts from the surface of milkweed seeds induce

penetration. Amino acids and starches were more important thereafter for influencing the continuation of sucking. Aphids ingest large amounts of fluid from the phloem sieve tubes and McLean, D. and Kinsey, M. (1968) found that *Acyrtosiphon pisum* fed for 22 hours out of 24. The rate of uptake is regulated according to apparent need as shown by Mittler, T. (1958) who found that *Tuberolachnus salignus* fed more slowly when the nitrogen level of the sap was high. Also it has been found that *Aphis fabae* feeds fastest when ants are in attendance (Banks, C. and Nixon, H. 1958). Practically nothing is known about the manner in which these regulatory mechanisms operate, and nothing is known concerning the action of chemoreceptors, or whether they adapt in such a continuously stimulating environment. Contact chemoreceptors are apparently absent on the labium and stylets of aphids so that monitoring of plant sap must occur by sampling into the food canal in the proximal mouthpart region to epipharyngeal receptors (the epipharyngeal organ) (Wensler, R. and Filshie, B. 1969; Tjallingii, W. 1980).

2 CONTINUATION OF FEEDING

Continued feeding generally depends on continued phagostimulation and an inadequate concentration of phagostimulants leads to early cessation of feeding (see Bernays, E. and Simpson, S. 1982; Barton Browne, L. 1975). This indicates that the pattern of feeding is not one which is simply switched on and then continues until repletion; it requires continued positive feedback, an important part of which is usually chemical feedback from the food. This is not true, however, of aquatic filter feeders which rely on mechanoreception to maintain the filtering mechanism, although phagostimulants do alter the rate of feeding by mosquito larvae (Dadd, R. 1970a); nor is it true in certain carnivorous insects where feeding may be independent of phagostimulants.

2.1 Phagostimulants

Sugars and, in particular, sucrose are the best-known and most-widespread phagostimulants. Bees, wasps, butterflies, moths and many Diptera, including blood-sucking species, feed on sugary solutions.

Table 3: The lowest stimulating concentration of various sugars to the blowfly *Phormia* (from Hassett, C. et al., 1950)

Sugar tested	Molar concentration at acceptance threshold	Sugar tested	Molar concentration at acceptance threshold
D-maltose	0.0043	Raffinose	0.200
D-fructose	0.0058	L-xylose	0.337
Sucrose	0.0098	D-xylose	0.440
Melezitose	0.064	D-galactose	0.500
L-fucose	0.087	L-arabinose	0.536
D-glucose	0.132	Cellobiose	5.01
L-sorbose	0.140	D-mannose	7.59
D-arabinose	0.144	D-ribose	8.99
Inositol	0.194	D-lyxose	42.27

In the fly *Phormia regina*, for example, maltose, fructose and sucrose are all very effective phagostimulants, while various other sugars initiate and maintain feeding but to a lesser extent (Table 3). Many studies of phytophagous insects including grasshoppers, beetles, caterpillars, aphids and

planthoppers have now been carried out and in all cases a range of sugars including sucrose stimulates feeding (Table 4). The effectiveness measured in different species, as the amount ingested in one meal or over an extended period, increases as the concentration increases up to a maximum above which

Table 4: Comparative stimulating effectiveness of different sugars for different phytophagous insects. + + + + + = highly stimulating, + weakly stimulating, - = no effect, . = not tested

	Locusts		Beetles		Caterpillars	
	<i>Locusta migratoria</i> ¹	<i>Schistocerca gregaria</i>	<i>Hypera postica</i> ³	<i>Leptinotarsa decemlineata</i> ^{3,4}	<i>Pieris brassicae</i> ⁵	<i>Spodoptera</i> spp. ⁶⁻⁸
<i>Pentoses</i>						
L-arabinose	+	.	.	-	-	-
L-rhamnose	-	-	.	-	-	-
D-ribose	-	-	.	-	-	.
D-xylose	-	-	.	-	-	-
<i>Hexoses</i>						
D-fructose	+++++	+++++	+++++	+	-	+++++
D-galactose	++	+	.	+	-	++
D-glucose	+++	++++	+	+	++	++
D-mannose	-	+	++	-	-	+
L-sorbose	+	+	.	-	-	-
<i>Disaccharides</i>						
D-cellobiose	-	+	.	-	-	-
D-lactose	+	+	.	-	-	+
D-maltose	+++++	++++	++	-	-	+++
D-melibiose	+++	+++	.	-	-	++
D-sucrose	+++++	+++++	+++++	+++++	+++++	+++++
D-trehalose	+	++	+	+	-	-
<i>Trisaccharides</i>						
D-melzitose	++++	+	+++	++	-	++
D-raffinose	++++	+++	.	-	-	+++
<i>Alcohols</i>						
inositol	+	.	.	-	-	-
sorbitol	+	+	.	-	-	-
mannitol	+	+	.	-	.	-

¹ Cook, A. 1977a; ² Dadd, R. 1960; ³ Hsiao, T. 1969a; ⁴ Hsiao, T. and Fraenkel, G. 1968; ⁵ Ma, W. 1972; ⁶ Ma, W. 1976; ⁷ Meisner, J. et al., 1972; ⁸ Khalifa, A. et al., 1974.

the amounts ingested may be reduced (Fig. 1 and see Dethier, V. 1976). The concentration causing maximum intake generally lies between 0.1 and 1.0 M. Moreover, in *Pieris brassicae* at least, there is a strong correlation between impulse frequencies from the sugar receptors and the amounts ingested (Blom, F. 1978). The comparative stimulating effectiveness of different sugars for six phytophagous insects is shown in Table 4. Interestingly, in *Oncopeltus fasciatus*, starches are more strongly stimulating than sucrose (Fier, D. and Beck, S. 1963).

Apart from sugars, in most phytophagous insects it is common for a selection of different nutrients normally present in the host plants to serve as phagostimulants. Among these are amino acids, although their effects vary with the species. Thus in acridids certain amino acids are weakly stimulating while in aphids *Oncopeltus fasciatus* and *Leptinotarsa decemlineata* a number of amino acids are strongly stimulating. The differences in response to amino acids by several phytophagous insects is shown in Table 5. Other nutrients which may stimulate feed-

ing include phospholipids, certain fatty acids and sterols, ascorbic acid and various salts (e.g. Cook, A. 1977b; Dadd, R. 1970b).

Combinations of nutrient chemicals used to test their phagostimulatory properties may cause different responses by the insect. With some combinations of amino acids the response is greater than the sum of the responses to each amino acid separately. In some instances an amino acid or secondary plant chemical stimulates feeding only in the presence of sucrose (Ma, W. 1972). In such cases where the behavioural response to two or more chemicals in terms of amount eaten is greater than the sum of the amounts eaten when the individual compounds are presented singly, then the chemicals are synergistic in their action (Dethier, V. and Kuch, J. 1971). In some cases the combinations are additive or less than additive (Bernays, E. and Chapman, R. 1978). Other examples of these effects are given by Dadd, R. (1970b).

For fluid feeders, water is commonly a phagostimulant, but this is a chemical in a special category, since it is universally required. Normally

Table 5: Comparative stimulating effectiveness of different amino acids on different phytophagous insects. ++ = stimulating, - = no effect, . = not tested, (+) = stimulating only in the presence of sucrose

	<i>Locusta migratoria</i> ¹	<i>Leptinotarsa decemlineata</i> ²	<i>Hypera postica</i> ³	<i>Pieris brassicae</i> ⁴	<i>Aphis fabae</i> ⁵	<i>Acyrtosiphon pisum</i> ⁶	<i>Oncopeltus fasciatus</i> ⁷
glycine	-	+	.	-	.	.	++
D-alanine	-	++
L-alanine	.	++	-	.	++	.	++
L-serine	+	++	-	-	++	.	+
γ -aminobutyric acid	-	++	-	-	.	.	+
L-valine	+	+	-	.	.	++	.
L-threonine	+	-	.	-	.	.	+
L-leucine	-	+	.	-	.	++	.
L-isoleucine	-	-	.	.	.	-	.
L-cysteine	-	+	.	.	-	.	.
L-cystine	-	-
L-methionine	-	-	.	(+)	++	++	++
L-aspartic acid	-	-
L-asparagine	-	+	.	.	.	-	.
L-glutamic acid	-	-	.	-	.	.	+
L-glutamine	-	-	.	-	.	.	.
L-lysine	-	-	.	-	.	-	.
L-arginine	-	-	.	.	.	-	+
L-histidine	.	-	.	-	++	-	+
L-phenylalanine	-	-	.	-	-	++	+
L-tyrosine	-	-	.	.	-	.	.
L-tryptophan	-	-	.	.	.	++	.
L-proline	+	++	-	(+)	++	.	.
L-hydroxyproline	.	+

1 Cook, A. 1977b; 2 Hsiao, T. and Fraenkel, G. 1968; 3 Hsiao, T. 1969a; 4 Ma, W. 1972; 5 Leckstein, P. and Llewellyn, M. 1974; 6 Srivastava, P. and Auclair, J. 1974; 7 Fier, D. and Beck, S. 1963.

Table 6: Stimulating effectiveness of adenine and some nucleotides for various insects which have been tested. ++ = highly stimulating, - = no effect, . = not tested

	Adenine	AMP	ADP	ATP	Other nucleotides	Reference
Phytophagous insects						
<i>Locusta migratoria</i>	-	-	-	-	.	1
<i>Schistocerca gregaria</i>	-	-	.	-	.	1
<i>Hypera postica</i> (L)	+++	+	+	+	+	2
<i>Sitona cylindricollis</i> (A)	+	+	.	+	-	3
<i>Leptinotarsa decemlineata</i> (L)	-	-	-	-	-	2
<i>Pieris brassicae</i> (L)	-	4
<i>Spodoptera exempta</i> (L)	++	+	+	+	-	5
Blood-sucking insects						
<i>Rhodnius prolixus</i>	-	+	+	++	+	6
<i>Culex pipiens</i> (A)	.	+	+	++	-	7
<i>Aedes aegypti</i> (A)	.	+	+	++	-	7
<i>Glossina austeni</i> (A)	-	+	+	++	-	8
<i>Xenopsylla cheopis</i> (A)	-	-	-	++	-	9
<i>Simulium venustum</i> (A)	.	+	++	+	.	10
Miscellaneous						
<i>Culex pipiens</i> (L)	-	-	-	+	.	11
<i>Musca domestica</i> (A)	.	-	-	-	+	12

A = Adult, L = Larva

1 Bernays, unpublished; 2 Hsiao, T. 1969b; 3 Beland, G. *et al.*, 1973; 4 Ma, W. 1972; 5 Ma, W. and Kubo, I. 1977 and Ma, W. 1977; 6 Friend, W. and Smith, J. 1972 and Huang Guo-Cheng 1981; 7 Hosoi, T. 1959; 8 Galun, R. and Margalit, J. 1969, 1970; 9 Galun, R. 1966; 10 Sutcliffe, J. and McIver, S. 1975, 1979; 11 Dadd, R. 1970a; 12 Robbins, W. *et al.*, 1965.

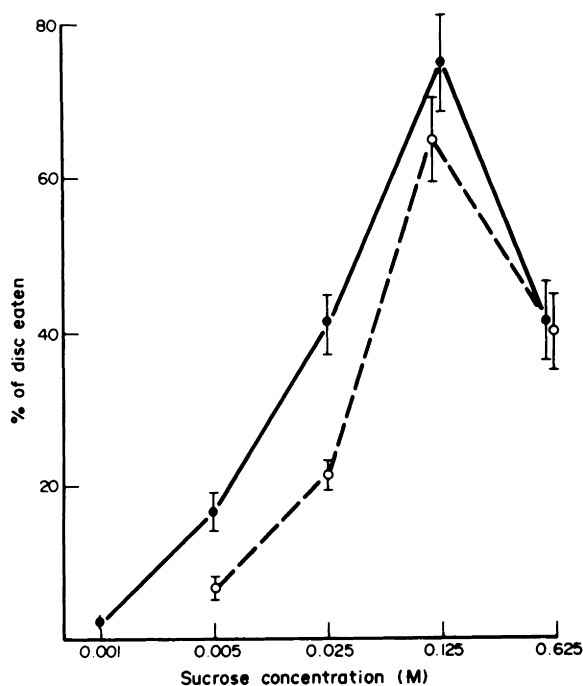


FIG. 1. Comparison between feeding levels on sucrose-impregnated pith discs determined over 18 h (●—●), and measured by meal size experiments (○—○) in nymphs of *Locusta migratoria*. Vertical lines represent standard errors. (After Cook, A. 1976.)

an adequate amount of water is ingested with the food but the case of desiccating conditions when it becomes a drinking stimulus is discussed in section 5.3.

Chemicals have sometimes been shown to be phagostimulants even though they are neither required nor utilized. A well-known example is the sugar fucose, which is strongly stimulating to flies and causes increased feeding yet is not used metabolically (Hassett, C. *et al.*, 1950). However, the significance of this is not known, since fucose is probably rarely encountered by a fly in the course of its normal activity.

Non-nutrient materials which are specific to the host plants stimulate feeding in some oligophagous species, and appear to function as sign stimuli indicating suitable food. For example a number of species feed on cruciferous plants containing glucosinolates: such compounds are commonly phagostimulants for these insects and increase food intake (see Schoonhoven, L. 1981 for a discussion). Thus a number of examples of oligophagy or monophagy among phytophagous insects appear to depend partly on the stimulating properties of some secondary plant compounds which are of chemotaxonomic significance. In polyphagous species such as the desert locust *Schistocerca*

gregaria, many secondary plant chemicals of no known value to the insect enhance food intake, but the interpretation of this can only be speculative (Chapman, R. and Bernays, E. 1977).

Although many blood-sucking insects feed on sugar solutions and sucrose is a phagostimulant, levels which occur normally in the host blood do not approach the sensory threshold. Such insects are commonly stimulated to gorge by the presence of certain nucleotides such as ATP (Table 6), but they may not always encounter optimal concentrations. Thus it is possible that food intake may be limited by low levels of such chemicals, although this is unlikely to be a major reason for the occasional ingestion of small meals, since the host is chosen before probing and the nucleotides will inevitably be present in the blood, and will stimulate continuous ingestion after the choice is made (Hocking, B. 1971).

Although many different compounds can stimulate feeding, usually only a few provide the major phagostimulatory input. The relative importance of the different phagostimulants clearly varies with the species. Among most phytophagous insects, sucrose and in some cases fructose are by far the most important materials, even though optimal food intake may require some other particular chemicals or a complex of them. The same is true for flies except when they exhibit a "protein hunger" associated with reproduction (see section 5.2).

Studies with artificial diets have shown that the balance of nutrients often affects the growth and development of insects. In most cases, however, natural foods and normal food selection behaviour ensure that the balance of nutrients is appropriate and only in a few groups of phytophagous insects is there any suggestion that balance *per se* is important in governing food intake (see House, H. 1965, 1971). In aphids much emphasis has been placed on the importance of the balance of nutrients. There is no doubt that selection and performance are greatly affected by imbalance (Mittler, T. 1972) but the evidence for its action on growth via regulation of natural food intake is scanty.

Specific requirements for individual nutrients or classes of compound, resulting from deprivation on the one hand or specific needs on the other, may affect feeding activity in some insects. Such specific effects are discussed in section 5.

2.2 Feeding deterrents

Evidence is accumulating that within the possible range of foods available to phytophagous insects in particular, deterrent chemicals play a large part in determining both the initial choice made and the amounts eaten (see Schoonhoven, L. 1982 for a recent review). There is a very wide range of secondary metabolites in plants which deter feeding in various insects. These chemicals include amines, alkaloids, terpenoids, phenolics and numerous types of glycosides. The deterrent effects are concentration-dependent, and may completely prevent feeding when concentrations are high. Oligophagous and monophagous species are more sensitive to the presence of deterrent compounds than are polyphagous species and the majority of non-host plants, or those eaten in small amounts, contain chemicals which are feeding deterrents (Jermy, T. 1961).

A relatively simple case is that of *Locusta migratoria* which is graminivorous: its restriction to grasses is determined by a wide range of feeding deterrents. Plants such as seedling grasses, which are eaten in small amounts, contain deterrent compounds which reduce the amount eaten (Bernays, E. and Chapman, R. 1976). The same is probably true of other graminivorous grasshoppers. Amongst polyphagous grasshoppers such as *Schistocerca gregaria*, there are many phagostimulants which tend to increase amounts ingested. Here too, however, deterrents play an important part, particularly in plants which are only eaten to a very small extent (Chapman, R. and Bernays, E. 1977).

The balance of phagostimulants and deterrents is probably the final determinant of the palatability of a material. In acridids it has been shown that low levels of deterrents will be ignored if the level of phagostimulants is very high (Fig. 2). In flea beetles which feed on Cruciferae, the amounts eaten depend largely on the combinations and amounts of phagostimulatory and deterrent secondary chemicals including various glucosinolates and flavonoids (Nielsen, J. 1978a,b). Other examples are known from the Lepidoptera (see Schoonhoven, L. 1973). Moreover Blom, F. (1978) has shown that the amount eaten is a reflection of the balance of inputs from sugar and glucoside receptors (phagostimulants) on the one hand and the

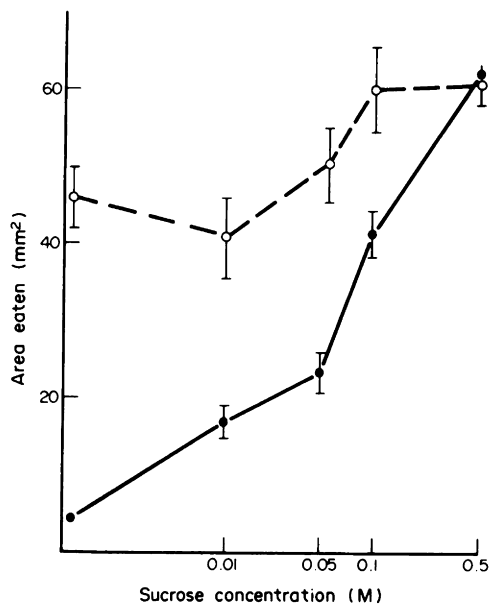


FIG. 2. The effect of different concentrations of sucrose on the amounts of wheat-flour water eaten, with 0.1% dry weight tomatine (●—●) or without tomatine (○—○). Vertical lines represent standard errors. (After Bernays, E. and Chapman, R. 1978.)

deterrent receptor (deterrents) on the other, in *Pieris brassicae* larvae.

2.3 Physical factors

Food intake is also regulated by the physical nature of the food. Hardness and toughness are parameters of the food which are of particular relevance to phytophagous and wood-boring insects. There are examples in a variety of species where hardness has been shown either to reduce feeding or to increase the time taken to ingest a given amount of food (e.g. Williams, L. 1954). Seed feeders may be unable to feed on particular seeds or they may eat less of the harder specimens (Smith, C. 1973). Other examples for certain crop pests are given by Beck, S. (1965). The effect of hardness may not necessarily be simply a matter of reduced food intake, but may involve other disadvantages such as inadequate nutrient intake for the effort required in ingestion. This, however, is difficult to separate from nutrient deficiencies related to an increased proportion of fibre.

In some situations where physical factors may be limiting, ingestion of food is affected by the presence of other insects. The larvae of the sawfly

Neodiprion pratti feed on certain pine trees, but when they hatch they have difficulty cutting into the tough cuticle. If one succeeds, the smell attracts others, which thereafter are able to feed in a group (Ghent, A. 1960). Similarly, a group of young sheep blowfly maggots is required to penetrate the skin of the sheep and create a lesion for feeding (Norris, K. 1959).

Physical form can also affect the ease of food intake, and the amounts ingested. Thus particle size affects ingestion rate in filter feeders such as certain mosquito larvae (Dadd, R. 1971). In phytophagous chewing insects, leaf shape may have an effect, since some of these insects prefer or require an edge and rolled leaves make feeding difficult (Bernays, E. and Chapman, R. 1970).

Many minor physical factors may affect food intake, but where insects are adapted for particular diets, physical factors play a minor role. Thus grasshoppers which are graminivorous have mandibular structures adapted for dealing with this hard material, and it is unlikely that the food intake is regulated by this alone. On the other hand, grasshoppers not specifically adapted for grass feeding are more commonly affected by hardness (Mulkern, G. 1967). In some situations physical features of the host, such as hairiness, have an indirect effect by interfering with behaviour prior to feeding. Such phenomena are reviewed by Chapman, R. (1977).

In the case of fluid feeders, viscosity can reduce food intake. For example the rate of feeding on high concentrations of sugars by flies is relatively low due to the high viscosity (Dethier, V. *et al.*, 1956). Insects which make use of host fluids under pressure may be affected by changes in the pressure of such fluids. For example, mosquitoes which insert their stylets into the capillaries of their vertebrate hosts feed faster than those which feed from small local haemorrhages which they cause in the host tissues. The same individual may feed in either manner, but larger meals are often ingested if feeding is directly from a capillary (Clements, A. 1963). Other physical factors influencing probing and ingestion in blood-feeding insects are temperature gradients, humidity, the thickness and texture and hairiness of the host skin, the osmotic pressure and pH of the food medium and host tissues (Friend, W. 1978; Friend, W. and Smith, J. 1977).

2.4 The balance of inputs

During feeding the central nervous system of the insect receives information from what may be a large number of sensilla, each containing a number of physiologically different receptor cells. The nature of this information is potentially extremely complex. The spectrum of responses of different sensilla and of individual receptors can vary considerably from those which respond to a wide range of stimuli to others which are extremely specific. Such highly specific chemoreceptors and their central connections have been termed "labelled lines". In addition, sensitivity to a single stimulus may vary both between similar receptors, and in an individual receptor with time. In some insects there is a basal firing rate or "noise level" in unstimulated cells, which also varies. In such cases a chemical stimulus may result in either an increase or a decrease in the basal firing rate, the same stimulus having opposite effects in different receptors. Further, differences in the latencies and rates of adaptation of receptors provide more potential information to the central nervous system.

Ultimately, the central nervous system integrates incoming information with input from other sensory systems to give the appropriate motor output. Some of this integration may occur peripherally, depending on the degree of electrical coupling between inputs from individual receptors. Generally there will be considerable convergence of peripheral inputs to second- and higher-order neurones, possibly in conjunction with selective filtering. In attempting to describe the manner in which the central nervous system may recognize a particular food, the concept of "across-fibre patterning" has been developed. Each material making gustatory contact with the mouthparts will produce a different net effect or response profile. Discrimination by across-fibre patterning involves the ability of the central nervous system to distinguish between such profiles. The degree to which the central nervous system uses labelled lines in analysing peripheral input has been a matter for conjecture. The concepts of labelled lines and across-fibre patterning have been discussed by Blaney, W. (1975, 1980), Boeckh, J. (1980a,b), Dethier, V. (1973, 1974, 1976), and van Drongelen, W. *et al.* (1978).

Such work on information processing concerns

the chemical discrimination of appropriate food, and the manner in which food quality is monitored. No attempt has yet been made to understand the complex neural regulation of the whole feeding process but a model of the behavioural sequences and the factors which appear to be relevant for an insect such as a grasshopper is given in Fig. 3.

3 TERMINATION OF FEEDING: CONTROL OF MEAL SIZE

Most insects eat their food in discrete meals with relatively long periods between them, and in the extreme case of some blood-sucking insects there may be only one meal in each instar. What regulates the amount taken in? It is assumed that the insect is ready to feed, has stimulating food available, and that the process of ingestion has begun. The significance of food quality in meal size regulation is discussed in section 2.

3.1 Acridids

Adaptation of chemoreceptors on the mouthparts has been suggested as a regulatory mechanism in the termination of a meal by *Chortoicetes terminifera* (Barton Browne, L. *et al.*, 1975). When drops of sucrose were placed on the mouthparts of restrained

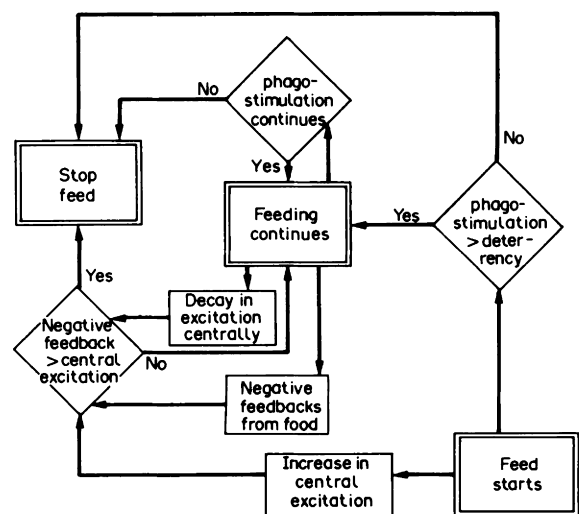


FIG. 3. A model of the processes involved in continued feeding in a locust. (After Bernays, E. and Simpson, S. 1982.)

insects, more were imbibed if they were alternated with drops of water than if they were given in an unbroken sequence. An interpretation of this in terms of sensory adaptation is reasonable, but a single chemical presented in this way is very unlike the natural situation where chemoreceptor adaptation to threshold levels during a meal on a normal solid food probably cannot occur, because the natural feeding process is such that a complex and continuously changing series of stimuli is presented to the mouthpart sensilla (Bernays, E. and Chapman, R. 1974a). For example adaptation of the palp receptors is reduced by palpation (Fig. 4, see also section 1.2). On balance, it must be concluded that while locust chemoreceptors do adapt to phagostimulants (Blaney, W. 1975), and sensory adaptation may play a role in terminating feeding when a single chemical is presented almost continuously, the evidence from naturally feeding insects which can feed continuously for 20 min suggests that this cannot be a major factor in the regulation of meal size.

The level of excitation associated with the start of feeding is enhanced by phagostimulation, and this effect is probably more extreme after a period of

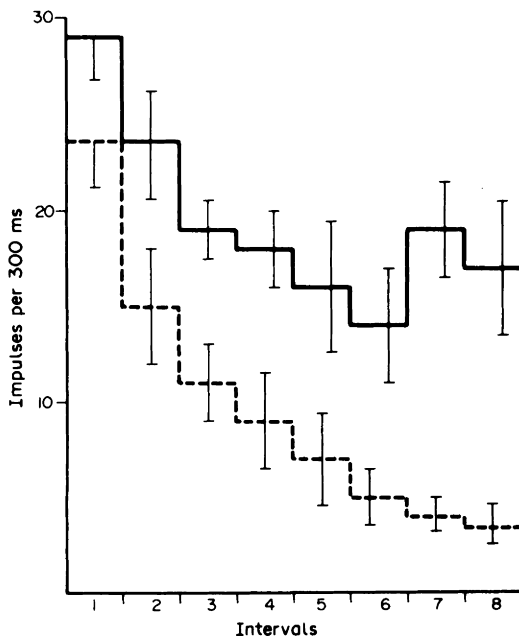


FIG. 4. Numbers of impulses from palp tip chemoreceptors of *Locusta migratoria* when the contact is intermittent (solid lines), as in palpation, or continuous (broken lines), over successive 300 ms periods. Vertical lines represent standard errors. (After Blaney, W. and Duckett, A. 1975.)

food deprivation (see subsection 1.2 and section 4). Various experiments with acridids have shown that heightened excitation may increase meal size (see Chapman, R. 1982 for discussion). It is also possible that towards the end of a meal the decay of the excitatory state is a cause of terminating that meal. The apparently enhanced state of arousal associated with feeding, indicated by palpation and movement, continues for a short period after the completion of a meal (Blaney, W. *et al.*, 1973; Simpson, S. 1982a). This suggests that a fall in an excitatory state is not a dominant reason for the termination of feeding.

Locusts feeding without imposed periods of food deprivation ingest their food in discrete meals, each of several minutes' duration, separated by longer periods, averaging about an hour, when no feeding occurs (Blaney, W. *et al.*, 1973; Simpson, S. 1981). If insects are deprived of food for long enough to empty the foregut, and then allowed to ingest a tough mature grass, the size of the meal taken by nymphs of *L. migratoria* is remarkably constant (Bernays, E. and Chapman, R. 1972). This suggests a sharp cut-off of feeding under these circumstances. Also meal sizes on such food, when the crop still contains food, tend simply to top up the crop to similar levels (Fig. 5).

In nymphs of *Locusta migratoria*, the backward movement of solid tough grass to the midgut in the course of a meal is slower than the ingestion rate,

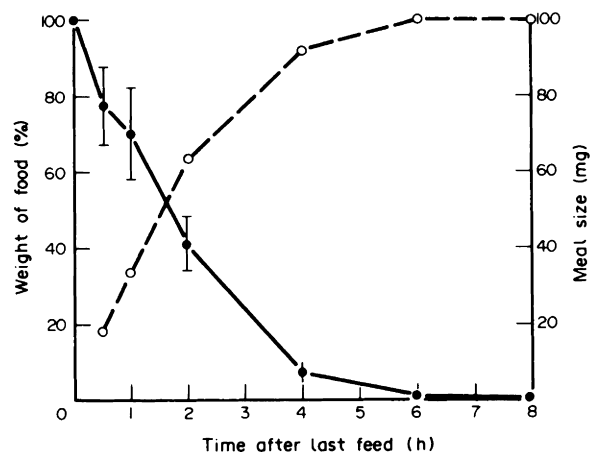


FIG. 5. Weight of food remaining in the crop at different times after a full meal in nymphs of *Locusta migratoria* (●—●) and the meal sizes taken by similar groups of insects (○—○). Temperature 30°. (After Bernays, E. and Chapman, R. 1972.)

and the foregut is filled from the posterior end forwards (Bernays, E. and Chapman, R. 1973). Hyperphagia results if the posterior pharyngeal nerves, at the front of the foregut, are cut; the insects attempt to feed continuously but are physically incapable of ingesting much more (Fig. 6). Sectioning other nerves to the foregut does not have this effect, but Rowell, C. (1963) observed hyperphagia in *Schistocerca gregaria* after sectioning the recurrent nerve. This operation has no effect on meal size in *L. migratoria*, but it is very easy to damage the posterior pharyngeal nerves while sectioning the recurrent nerve, because their positions are very variable and they often branch from the recurrent nerve itself. It may well be that the observations made by Rowell resulted from damage to the posterior pharyngeal nerves. These nerves supply the anterior part of the foregut, the last part to fill during a meal. Over this region is a network of nerves containing approximately ten large cells and these are probably the perikarya of stretch receptors. It is suggested that input from these cells, indicating complete fullness of the foregut, is the signal for cessation of feeding.

When, however, the interval between meals is less than 4 h, feeding often stops before the foregut is fully distended (Bernays, E. and Chapman, R. 1972). This is most obvious if the food consists of soft lush vegetation which passes to the midgut faster than tough and relatively dry food (Simpson, unpublished), so that some other mechanism may be involved. Barton Browne, L. *et al.* (1976), working on adults of *Chortoicetes terminifera*, found that meal size was correlated with weight loss during the

previous period of food deprivation. However, their food source was water, or water with sucrose, which cannot provide adequate pressure to stimulate the stretch receptors in the way that normal solid food does. Further, the insects were in a state of negative water balance, and drinking responses have been shown to be affected by a reduction in body volume (see section 5.3).

In adult female *C. terminifera* it was also suggested that total body volume may provide a negative feedback regulating meal size (Moorhouse, J. *et al.*, 1976). This was not apparent in nymphs of *L. migratoria* deprived for 5 h and then fed on a tough mature grass; body volume did not alter because the full foregut displaced air from thoracic airsacs (Bernays, E. and Chapman, R. 1973). It is possible that, in the *C. terminifera* experiments, the effect was a drinking response related initially to reduced body volumes. An abdominal feedback may be important in some situations, particularly where the insect has continuous access to a soft lush food having a high water content, because such food passes back to the midgut relatively quickly, and with this food the crop is sometimes only half-filled at the end of the meal. In such cases there is now evidence that a volumetric feedback is acting from the midgut or ileum via nerves from the terminal abdominal ganglion (Fig. 7).

Finally there is the possibility that haemolymph factors limit meal size. In *L. migratoria* nymphs, altering nutrient concentrations and osmotic pressure during the course of a meal via a chronically implanted cannula had no effect on the size of that meal. Likewise, corpus cardiacum extracts

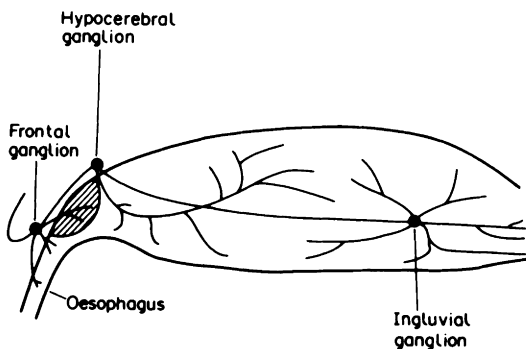


FIG. 6. Diagram of the main nerve supply to the foregut of *Locusta migratoria*. Nerves supplying the shaded area at the front of the crop relay information on crop fullness to the brain. (After Bernays, E. and Chapman, R. 1973.)

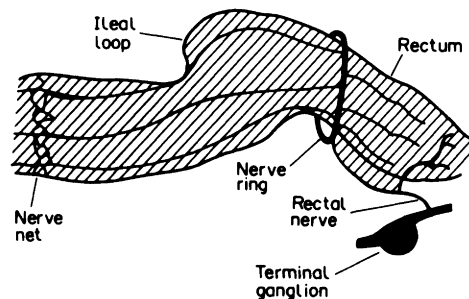


FIG. 7. Diagram of the main nerve supply to the hindgut of *Locusta migratoria*, showing three of the six longitudinal nerves running between the nerve ring near the rectum and the nerve net anteriorly. These nerves are stretched out when the ileum is full and the ileal loop extended. (After Simpson, S., 1983.)

were without effect. On the other hand, if the haemolymph osmotic pressure was raised without a significant volume change about 20 min before food was presented, meal size was reduced. Such high levels of haemolymph osmotic pressure do occur at certain times such as late in the instar, and may contribute to the reduction in meal size which occurs then (Bernays, E. and Chapman, R. 1974a,b). In general, however, the effect is relatively small compared with volumetric factors, and the role of the haemolymph is more significant in determining the length of the period between meals (see section 4.2).

3.2 Flies and other fluid feeders

Chemosensory adaptation has been given a lot of attention in the blowfly *Phormia regina*. When feeding on sugar solutions, blowflies seldom feed for more than 2 min, and then may not feed again for 2 h or more. The meal taken is not continuous, a relatively long initial bout of feeding being followed by successively shorter ones (Gelperin, A. and Dethier, V. 1967). The first bout is lengthened if the feeding stimulus is stronger (except at very high concentration ranges). The sensory adaptation to a threshold level is faster when the stimulating solution is in low concentration, so that this adaptation of the chemoreceptors may play a part in regulating the length of the bout (see Dethier, V. 1976 and section 1.2). Since, however, time between bouts allows for at least some disadaptation, it is ultimately the number of bouts which will relate to meal size. This is less likely to be a function of chemosensory adaptation.

As with locusts, a "central excitatory state" is generated by contact with phagostimulants, which temporarily lowers the behavioural threshold for responsiveness to less stimulating material (Fig. 8). Loss of contact with the food during the excitatory state leads to the so-called fly dance which increases the chances of locating food again (Nelson, M. 1977). As with locusts, the main effect of such a heightened state of excitation is to maximize feeding processes when food is in the vicinity, although decay of such excitation during the meal could be a significant factor in terminating feeding (see Barton Browne, L. 1975). This is because more highly phagostimulatory solutions are ingested in larger

amounts, and such solutions induce a higher level of excitation which takes longer to decay. The relative importance of phagostimulation acting directly on motor systems as compared with phagostimulation enhancing excitation and indirectly stimulating feeding is considered further in section 1.2.

The exact role of the decay of the excitatory state in the termination of feeding on an optimal food is difficult to assess, but it probably interacts with direct negative feedbacks such that these become dominant when the level of excitation falls. Attempts at feeding actively continue for a long time when volumetric feedbacks inhibiting feeding are removed, so that a fall in the excitatory state as a result of continuing contact with food is unlikely itself to lead to the cessation of feeding. It may be, however, that the inhibitory inputs themselves influence the rate of decay of the excitatory state as well as directly terminating feeding.

During the early stages of a meal on sugar solution, some fluid passes directly into the midgut and some into the crop which is a diverticulum of the oesophagus. Towards the end of a meal food is directed entirely into the crop, and finally, at the end of a meal, the crop is closed by a valve (for a detailed account see Knight, M. 1962, and Green, G. 1964a). The crop is in a more or less central position in the

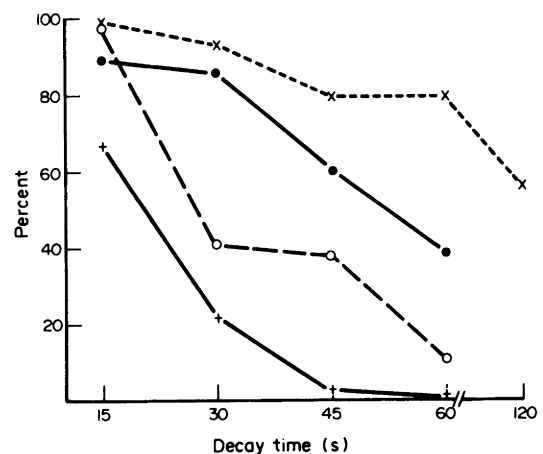


FIG. 8. Percentage of insects extending the proboscis during stimulation with water over 2 minutes, following stimulation with different concentrations of sucrose solution. Prior stimulation with more strongly stimulating solutions induces a longer-lived responsiveness. \times — \times = 0.25 to 0.5 M; \bullet — \bullet = 0.06 to 0.125 M; $+$ — $+$ = 0.02 to 0.03 M. (After Dethier, V. *et al.*, 1965.)

abdomen so that its filling also enlarges the abdomen (Fig. 9). The first reports that cutting the ventral nerve cord produced hyperphagia in *Phormia regina* and related flies suggested that receptors in the abdominal body wall were involved (Dethier, V. and Gelperin, A. 1967; Nuñez, J. 1964). It has now been shown that branches of the abdominal nerve form a loose basketwork over the crop, and several stretch receptors within the basketwork have an increased firing rate when the nerves are extended, a situation which arises towards the end of a meal when the crop is distended. The input from these receptors probably provides the brain with the information required to inhibit further feeding.

A second negative feedback mechanism occurs in flies. At the end of feeding on a sugar solution, when the midgut and crop are expanded, there is a certain amount of food in the oesophagus. At intervals, small quantities of food from the crop are returned to the oesophagus and then passed into the midgut. Stretch receptors in a branch of the recurrent nerve which innervates the foregut are stimulated by oesophageal expansion and cutting the recurrent nerve anterior to this branch results in overfeeding. Thus it is believed that input from the stretch receptors here also inhibits further feeding. Full accounts are given by Gelperin, A. (1971a, 1972) and Dethier, V. (1976). Both mechanisms depend on a volumetric component rather than feedbacks involving nutrient or energy reserves.

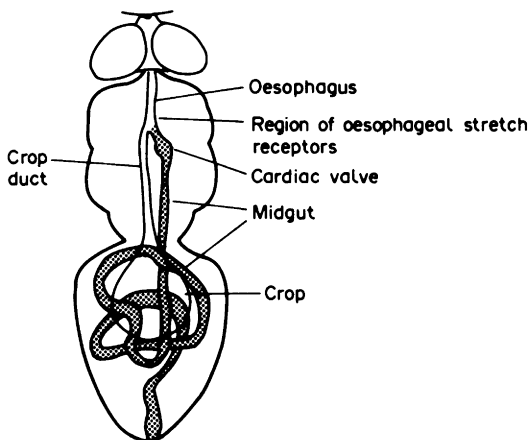


FIG. 9. Diagram to show the arrangement of the gut in the body of the fly.

Protein-deprived flies which take a full sugar meal will then take a protein meal if given the opportunity. The size of this meal depends upon the amount of sugar solution previously ingested. Even if the fly is severely bloated after ingesting 2 M sucrose, some protein is ingested subsequently. The separate control of protein and sugar meals in *Phormia regina* has been studied by Belzer, W. (1978a-c, 1979). Frontal ganglionectomy (and the presumed removal of a negative feedback via the recurrent nerve) led to sugar or protein hyperphagia in both protein-deprived and gravid females, when either food source was provided. Operated protein-deprived flies, given a choice of foods, ingested more sugar than protein. Unoperated flies, however, preferred protein. These results have been interpreted in the following way: negative feedback via the recurrent nerve exerts some control on both protein and sugar meals, with the effect being stronger for sugar.

Sectioning the abdominal nerve led to protein hyperphagia or some elevation of sugar ingestion in protein-deprived flies when either food source was presented. In gravid flies the operation led only to a slight increase in protein ingestion, suggesting that abdominal feedback is most important in regulating protein ingestion, with sugar ingestion being regulated primarily via the recurrent nerve feedback. Belzer, W. (1979) demonstrated that the presence of mature oocytes reduced protein intake because of feedback from abdominal stretch receptors. By having recurrent nerve feedback as the primary regulator of sugar ingestion, a gravid female can still take the sugar meals necessary for survival despite a high level of abdominal nerve feedback due to the presence of the oocytes. Similarly, by having two different volumetric controls, a protein-hungry fly which has just fed to repletion on a sugar solution can then take a protein meal if it is available. Alternatively, a fly which has just taken a protein meal may ingest a sugar solution immediately afterwards. By integrating incoming chemosensory information on the nature of the food with volumetric information from the oesophagus and abdomen, a fly can make the best use of available resources.

Rhodnius prolixus takes just one blood meal of about six times its own weight in each nymphal instar and severe hyperphagia results from cutting

the ventral nerve cord. Cutting a hole in the abdomen and midgut, such that the ingested blood can leak out, also greatly increases the duration of feeding and the volume ingested (Maddrell, S. 1963). This suggests that negative feedback from stretch receptors is a probable control mechanism. Appropriate stretch receptors in each complete abdominal segment have been described, and their adapted discharge frequency increases with the intensity of stretching (Anwyl, R. 1972).

In several species of mosquito, sectioning of the ventral nerve cord anterior to the second abdominal ganglion resulted in about a four-fold increase in the volume of blood consumed. In *Aedes aegypti* meal size depended on the point at which the cord was sectioned: the more anterior the cut, the greater was the size and duration of the meal taken (Table 7). It is apparent that inhibitory inputs resulting from abdominal distension bring about the termination of feeding, and that there are probably a number of receptors involved which are segmentally arranged. There has been no investigation of carbohydrate meals, which may be separately controlled as in blowflies, particularly as the partitioning of these into the crop, with blood going into the midgut, is usual in this group (Hosoi, T. 1954).

In *Oncopeltus fasciatus* it has been suggested that sensory adaptation is a likely cause of the cessation of feeding (Fier, D. and Beck, S. 1963). The argument was based on the fact that the length of a probe (meal) was greater on a substrate of cellulose or starch than on sucrose. There are, however, other interpretations of this phenomenon. There is a sug-

gestion that adaptation may play some part in aphids since, when given artificial diets alternating with water, they ingest more than the same aphids given the artificial diet continuously (Cull, D. and van Emden, H. 1977). Results of McClain, E. and Fier, D. (1973) give evidence for the presence of a volumetric feedback in *O. fasciatus*. When 4 μ l of distilled water was injected into the haemolymph less of both liquid and solid diets was ingested than after injection of only 1 μ l. On the other hand, a number of amino acids had different effects on the lengths of subsequent meals on both liquid and solid diets after injection into the haemolymph. For example, glycine reduced meal length on milkweed seeds while histidine increased it. These results are difficult to interpret since the final haemolymph concentrations were probably higher than those occurring naturally, but they do suggest that the effect is not a simple osmotic one.

Finally it has been suggested that in *O. fasciatus*, the depletion of salivary secretions is a cause of cessation of feeding (Miles, P. 1959). At the end of a meal, if a drink is taken, feeding can again be initiated (Fier, D. and Beck, S. 1963).

3.3 Synthesis

The regulation of meal size is a means of preventing physical damage due to overeating, and probably of ensuring that the most effective amount for optimal digestion and conservation of effort is eaten. In all cases examined so far, the major component in this short-term regulation of feeding is a volumetric factor mediated by stretch receptors which are variously

Table 7: Effect of cutting the ventral nerve cord at various sites on feeding time, blood meal size, and egg development in female *Aedes aegypti* (after Gwadz, R. 1969)

Treatment: ventral nerve cord cut anterior to abdominal ganglion	No. females/treatment	Mean for treated females (\pm 95% confidence limits)		
		Feeding time (min.)	Blood meal weight (mg)	No. of eggs developed
No. 2	76	5.3 \pm 0.2	12.0 \pm 0.5	103.3 \pm 4.3
No. 3	42	3.2 \pm 0.3	7.6 \pm 0.7	97.2 \pm 4.0
No. 4	36	2.7 \pm 0.2	5.1 \pm 0.4	92.3 \pm 2.8
No. 5	40	2.2 \pm 0.2	4.2 \pm 0.5	88.9 \pm 4.2
No. 6	36	2.0 \pm 0.2	3.6 \pm 0.2	87.1 \pm 4.3
Sham-operated	62	1.8 \pm 0.1	2.9 \pm 0.2	85.8 \pm 3.0
No treatment	64	1.9 \pm 0.1	2.8 \pm 0.3	86.1 \pm 3.3