METHUEN'S MONOGRAPHS
ON BIOLOGICAL SUBJECTS

SOCIAL BEHAVIOUR IN INSECTS

A. D. IMMS

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BY

A. D. IMMS, M.A., D.Sc., F.R.S.

AUTHOR OF "A GENERAL TEXTBOOK OF ENTOMOLOGY," ETC.

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Methuen's Monographs on Biological Subjects

General Editor: G. R. de Beer, M.A., B.Sc.

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GENERAL PREFACE

BIOLOGY has long since reached the stage when it is impossible for one person to specialize in all its branches, or even to keep abreast of the latest developments in all of these. This is the more regrettable because it seems likely that many problems which baffle frontal attacks may be circumvented with the help of concepts and techniques of other branches of science, and that knowledge may thereby be extended. The present series of monographs attempts to give brief but authoritative accounts of the present states of knowledge in various departments of biology, and to convey information which can be obtained only at the cost of considerable time and trouble by a person who is not engaged in that particular branch. Teachers and students will find up-to-date accounts of their own subjects, and research workers will be aware of the progress made by their colleagues in other departments. At the same time, the general reader with a taste for biology will be able to follow the most recent developments in the various branches of the science.

G. R. DE B.

MERTON COLLEGE
February, 1931

PREFACE

THE habits and economy of social insects form one of the most remarkable chapters in biology. Their manifestations exemplify the heights to which mutualism and co-operation can attain, even when determined by causes other than intelligence. Since the social organization of insects has been evolved on a physiological and instinctive basis, it can be reviewed with greater detachment and impartiality than the more complex human system, which presents accomplishments that have been developed and integrated along a different line. The fact that the independent communal organizations of insects and man present many features in common, widens the horizon of our subject, and brings it into relations with both sociology and psychology. To the biologist social insects present no lack of fundamental problems with which he is directly concerned. Among them are displayed many functional adaptations, peculiar developments of symbiosis and the most complex and advanced phases of polymorphism. He is exercised with the problem as to how to account for the regular production of sterile individuals, generation after generation, and its relation to nutritional influences on the one hand and to hereditary factors on the other. Students of animal behaviour find in such creatures the culminating expression of instinctive habits. Practically-minded people preserve the hive bee for economic reasons: with the rest of such fauna they are exercised, either with means of its extermination, or with leaving it severely alone.

This little book endeavours to present an outline of the essential features of the structure and habits of social insects: the main paths which their evolution has traversed and the basis upon which their behaviour depends. Effort has been made to avoid undue technicality and to present the subject in a form acceptable to readers other than entomological specialists.

It is difficult to imagine any present-day author of a book on social insects who can afford to neglect the works and expositions of Prof. W. M. Wheeler. Possessing a unique acquaintance with all that pertains to the lives of such animals, and philosophic insight in interpreting their behaviour, Prof. Wheeler has done much to co-ordinate, and bring into daylight, a subject of perennial interest. Opportunity, therefore, is taken here to express, to my distinguished friend at Harvard University, indebtedness to his influence, without which this book would not have been written.

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A. D. IMMS

HARPENDEN, HERTS
January, 1931

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CHAPTER I

THE SENSE ORGANS AND INSECT BEHAVIOUR

THE behaviour of an insect, as of any other animal, consists of acts which are the ultimate effects of stimuli upon its particular type of anatomical structure. The stimuli themselves originate either from the environmental forces of the outer world or from causes operating within the insect's body. External stimuli act very largely through the organs of sense, which are special receptors for the purpose, whereas internal stimuli arise from biochemical activities going on within the tissues.

The most usual reactions to external forces are by movements. A given stimulus impresses itself upon the sensory cells concerned, and an impulse is conveyed by afferent nerve fibres to an association centre located within the central nervous system. The association centre, in its turn, is linked up with a motor centre which sends out afferent nerve fibres terminating in a muscle or group of muscles (Fig. 1). The association centre is a kind of two-way connexion between the roots of the sensory and motor nerves. Its degree of development varies greatly, and in the brain, for example, there is a large number of such centres whose nerve

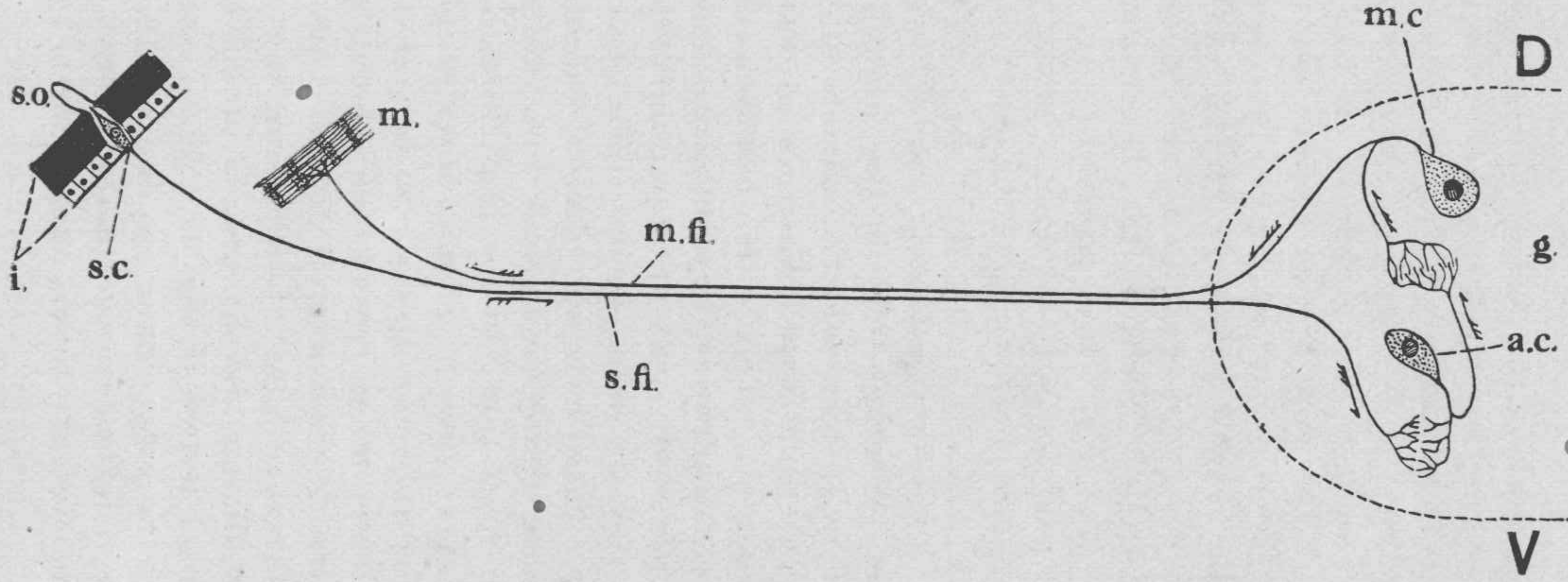

FIG. 1.—Diagram of the Reflex Mechanism of the Nervous System of an Insect

One half of a ganglion, *g.* of the ventral nerve cord is represented in outline. *D*, dorsal aspect; *V*, ventral aspect. A motor fibre (*m.fi.*) and a sensory fibre (*s.fi.*) of a lateral nerve are shown; *i.*, integument; *s.o.*, sense organ; *s.c.*, sensory cyton or cell; *m.*, muscle; *a.c.*, association cyton; *m.c.*, motor cyton. (The course traversed by a stimulus, received by the sense organ, is represented by arrows.)

fibres link different parts of the nervous system together. This type of nervous mechanism, known as the composite reflex arc, prevails in all animals with a central nervous system, differing only in its degree of elaboration. In insects, however, there is this difference as compared with vertebrates. The only known afferent nerve-cells are peripheral in situation and none have been found in the central ganglia as in vertebrates: their fibres when traced to their particular ganglionic centre end in terminal arborizations. Whether this distinction is a fundamental one we are not in a position to say, since histologists have paid too little attention to the origin and growth of the finer components of the insect nervous system.

By no means all stimuli affecting insects originate from the outside. Whether their bodies contain anything comparable with the endocrine glands of vertebrates, that control important phases of growth and behaviour, is unknown. There are, however, certain ductless organs, which appear to be glandular in function, that are almost universally present among insects. The corpora allata, or small paired bodies, present in close relation with the sympathetic nervous system, and the œnocytes, which are segmentally grouped nests of highly specialized cells, may possibly be important in this respect. All that is known is that internal stimuli exercise a profound influence upon insect behaviour, but as regards the nature and sources of these stimuli we are completely ignorant. Such stimuli are most probably products of metabolism which function as messengers activating or modifying specific phases of behaviour. Many instincts are initiated in this way as, for example, those involved in the processes of cocoon-formation and of oviposition, and in the transformation of the caterpillar into the chrysalis: internal stimuli further deter-

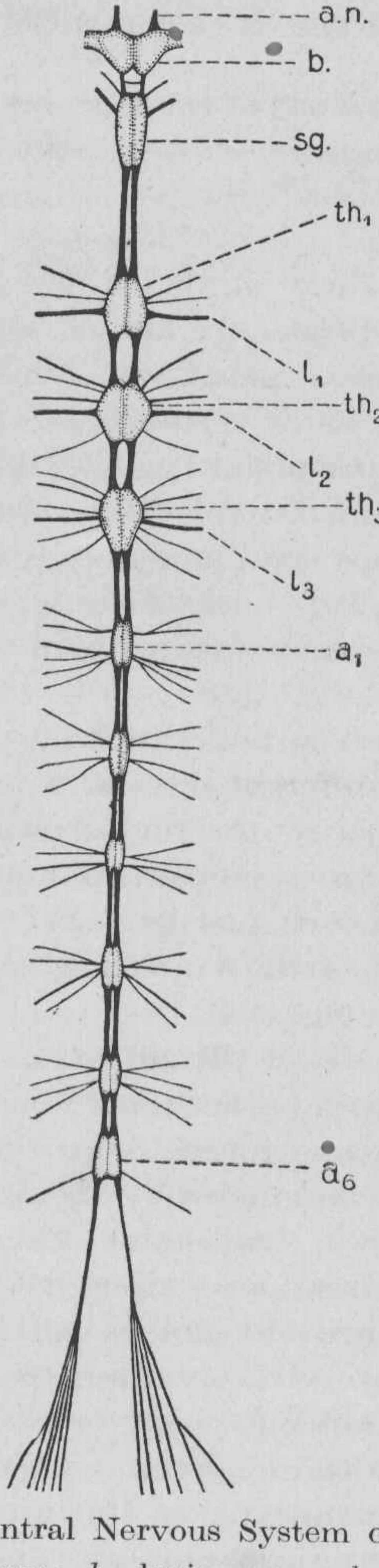

FIG. 2.—Central Nervous System of an Earwig.

a.n., antennary nerve; *b.*, brain; *sg.*, subœsophageal ganglion: th_1–th_3, thoracic and a_1, a_6 abdominal ganglia, forming the ventral nerve cord; l_1–l_3, nerves to the three pairs of legs.

mine differences in reactions to the same external forces during different phases of an insect's life, and other features of behaviour.

THE NERVOUS SYSTEM

The central nervous system of an insect (Fig. 2) consists of a dorsal ganglionic centre, the cerebral ganglion or brain, which is situated in the head immediately above the œsophagus. The brain is joined by means of a pair of lateral nerve connectives with a ventral or subœsophageal ganglion, located beneath the œsophagus. The latter ganglion is united by paired longitudinal connectives with a chain of ganglia forming collectively the ventral nerve cord. For the most part there is a separate pair of ganglia to each segment of the body but, in different insects, a varying amount of fusion between adjacent ganglia takes place, particularly between those at the posterior extremity of the ventral chain. A visceral or sympathetic nervous system is also present, together with a peripheral sensory system innervating the integument.

The brain (Fig. 3) is the principal seat of sensation and is also the most important co-ordinating centre of the body. All investigators have observed the large number of sensory and motor nerve tracts, from different regions of the body, that enter and become localized in the brain. These are concentrated in a pair of special areas termed the mushroom bodies, and there is good reason for believing that, in these bodies, the main sensory impressions are recorded, actions are co-ordinated and associations once acquired are impressed. The greatest development of the mushroom bodies is found in the order Hymenoptera: here they attain a size and complexity not found elsewhere, and it is in this order that psychic development attains its highest expression. In the Hymenoptera, and in some other orders, the size and complexity of the mushroom bodies corresponds in a general way with complexity and specialization of behaviour or, in other words, they

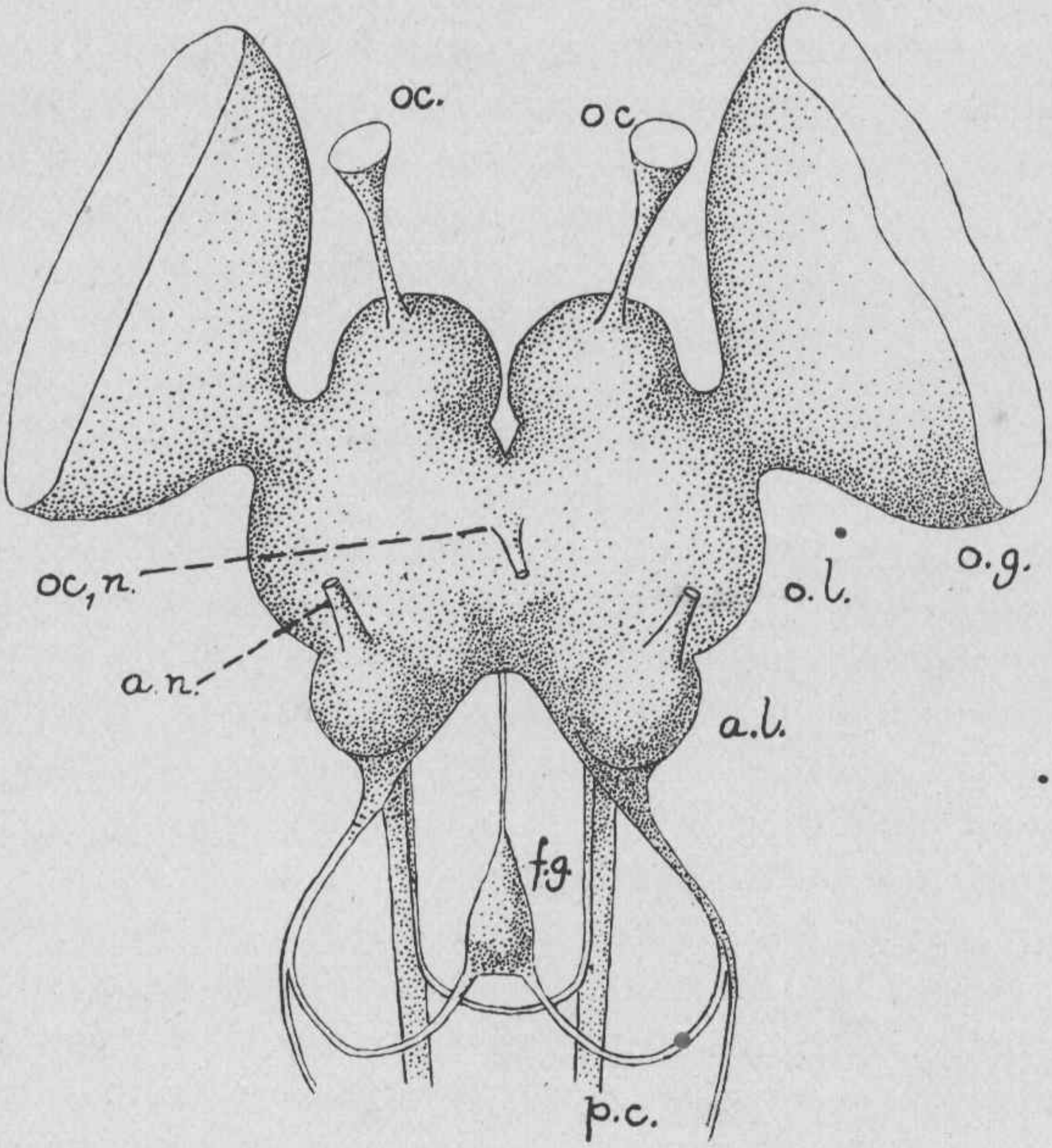

FIG. 3.—Frontal View of the Brain of a Locust

a.l., antennary or olfactory lobe ; *a.n.*, antennary nerve ; *f.g.*, frontal ganglion of sympathetic system ; *oc.*, lateral ocelli and nerves ; *oc, n.*, nerve to median ocellus ; *o.l.*, optic lobe ; *o.g.*, optic ganglion ; *p.c.*, connective to subœsophageal ganglion. From Burgess.

provide a kind of mental index. One of the most experienced insect neurologists, Jonescu, has shown that the mushroom bodies are more greatly developed in the worker hive bee than in either the drone or the queen—a fact that would be expected if they are the centres of instinctive behaviour. Other investigators, notably von Alten, in 1910, and Armbruster, in 1919, have made comparative studies and careful measurements of the brain in various Hymenoptera. By taking numerically expressed relationships between two dimensions of the mushroom bodies, and a constant in the same brain, a kind of 'intelligence index' was obtained. If the Hymenoptera be arranged in an ascending series upon this basis, the sawflies come lowest on the list, the social Hymenoptera highest, while the solitary bees occupy an intermediate position. This conforms well to what is known of behaviour in those several groups.

The subœsophageal ganglion controls and co-ordinates the movements of the mouth-parts. The experiments of Kopéc suggest that it also functions as a reflex-inhibiting centre. After the excision of this ganglion very strong reflex movements result from certain artificial stimuli, whereas similar stimuli are ineffective in the uninjured insect. By decapitation, both the initiatory and inhibiting centres are lost, and headless insects can be artificially induced to perform complicated reflex acts.

Each ganglion of the ventral nerve cord is a reflex centre, combining both sensory and motor functions, with respect to its particular segment. In addition to its ganglionic autonomy, the ventral cord as a whole exhibits considerable powers of co-ordination. It is this capacity which enables a decapitated insect to walk, fly, lay its eggs, and perform other actions, provided requisite artificial stimulation be applied. Their normal initiation and full co-ordination, however, are not possible unless the brain be intact.

Sensory Perception

Insects are able to perceive very much the same stimuli which impart definite sensations in man. Such stimuli make certain impressions upon the insects' nervous system which result in their behaving accordingly. Light, chemical stimuli (smell, taste), tactile stimuli and sound vibrations exercise their respective influences to a varying extent among different species. There are no grounds, however, for concluding that these impressions bear any real resemblance to those which we ourselves perceive. One of the most important differences lies in their reactions to different amplitudes of these stimuli which involve ranges outside human capacity. Insects respond, for example, to chemical stimuli too dilute or too delicate for perception by our olfactory or gustatory organs: they react in some cases to pitches of sound incapable of appreciation by the human auditory organ: and their range of colour discrimination does not involve the whole spectrum visible to human beings, yet, at the same time, they are able to appreciate ultra-violet rays. Whether sensory reaction in insects also embraces responses to other types of stimuli, imperceptible to human senses, is a possibility which has often asserted itself without being, as yet, definitely proved.

The essential components of a sense organ are known as sensillæ. The most generalized types of sense organs consist of single sensillæ only, while in their more complex developments large numbers of these elements become compacted together to form highly evolved localized structures. A sensilla always exists in relation with the external cuticle and consists of a specialized hypodermal (epidermal) cell, connected with the fibre of a sensory nerve. In association there are usually one or more unmodified hypodermal cells, and the whole is invested externally by a differentiated portion of the cuticular covering of the body (Fig. 4). The simplest and most primitive sensillæ are merely innervated hairs, and a