CHAPTER XVII

THE VISION OF INVERTEBRATES

I am introducing this chapter on the function of the eyes of Invertebrates with the photograph of KARL VON FRISCH (1886 —) (Fig. 728), who has devoted his long and fruitful life to the fascinating study of animal behaviour—and still continues to do so. Born in Vienna, he studied in Munich and successively became Professor and Director of the Zoological Institutes at the Universities of Rostok (1921), Breslau (1923), Munich (1925), Graz (1946), and again Munich (1950) where, as this book is being written, he is still pursuing his close and intimate study of the habits of insects. Taken as a whole, his life as a biologist, spent observing the behaviour of his experimental friends in the water and in the countryside, must have been a delightful one ; he obviously enjoyed it and no one can read his published works without realizing that fact can indeed be more exciting and of more interest than fiction. The greater part of the first years of his studies was devoted to the vision, and particularly the colour vision, of fishes, a subject in which, as we shall see in the following chapter, he became a great authority, opposing the views of Carl von Hess (Fig. 735) and eventually winning the battle. The latter part of his life has been largely spent observing the habits of bees. Much of the fruits of this we have already studied in the chapter on the influence of light on movement.[1] There are few romances in science more pleasant than the convincing and far-reaching results he has obtained in the study of the extraordinarily complex behaviour of these insects in the meadows of Central Europe ; and there are few pieces of biological work carried through with greater perseverance, with greater thoroughness and to greater purpose.

METHODS OF INVESTIGATION

The scientific estimation of the visual capacity of animals is notoriously difficult. It is a difficult problem even in man for sensations are individualistic and subjective and the language of introspection is usually unsafe ; in the lower animals the difficulties become in-finitely greater for the only criterion whereon we can pass judgment is the observation of their reactions to various stimuli ; we have no knowledge of how far their experiences coincide with our own, and no right to equate the two.[2]

From the scientific point of view the observation of animal behaviour in ordinary uncontrolled circumstances can provide much useful information regarding their sensory experiences, but from such evidence our conclusions can only be drawn with reserve. This approach is full of pitfalls even in human subjects. A red-green colour-blind person will say that he can appreciate red and green and usually behaves as if he does so ; and we have little idea of what

p. 70.   [2] p. 108.

Fig. 728.—Karl von Frisch (1886——).

indeed he does see. For this reason König gave up the method of introspection entirely and trusted only to colour-matches in his investigation of colour-blindness ; only if every colour in the spectrum could be matched by a mixture of a given pair of colours should the subject be considered a dichromatic colour-blind. There are occasions, however, when the observation of the behaviour of animals in their natural surroundings can yield satisfying results. We have already noted many instances of such œcological research, for example, in the study of the conduct of different Arthropods in their orientation towards light ; a particularly good example is von Frisch's experiments on bees, or the means of orientation employed by birds in navigation. These methods, however, valuable as they are, are applicable only to certain restricted types of complex behaviour of a nature such that other incidental variables can be neglected.

Two more generally applicable methods of research are available. In the *objective methods* of approach a measurable physical phenomenon presumably determined by a specific stimulus is observed—a contraction of the pupil to light, for instance, or an electroretinographic response—and it is assumed that this reaction bears a relatively constant relation to events on the sensory level. If a response of this nature follows stimulation by one band of wave-lengths of light and not by another, for example, it is probable that the first gives rise to a sensation and the second does not. A further analysis is possible by the study of reflex responses. If an animal exhibits characteristic reflex reactions to varying stimuli it is reasonable to suppose that these affect it in different and specific ways. The optomotor reaction illustrates this. If an animal, be it insect or vertebrate, is faced with a revolving striped drum and reacts to the succession of stimuli thus presented to it by compensatory movements of its eyes or its body, we can assume that the alternating stimuli have a different effectivity ; or if an animal salivates when presented with one stimulus associated by training with food and not with another, the deduction seems inescapable that a discrimination is made between the two stimuli ; but whether the differentiation remains on the reflex level or is appreciated as a sensation is sometimes problematical.

The elicitation of such reflex responses, however, although suggestive, gives us little idea of the conscious appreciation of sensations and their effectiveness in determining conduct. A more satisfying approach is the *subjective method* of the study of what appears to be conscious behaviour. The simplest technique in this respect is a study of " preference " : if an animal goes towards light and avoids darkness, or vice versa, it evidently can distinguish between them ; a similar argument applies to a fish which swims towards a red rather than a green light. How far this conduct implies that the discrimination is

based on different sensory experiences is, however, doubtful. It has been generally accepted in the case of the worm which emerges in twilight and hides again in daylight ; but does it equally apply to the protozoan which shows the same response ? We do not know the answer to this riddle.[1]

A more analytical method is the application of *training techniques* which, incidentally, are more susceptible to scientific control. Thereby an animal is trained to respond to or reject one stimulus to the exclusion of all others by an appropriate reward or punishment, the stimulus
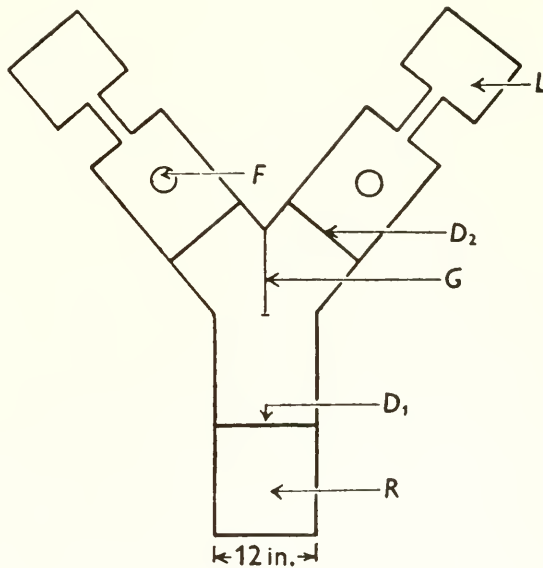

Fig. 729.—GROUND PLAN FOR DISCRIMINATION BOX.

L, light box. *F*, food ; *D₁*, hinged door ; *D₂*, hinged door with 3 × 3 in. opal glass panel ; *G*, glass partition ; *R*, restraining chamber. The box is 13 in. high (R. Gunter, *J. Physiol.*, 1951).

being more minutely differentiated from related stimuli as the process of training proceeds. The disadvantage of the method is the limitations of its applicability since it requires more intelligence, consistency in behaviour and amenability than most animals possess ; moreover, an experiment of this type must excite the animal's interest so that the technique would be expected to break down if the sensation in question were not of importance in its life.

A simple and typical experimental set-up for such a training experiment is seen in Fig. 729. In its essentials it is a Y-shaped " discrimination box " or maze wherein the animal is first retained in an outer chamber and then, entering

[1] p. 102.

the main chamber, is offered the choice of two stimuli ; these, for example, may
be light stimuli made up of two illuminated milk-glass panels set into hinged
doors and lit from behind so that they can be suitably varied in intensity, hue
or saturation. Either of these the animal can open to receive a reward (food)
or punishment (an electric shock). Trained initially to go towards one (the
positive) of two well-differentiated alternative stimuli and to avoid the other,
the negative stimulus is approximated progressively to the first until the limit
of discrimination is reached. Throughout the experiment the relative positions
(right or left) of the two stimuli are randomly alternated, while other stimuli
(olfactory, etc.) are eliminated as by placing similar food in each box, that in
the negative box being inaccessible. Such training techniques, of course, are
laborious, several hundred " runs " being usually required in each experiment ;
moreover, they are time-consuming for much cannot be accomplished at one
session lest fatigue be induced or interest lost ; and they are restricted to species
which are relatively intelligent and docile, for a stupid or an untrainable animal
or one that gets cross or sulks is useless.

It is also to be remembered that any response of this nature made
by an animal depends upon complex factors ; few stimuli are in fact
simple, most involve more than one receptor, and all responses are
complicated by mutual excitations and inhibitions, for the animal
reacts not to one stimulus alone (such as food) but to a complex
situation wherein each stimulus must be differentiated against a
changing background and varies with past experience and its present
psychological state. Even in the most adequately controlled experi-
ments in the laboratory an ideal environment can rarely be realized.
The very fact of the artificial isolation of the stimulus is outside the
animal's natural experience and thereby something important in the
experiment is lost. It follows that the results of such analyses can be
accepted only with reservation ; indeed, any claim that a scientifically
exact appreciation of the physiology or psychology of any animal can
be based on conditioning experiments is illusory.

Within these limits, the method undoubtedly produces results in
terms of sensational responses of greater reliability than any other
and forms the best means of analysing the nature of the sensation
concerned. Considering these difficulties, however, as well as the varia-
tion in psychology between different members of the same species and
the probable differences in apperception and interpretation between any
species and our own, it is not surprising that the results thus obtained
have often been inconsistent.

THE LOWER INVERTEBRATES

PROTOZOA. We have already seen that Protozoa exhibit fixed
reactions to a variety of " sensory " stimuli—light, heat, gravity,
contact, electrical shock—the only observable response being a tropism.
We have also seen that there is no observable difference in behaviour

in respect to these different modalities but that, on the other hand, they may be additive in their effect. Whether the reaction is positive or negative there is no evidence that the response is associated with subjective awareness ; and although a temporary process of conditioning may exist due to the cumulative effects of previous stimuli,[1] there is little evidence of any true capacity for learning. Soest (1937), for example, claimed that an association with electric shocks could condition an avoidance of light in *Paramœcium*, but this behaviour may well have been determined by the accumulation of metabolites (Dembowski, 1950). It would therefore seem that apart from responses which are explicable on a purely physico-chemical basis, we have no knowledge of " vision " in the sense of perceptual awareness in this phylum (see Wichterman, 1953).

Paramœcium

CŒLENTERATA. Among Cœlenterates there is more evidence for assuming the existence of a lowly organization of some aspects of conduct on a reflex level as well as the presence of associated memory. The spontaneous movements exhibited by several species either of swimming or " stepping " whether the environment is changed or remains constant, are obviously the result of controlled activation and inhibition [2] ; the same type of conduct is seen in the daily rhythms in the activity of sea-anemones and jelly-fish, such as those determined by tidal changes, which may persist for some considerable time after the stimulus has been artificially removed.[3] That purposive reactions with memory associations also exist is suggested by such types of behaviour as the assumption by the anemone, *Actinia*, of the same position in an artificial aquarium as it occupied in its natural rock (van der Ghinst, 1906 ; Bohn, 1908), the apparent intelligence of the anemone, *Antholoba*, in climbing on the back of a crab (Brunelli, 1910), or the rejection of unsuitable food after several trials by such anemones as *Actinia, Tealia* and *Cribrina* (Fleure and Walton, 1907 ; Gee, 1913 ; and others). In spite of these activities, however, so far as we know, the phototactic reactions of this group are completely automatic and fixed, and indeed have been found to remain unchanged after two generations have been exposed to abnormal lighting conditions (Ewer, 1947).

Sea-anemone

Jellyfish

ECHINODERMATA. In this phylum, again, although some training ability in the starfish, *Asterias*, is suggested by the observations of Jennings (1907) on its capacity to right itself, or of Ven (1921) on its ability to escape from a confined position, there is no proof of any visual reaction except a rigid and unvaried phototactic response without detectable evidence of subjective appreciation.
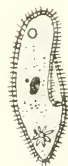

Starfish

[1] p. 36.
[2] Haug (1933) in *Hydra* ; Batham and Pantin (1950) in the sea-anemone, *Metridium*.
[3] Piéron(1909) in sea-anemones ; Horstmann (1934) in the jellyfish, *Aurelia*.

THE VISION OF WORMS

As would be expected from the extreme primitiveness of their ocular structures, the vision of worms is limited to an appreciation of the presence or intensity of light associated with a light-shadow reflex usually of a photo-negative type ; as we have seen, in some species a directional localization may be possible. In the UNSEGMENTED WORMS the simple photo-negative reaction is the only response. Planarians, for example, are always found in dark places beneath stones or the leaves of water plants, vigorously retreating from light whenever they are exposed to it (Taliaferro, 1920). Some such response to light still remains when the eyes have been removed, the animal depending on light-sensitive cells scattered over the surface of the body. There is evidence, however, for the first time in the animal kingdom, that the rigid phototactic response can be modified in a very crude manner by training. The Polyclad, *Leptoplana*, for example, is quiescent in the dark and moves when illuminated, but contact of the head-end with a solid object stops the forward movement. Hovey (1929) found that by simultaneously illuminating the worm and touching it so as to prevent it from creeping forward, the photo-kinetic reaction was completely inhibited ; a similar conditioning process to electric shocks was demonstrated in *Planaria gonocephala* by Dilk (1937). After removal of the cerebral ganglion these modifications of the simple phototactic response cannot be elicited, so that this structure is necessary for the development of this elementary learning process. In assessing the importance of these reactions to light in the life of the animal, however, it must be remembered that the general behaviour of unsegmented worms is determined not so much by their light-sense as by the more fully developed chemical sense and the sense of touch which responds with great sensitiveness to the slightest movement of the water in which they live or to objects with which they come in contact.

More work has been done on the light-sense of SEGMENTED WORMS, particularly upon the earthworm, *Lumbricus*.[1] It will be remembered [2] that in this animal the light-sensitive cells are concentrated mainly at the two extremities. In very dim illumination (less than 0·00118 m.c., W. N. Hess, 1924) the animal is photo-positive, and in ordinary daylight illumination, photo-negative—it must avoid light since, in fact, exposure to strong sunlight for one hour may cause paralysis, for several hours, death. It follows that on emerging from its burrow at any time except at night or in the dim twilight of morning or
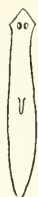
Planarian

Leptoplana

Lumbricus

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[1] Hoffmeister (1845), R. Hesse (1896), W. N. Hess (1924), v. Buddenbrock (1930), Segall (1933), Unteutsch (1937–38).

[2] 190.

evening, either end will at once retract into the safety of its retreat. Its more complex reactions to light when travelling on the ground have already been described.[1] A similarly high degree of sensitivity is seen among certain polychæte worms, particularly the tubiculous types. In these the light-and-shadow reflex is very marked ; so sensitive are they to light that Andrews (1891) found that if a hand were moved in the air at a distance of a metre from the water containing the animals, they withdrew themselves into their tubes as soon as the shadow fell upon them.

In segmented worms, however, the potentialities of habituation and learning have evolved to a considerably greater extent ; that earthworms, indeed, have a modicum of intelligence was known to Darwin (1881) who noted the deft way in which by trial-and-error, profiting by previous experience, they transported leaves of various types to their burrow or collected little stones to guard its entrance.[2] Again, *Hydroides*, if collected from shallow water, reacts promptly to shadows in the aquarium, but individuals collected from deep water remain inactive presumably from lack of experience in a shadowless environment ; a like passivity is rapidly assumed by reactive specimens from shallow water if they are isolated from shadows for some time in the laboratory (A. W. Yerkes, 1906 ; Hargitt, 1906–9). Similar habituations to light-and-shadow stimuli have been found also in polychæte worms (Bohn, 1902) and leeches (Gee, 1913). Moreover, in these species the normal response can be varied by conditioning. Thus the polychæte, *Nereis*, if presented with food together with a sudden increase or decrease in illumination, can be trained after only six trials to respond to the change in illumination alone whether it is positive or negative (Copeland, 1930), while by a similar association with tasty food or other stimuli a reversal of the usual reaction to light can be induced in a number of worms such as *Hydroides* (A. W. Yerkes, 1906), *Nereis* (Copeland and Brown, 1934), *Lumbriculus* (Raabe, 1939) and *Lumbricus* (Wherry and Sanders, 1941). Finally, several Oligochætes and Polychætes have shown a considerable ability to learn the correct turning in a simple T- or Y-maze ; propelled forwards by illumination of the hind region, rewarded by a warm dark cell or punished by an electric shock or an unpalatable salt solution, they can after many trials (up to 200) be taught to turn in the required direction, a capacity unimpaired by excision of the supra-œsophageal ganglion.[3]

In worms, therefore, in which a ganglionated nervous system first appears, *for the first time in evolution the response to light has been shown*
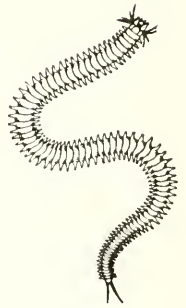
Nereis

[1] p. 53.
[2] See also Málek, 1927.
[3] In Oligochætes : *Allolobophora* (R. M. Yerkes, 1912), *Eisenia* and *Lumbricus* (Heck, 1920), *Heliodrilus* (Swartz, 1929) ; in the polychæte, *Nereis* (Copeland, 1930 ; Fischel, 1933 ; Copeland and Brown, 1934).

to become something that is not rigid and entirely automatic ; it can be modified by experience and training, while vision, although still a secondary sense, apparently becomes endowed with some degree of awareness and meaning.

THE VISION OF MOLLUSCS

From the functional point of view in most Molluscs vision is secondary to the olfactory or tactile sense ; this would be expected in view of the primitive structure of the eyes of most types for, with the exception of Cephalopods, they are rarely capable of detailed visual resolution. It has been contended that land Molluscs (snails, slugs, etc.) which seldom emerge except in twilight and retract their eyes within their tentacles on exposure to bright light, are blind (Yung, 1913) (Fig. 188). A directional appreciation of light is possible, however, and quick movements can be readily detected (Föh, 1932 ; Grindley, 1937) ; but there is no evidence of the appreciation of colour (Mundhenke, 1955). These animals, however, are highly myopic and experiment has shown that objects can rarely be appreciated more than a few centimetres away, although farther in subdued than in bright light (Willem, 1892). Vision does not thus appear to dominate behaviour. On the other hand, Gastropods are extremely sensitive to the slightest movement of the air or any jarring of the surface on which they crawl, while their sense of smell is so acute as to dominate most of their behaviour : food, for example, is sought almost by scent alone.

In littoral lamellibranch Molluscs it would seem probable that vision is generally limited to the appreciation of light and shadow, but this appreciation may be unusually acute. Whether the ocelli are situated on the siphon or the mantle-edge the slightest shadow often induces a response. Thus Patten (1886) found that in the Noah's-ark shell, *Arca*, the mantle contracted and the valves closed quickly if the faint shadow of a hand or a pencil fell upon them. It is interesting that sensitivity does not always vary with the elaboration of the structure of the eye, for the same observer found that an even more sensitive response was given by *Avicula* which is provided with only a few ill-developed ocelli; even the eyeless mussel, *Anodonta*, reacts to a passing shadow owing to its dermal sensitivity to light (Braun and Faust, 1954).[1] The rapidity with which oysters close their shells on the passing of the shadow of a man or a boat is well known. A similar sensitivity to passing shadows characterizes the ocelli in the siphons of littoral Lamellibranchs (Hecht, 1919 ; Koller and v. Studnitz, 1934, in *Mya*) ; and it is obvious that such types which live between the tide-marks and protrude their siphons and occasionally
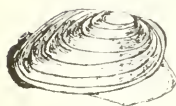
Snail

Slug

*Avicula*

Anodonta

Mya

[1] p. 114.

portions of their shells outside their burrow, will depend much for their survival on their ability to withdraw into safety before the arrival of their many enemies. *Pecten*, with its elaborate eyes, is an exception, perhaps because this animal may use sight to direct its unusual activity as it " flies " on the water for considerable distances by flapping its valves and expelling water from the apertures near the fringe. Even if this is not so, the experiments of Wenrich (1916), who determined the smallest white card which produced a shell-closing response in this scallop, showed that the animal was extremely sensitive to minimum changes in brightness. On the other hand, in abyssal or underground Molluscs, visual organs tend to be less elaborate, and vision takes a secondary or negligible place in the creature's activities.

Pecten

Snails have been trained to negotiate a T- or Y-maze (Garth and Mitchell, 1926 ; Fischel, 1931 ; Brandt, 1935), while a number of Molluscs demonstrate a remarkable ability to seek their habitual homes from a distance.[1] The mechanism employed is unknown ; an association of several senses is possibly involved among which touch probably figures largely and vision little if at all.

CEPHALOPODS are visually in a very different class. There can be little doubt that they use their eyes for the actual observation of objects and in this respect, depending on vision rather than smell, they are unique among Molluscs. Functionally their eyes are capable of a considerable degree of pattern-vision, they have a good perception of movement, and have adaptive and accommodative powers. They are the only Invertebrates which exhibit pupillary reactions remotely resembling those characteristic of Vertebrates (Magnus, 1902) ; these reactions are most readily excited by yellow-green light of the same spectral range which induces the most active phototactic responses. Although many Cephalopods change their integumentary colour to harmonize with their background by reflexes originating in the eyes,[2] Carl von Hess (1921–22) found no evidence to suggest that colour vision is present ; and the positive claims made by Goldsmith (1917), Bierens de Haan (1926), Tinbergen (1939) and Kühn (1930–50) that, as judged by behavioural experiments, they can differentiate hues are open to serious criticism (Carter, 1948).

The visual capacity of *Octopus* has received a considerable amount of attention by such writers as von Uexküll (1905), Polimanti (1910), Goldsmith (1917), ten Cate and ten Cate-Kazejewa (1938), and particularly by Boycott and Young (1950–56) and Young (1956). The standard lay-out of their experiments was to allow an octopus to attack and eat a crab associated with a particular geometrical figure, but to
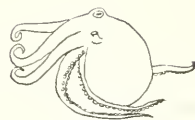
Octopus

[1] *Chiton*, Pelseneer, 1935 ; the limpets, *Patella* and others, Davis, 1885–95 ; Lloyd Morgan, 1894 ; H. Fischer, 1898 ; Piéron, 1909 ; Thorpe, 1956 ; the littoral Pulmonate, *Onchidium*, Arey and Crozier, 1918.

[2] p. 93.

punish it with an electric shock if it attempted to attack a crab associated with another figure. In such experiments the octopus is eminently trainable. The form vision of the animal is surprisingly good.
It can distinguish a square of 4 cm. from a square of 2 or 8 cm., between
a square and a rectangle of equal area, and between figures of various
orientation such as three sides of a square, an L, a vertical or horizontal
line, a cross, and so on ; curiously it was found that difficulties were
experienced in differentiating oblique lines or a circle from a square.
Further, a square of 4 cm. was not confused with a square of 8 cm. at
twice the distance, a differentiation which indicates some spatial
perception.

The facility of *Octopus* in learning to differentiate between horizontal and
vertical lines and its relative difficulty in differentiating oblique lines or such
figures as a diamond and a triangle, suggested to Sutherland (1957) and Dodwell
(1957) that the vertical and horizontal axes have a special status in the discrimination of shape. On this basis Sutherland advanced a theory that the
output from the visual cells of the octopus was so projected in the optic lobes
as to correspond with a vertical and horizontal system of coordinates ; they
would thus correspond with the fundamental coordinates of orientation in space—
the vertical depending on gravity and the horizontal aligned to the visual
horizon.[1] This hypothesis would account for some similar experimental results
obtained by Fields (1932) and Lashley (1938) on the sense of discrimination in
rats ; and it is also interesting that in man, reference to vertical and horizontal components seems to be of primary importance, in association, of course,
with other systems of coordinates, in referring a point in the environment to
the centre of the visual field.

Sepia

Somewhat similar visual reactions can be elicited in the cuttlefish, *Sepia* (Sanders and Young, 1940) ; and the perception of movement by this mollusc is good with an optimum angular velocity of
about 7° per sec. (Boulet, 1954). Indeed, it would seem that *Sepia* is
in some ways more amenable to training than *Octopus* ; if a prawn is
presented as prey and placed behind a transparent glass partition, the
former will desist attacking after several attempts while *Octopus* will
persistently swim straight into the screen ; moreover, the cuttlefish
will pursue a prawn visually round a corner, while *Octopus* will give up
the hunt unless the invisible prey is reached and can be touched by
its exploring tentacles (Sanders and Young, 1940 ; Boycott, 1954)
(Fig. 730). It would seem, therefore, that the two species vary considerably in their dependence on vision for hunting. It would appear,
also, that the former possesses considerable intelligence in that it can
pursue its purposes by indirect means and shows some capacity for
learning.

There seems little doubt, however, that these capacities have been
exaggerated. Pliny—that prolific purveyor of intriguing inaccuracies—in his

[1] p. 669.

Natural History described how *Octopus* would insert a stone between the open shells of a bivalve so that the soft mollusc could be devoured at leisure, an observation repeated by Jeannette Power (1857) to demonstrate the importance of vision in the behaviour of this creature. In her aquarium, she wrote, an octopus holding a fragment of rock in one of its arms, intently watched the lamellibranch, *Pinna*, until it opened its valves. As soon as these were fully opened, she reported that with incredible address and promptitude the octopus slipped the stone between the valves so that they could not close again, and thereupon set about devouring its victim.[1] Piéron (1909) claimed that Octopods were able to uncork a bottle in order to obtain crabs seen through its glass walls ; and other somewhat similar statements appear in the semi-scientific literature. In view, however, of the apparent inability of the octopus to use a " tool," it may well
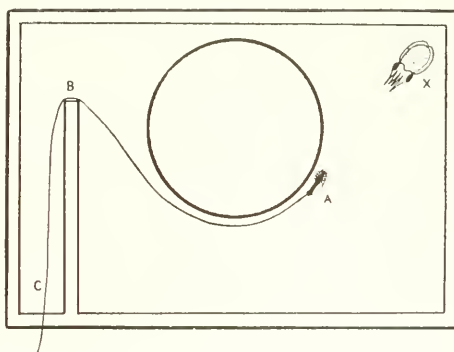

Fig. 730.—The Hunting Capacity of *Sepia*.

Within a tank the cuttle-fish is situated at X. In the tank is a circular opaque bucket and an opaque enamel plate. A prawn to which is attached a long thread is placed at A within sight of the octopod. As soon as its attention had been drawn to it and it had begun to follow the prawn, it was pulled by the thread to position B behind the opaque bucket. The octopod followed, whereupon the prawn was pulled behind the opaque plate to C, again out of sight of its pursuer. The latter would follow around B and thereupon it was allowed to devour its prey (Sanders and Young).

be that such stories are fairy tales or that the incidents were determined rather by chance than by purposive behaviour (Boycott, 1954).
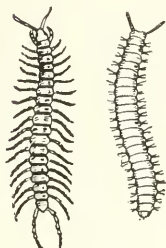
THE VISION OF ARTHROPODS

ARTHROPODS are a phylum so large and amorphous that a study of the visual perceptions of the various types must be taken separately ; this diversity in function follows from an equally marked diversity in habit and is to be expected within a group which contains members smaller than some Protozoa with great simplicity in organization, and others (particularly Insects) which are rivalled in their visual capacity and learning ability only by the higher Mammals. Apart from Insects, however, relatively little is known of the visual

[1] A somewhat similar story was recorded by Leonardo da Vinci (Manuscript H 14) who described how crabs inserted a stone or twig into the open shell of an oyster.

Onychophore,
Peripatus

Centi-   Milli-
pede   pede
(Myriapods)

Daphnia

Lobster

Leander

performance of Arthropods. Among the lower types the tactile sense takes pride of place in biological utility ; in Insects vision is dominant with the sense of smell (centred in the antennæ) a good second.

The ONYCHOPHORA are provided with eyes which merely differentiate the presence or absence of light from which the creature persistently flees. A crude image-formation is possible among the MYRIAPODS ; although *Lithobius* is trainable to the extent that it can master the single turn of a simple T-maze, it does so by its tactile sense on the basis of the texture of the walls (Scharmer, 1935). The visual sense of the smaller CRUSTACEANS is almost certainly similarly crude, but light perception at any rate, with phototactic responses while swimming is well developed. In the Cladocera, particularly the water-flea, *Daphnia*, it has been established by a large number of observers that the phototactic response varies with the wave-length of light so that a differential sensitivity would appear to exist, particularly affecting red and blue.[1] Moreover, an elementary degree of training is possible even in these minute creatures since the positive taxis of *Daphnia* to a source of light through a narrow tube can be rendered less clumsy with experience (Blees, 1918) ; but any such feat as the negotiation of the single turn of a T-maze seems to be beyond the capacity of the small Crustaceans (*Daphnia* and *Simocephalus*, Agar, 1927). These creatures thus seem to be inferior to earthworms in this respect.[2] Some directional sense to light stimuli is probable, and Exner (1891) suggested that the Copepod, *Copilia*, made the most effective use of its simple ocular apparatus, by scanning movements of the stalk-like eye controlled by its system of muscles (Fig. 139).

Not much more is known about the visual functions of the higher Crustaceans, although the anatomical elaboration of their compound eyes with their complex nervous connections would indicate visual potentialities of considerable proficiency. In the lobster, for example, optomotor reactions are readily elicited when the animal is confronted with a black-and-white striped rotating drum [3] ; moreover, reactions differ depending on the colour of the stripe, suggesting the presence of a colour sense or, at any rate, a differential reflex action to different wave-lengths of light.[4] Many of these animals, however, are essentially nocturnal or frequent ocean depths where the paucity or absence of light must preclude acute vision. It is probable, indeed, that as determinants of behaviour the eyes are of secondary importance to the

[1] v. Frisch and Kupelwieser (1913), Ewald (1914), Koehler (1924), Eckert (1935), Heberdey (1936), Heberdey and Kupka (1942), Smith and Baylor (1953). It is to be remembered that these differential responses may be served by different mechanisms—the dermatoptic and the ocular.

[2] p. 573.

[3] *Homarus*—v. Buddenbrock *et al.* (1952).

[4] Schlieper (1926–27), Kästner (1949) in the crab, *Carcinus*, the shrimp, *Crangon*, the prawn, *Leander*.

sensory bristles which are distributed all over the body and appendages, particularly the antennæ. These are of two types, being sensitive to touch or chemical stimuli, and are present in enormous numbers ; in the lobster, for example, there are said to be 50,000 to 100,000 on the pincers and walking legs alone.

A considerable aptitude to training is evident among the Malacostraca but it is based on the tactile sense rather than on vision ; the feat of mastering a T-maze is easily acquired by those species which have been investigated but the aptitude is based on the texture of the walls (Agar, 1927 ; Gilhousen, 1929 ; ten Cate-Kazejewa, 1934 ; and others), and is equally shown by the blind Isopod, *Asellus* (Bock, 1942).
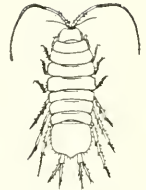
Asellus

THE VISION OF ARACHNIDS

The function of the eyes of ARACHNIDS is very variable and often crude. The smaller species (Acarines) merely respond to the intensity of light, and training experiments with water-mites (Hydracarina) utilizing any sense have been unsuccessful (Agar, 1927). The larger representatives, however, have more fully developed visual functions. The jerrymanders have relatively good vision ; but with the exception of spiders the other Arachnids probably only perceive variations in the intensity of light and movement ; the optics of their ocelli is poor and the number of visual cells small, while visual impressions seem to play an insignificant part in their behaviour.

Jerrymander

THE VISION OF SPIDERS has received more attention than that of any other type (Petrunkevitch, 1907–11 ; Homann, 1928–53 ; Millot, 1949 ; Drees, 1952). It is true that the web-spinners with their rudimentary ocelli of a short effective visual range are not particularly visually conscious, for their behaviour is dominated essentially by their exquisite sense of touch ; any tremor on the web caused by an alighting insect excites their immediate attention, probably while the object causing the tremor is still out of the range of their vision. It is interesting that this sense of vibrotropism is purely reflex, for photography has shown that the waiting spider orientates itself so that the vibrations of the web stimulate the legs on each side equally and then sets out in a straight path for its victim. Similarly, ripple-spiders sit at the water's edge resting their forelegs on the surface waiting to appreciate the ripples set up by an alighting insect. In the same way the vibrations of a tuning fork on the web or in the water will excite the spider to run out as if to capture prey. The more active hunting types, however, which move abroad to chase their prey, base their behaviour progressively upon vision, each element in the ocellar system having a particular function and the whole acting in a curiously reflex manner.

Web-spinner,
Aranea

Wolf-spider,
Lycosa

Evarcha blancardi

The behaviour of the jumping spider, *Evarcha blancardi*, the arrangement of the ocelli of which is shown in Fig. 216, may be taken as an example. It sees its prey (or mate) with the posterior lateral eyes which, situated far back on the head, have a wide field of vision and respond to moving stimuli only ; a stationary object excites no reaction. As the image of the moving object crosses the retinæ of these ocelli, the spider reflexly turns its body in the direction of the object with the result that the image falls on the retina of one of the anterior lateral ocelli, whereupon a further turning movement throws the image on both anterior lateral ocelli and the two central ocelli. If the former ocelli are covered, this second turning movement does not occur. It would seem that the function of these ocelli is to judge distance binocularly, that of the central ocelli, which have a small field and a short range, to perceive the form of the prey ; in each the lens is capable of forming sharp images. A male, for example, acts as if it can distinguish between a female of its own species or a male of its own or another species at a distance of 2 to 3 cm. At a distance of 1·5 cm. it leaps upon its victim with accuracy, but if the lateral anterior ocelli are covered the distance of the leap is misjudged. The posterior lateral ocelli therefore act as the peripheral retina of man, collecting impressions from the whole visual field ; the front row of four eyes acts together as the human fovea, the lateral pair being most useful binocularly at a short distance, the central pair being the chief agent for visual analysis. The small posterior median pair of ocelli, on the other hand, are used for the detection of movement behind the spider.

The reflex nature of the response is illustrated by the automatic movements of the limbs following retinal stimulation. Homann found that on covering the two median ocelli the first pair of legs was held up by the contraction of the femoral muscles and as the animal ran forwards they merely clawed the air instead of touching the ground ; if one of these eyes were covered the foreleg on the blind side alone was held up and the body was tilted sideways.

Despite the apparent automatism of this reflex response, however, spiders display a very considerable degree of visual intelligence. Nowhere is this more aptly illustrated than in the stalking of a fly on a creviced wall by a jumping spider. Spying a fly settled on the wall some distance away, the spider, knowing that the attention of the fly will be excited at once by a moving object, creeps with the greatest care to the nearest crevice in the brickwork. Arrived there, knowing that the fly will soon take wing, it scampers rapidly along the crevice hidden from view until it comes within range of its victim ; thereupon, anchoring it-self by a life-line of silk to the brickwork, it leaps upon its victim with incredible rapidity, hoisting itself back to safety by the silken cord.

Moreover, in their visual activities a considerable degree of sensory analysis exists, for jumping spiders can be negatively conditioned to unpalatable prey, and Drees (1952) found that their form vision is sufficiently effective to allow negative conditioning by means of an electric shock to a response acquired by training to visual stimuli such as triangles and crosses. It is also of interest that the jumping spider has been shown by its response to the optomotor reaction to have a selective sensitivity to orange (Kästner, 1949), a response which may indicate some degree of " colour vision " on a reflex level.

The mastery of a new element and the adventure of the experiences afforded by a third dimension would be expected to give a fillip to the sensory reactions of Insects, while the development of flight with the consequent ease and speed of exploring new environments must stress the importance of efficient distance receptors in the gathering of adequate data for effective orientation. These expectations have been realized ; and to Insects much the most important receptor-organs are the eyes. Indeed, in their efficiency, their capacity to resolve a pattern or to interpret movements, the eyes of Insects excel those of most Verte-brates ; moreover, alone among In-vertebrates many species have a fully developed colour sense, while they have assumed a faculty apparently unique to Arthropods—the power to analyse the plane of polarization of light and orientate themselves there-by. Finally, small though the insect brain may be, and dominated though the creature is by automatic and rigid reflex reactions, it shows an amenability to learning and a power to remember unique in the inverte-brate world.

FIG. 731.—THE HEAD OF THE MOTH SHOWING THE EYES AND THE ENOR-MOUS ANTENNÆ (Richard Cassell).

In the behavioural activities of Insects other senses are also important. The olfactory sense, indeed, would seem to be more fundamental than vision ; thus it has been shown by Schremmer (1941) that newly emerged specimens of the moth, *Plusia gamma*, seek flowers by scent only, this faculty being presumably innate, but that once an association with a particular flower has thus been established, further visits are determined by vision and scent. Moreover, in the recognition of their fellows and as a guide to homing when illumination is ineffective, odour is often a major determinant of conduct ; the male moth, for example, with its extremely sensitive antennæ, is said to find a female a mile or more distant by this means alone (Fig. 731) (Bonnett, 1779–83 ; Turner, 1907 ; Schneirla, 1929–33 ; Carthy, 1950 ; Vowles, 1955 ; Dethier, 1957).

The organs of smell are situated on the last 8 segments of the antennæ and consist of minute pits which are present in large numbers, sometimes up to a thousand on a single joint. The taste organs occur not only on the mouth and labial palps but also sometimes on the antennæ and the feet. The sense of touch is subserved by minute hairs associated with the antennæ, the maxillæ and the face ; the setæ are non-living but each has a sensory cell at its base with nervous connections. Many species are without ears but they are certainly well developed in insects capable of producing sounds : when they are present each

ear consists of a pit filled with air or fluid across the opening of which is stretched a drum-like membrane. In some Orthoptera the ears are on the shanks of the front pair of legs or on the sides of the abdomen above the base of the third legs ; in others on the first segment of the body ; in blow-flies under the bases of the wings ; in gnats on the bases of the antennæ ; and so on. In all the sense organs there is a considerable variation between species, while there may well be one or more types of sense organs with which we are not familiar that have no counterpart in the vertebrate sensorium.

The visual function of the LARVÆ OF INSECTS is relatively crude, a necessary corollary of the simplicity of the structure of the stemmata. In the more simple forms a crude sensitivity to light is the only possible response, but in the more elaborate forms, particularly when the eyes occur in groups, a coarse mosaic imagery with some degree of form vision is possible.[1] It may well be that the pendular movements of the anterior part of the body exhibited by so many caterpillars are an expedient to mediate form vision by scanning movements with the simple apparatus available, the visual impressions being perhaps coordinated with proprioceptive stimuli derived from the motion. The entire group of stemmata functions as a unit and if all are covered except one, form perception is lost and only phototactic responses remain (Friederichs, 1931 ; Dethier, 1942–43). The fact that the caterpillars of butterflies (*Vanessa*) are attracted by green leaves or paper of the same colour suggests the possibility of a crude colour sense (Götz, 1936). Finally, the stemmata of some species are capable of utilizing the pattern of polarization of light as a means of orientation.[2]
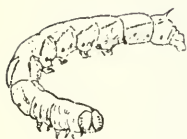
Caterpillar

The function of the DORSAL OCELLI OF ADULTS is more problematical ; since their principal focus does not coincide with the retinal plane, they are ill-designed for image-formation although well adapted to admit light (Homann, 1924 ; Wolsky, 1930–31 ; Cornwell, 1955). Any capacity for the perception of form is therefore probably negligible. In view of the facts that some insects with only their ocelli uncovered behave as if blind and that the reflex responses of the compound eyes to light are less rapid when the ocelli are covered, it has been suggested that the ocelli are stimulatory organs which accentuate, although they do not initiate, phototactic responses.[3] In other species, however, they have been shown to participate fully in the activities of the animal,[4] while they are the only effective organs in those species in which compound eyes are lacking.[5] Moreover, it was shown by Wellington (1953) that the ocelli of the flesh-fly, *Sarcophaga*, are sensitive to

Sarcophaga

[1] Larvæ of the tussock-moth, *Lymantria*—de Lépiney (1928) ; of the beetle, *Cicindela*—Friederichs (1931).

[2] Saw-fly, butterfly—Wellington *et al.* (1951), Wellington (1953) (p. 66).

[3] In ants—Homann (1924) ; bees—Müller (1931) ; the fly, *Drosophila*—Bozler (1925), Parry (1947), Cornwell (1955).

[4] In the bug, *Cryptotympana*—Chen and Young (1943) ; the flesh-fly, *Sarcophaga* Wellington (1953).

[5] p. 221.

changes in polarized light and thus aid in orientation. In the locust, illumination of the compound eye produces on- and off-spike potentials in the ventral nerve cord, of the ocelli off-responses only (with perhaps a very brief on-response, Hoyle, 1955) ; the former responds to movements of an external object while the latter does not (Burtt and Catton, 1954–56). It would thus seem obvious that the function of the ocelli of Insects varies in different types depending on such factors as the degree of development of the compound eye and the habits of the species.

Locusta

THE COMPOUND EYES OF INSECTS, on the other hand, possess functional attributes of a high order which have been extensively investigated [1] ; their appreciation of light and colour as well as form, movement and spatial relationships compares well with that of many types of Vertebrates. Moreover, in some insects the compound eye, occasionally in addition to the ocelli, can appreciate changes in the polarization of light.[2]

More study has been devoted to the function of the compound eye of Insects than to the eyes of any other Invertebrate. The two classical methods of approach [3] have been adopted—behavioural experiments and reactions based on the electro-physiological characteristics of the eye on stimulation by light. The first is the more informative in that it gives some idea of the sensations appreciated by the insect concerned, but insofar as many insects are untrainable perhaps because of their automatism, perhaps because of lack of intelligence, the method is by no means universally applicable. It is always to be remembered, of course, in interpreting the results of the second method, that physiological responses on a reflex level need not necessarily ascend into the level of consciousness and can only be translated with the greatest reserve into terms of sensation.

Behavioural experiments depending on the laying down of conditioned reflexes can be made available for the investigation of the responses of many insects ; the honey-bee, *Apis*, for example, can be trained to go to a container with sugar placed beside a black disc and avoid one marked with a black cross (v. Buddenbrock, 1937). Unconditioned reflex responses such as the optomotor reaction to black and white stripes on a moving drum are also readily elicited in many insects. Again, the honey-bee is very sensitive to stimulation of this type, responding if stationary by a reflex sideways movement of the head and thorax ; if it is crawling it makes a sudden change of direction opposite in sign to that of the movement of the environmental pattern. In similar circumstances the fruit-fly, *Drosophila*, will completely

Apis

Drosophila

[1] See among others, Eltringham (1933), v. Frisch (1950), Wigglesworth (1953).
[2] p. 66.   [3] p. 568.

reverse its direction of movement, a reaction repeated with dramatic precision on each occasion and in rapid succession on repeated stimuli. If the field is kept stationary a moving insect shows the same type of response to the shift of the retinal image produced by its own movement (v. Buddenbrock and Moller-Racke, 1952).

The electro-physiological characteristics of the visual mechanism have recently been applied with considerable success to the physiology of the compound eye. Depending on the type of electrical response on stimulation by light, two distinct physiological types have been differentiated by Autrum and his co-workers (1948–53).

(1) FAST EYES, *found in rapidly flying diurnal insects* (the blow-fly, *Calliphora*, the bees, *Apis* and *Bombus*, the wasp, *Vespa*, and so on). On stimulation by light the electro-physiological characteristic of such an eye is a diphasic wave made up of an initial positive response indicating the on-effect, followed by a terminal negative response indicating the off-effect ; on prolonged stimulation the initial positive response subsides rapidly. In such an eye there is a high temporal resolution with a response to intermittent stimulation in the form of flicker up to 250 or 300 stimuli per sec. The absolute threshold of sensitivity to light is, however, high ; the reaction is little affected by light- and dark-adaptation ; and the optomotor response shows an ability to discriminate between stimuli of 200 per sec.

(2) SLOW EYES, *seen in nocturnal, aquatic or slow-moving insects* such as the grasshopper, the water-beetle, *Dytiscus*, and cockroaches (as well as *Limulus*). Such an eye is characterized by a low threshold of flicker to intermittent stimulation up to 40 to 50 per sec. ; the absolute threshold of sensitivity is low ; the reaction changes markedly in light- and dark-adaptation ; and the subjective optomotor response can be obtained only by stimuli up to 5 to 10 sec.

The experimental evidence makes it probable that the characteristic properties of these two types of eye are attributable more to the central neurones than to the end-organ, particularly to the first optic ganglion [1] (Autrum, 1951–54 ; Autrum and Gallwitz, 1951). The optic lobes of both types are the source of spontaneous electrical oscillations [2] elicited by the onset or cessation of stimulation ; in the slow type of eye the frequency of these rhythms lies between 20 and 35 cycles/sec.; in the fast type, between 120 and 160/sec. (Adrian, 1937 ; Roeder, 1939–40 ; Crescitelli and Jahn, 1942 ; Massera, 1952 ; Autrum, 1952 ; Burkhardt, 1954), and it is noteworthy that the fast type can be converted into the slow type by the surgical removal of portions of the optic lobe (Autrum and Gallwitz, 1951 ; Autrum, 1951–52).

In general, insects respond to the short waves of the spectrum rather than to the long. The cornea (of the bee, *Apis*, and the flesh-fly, *Sarcophaga*) is transparent to wave-lengths as short as 253mμ, the

Bombus

Vespa

Dytiscus

Cockroach

[1] p. 524. [2] p. 524.

tracheal tapetum fluoresces in ultra-violet light and it would seem probable that the retinal cells are sensitive to rays of this type (Lutz, 1924–33 ; Bertholf, 1930–32 ; Lutz and Grisewood, 1934 ; Carter, 1948). Photo-negative insects such as the ant thus take shelter from ultra-violet light unseen by the human eye (Lubbock, 1885 ; Forel, 1886) and light-seeking insects such as moths and bees are attracted by it (Fig. 732) (Lutz, 1924–33 ; Lutz and Grisewood, 1934). On the other hand, although some species [1] undoubtedly respond to red (up to 690 mμ), most are not attracted by this colour because of the high threshold but treat red as black.[2]

In optomotor experiments when dark and light grey stripes are

Ant

Moth

578 · 492 436 405   365

FIG. 732.—THE SPECTRAL SENSITIVITY OF THE HONEY-BEE.
Indicating the attraction of the ultra-violet part of the spectrum. The numbers indicate wave-lengths in mμ (Tinbergen, after Kühn).

used, the *discrimination of luminosity-differences* is found to be generally low—about 20 times lower in the bee than in man, and in some other insects poorer still (Wolf, 1933 ; Hecht and Wald, 1934 ; v. Budden-brock, 1935 ; Hundertmark, 1937–38). When coloured light is used as a stimulus it is found that the most effective parts of the spectrum are generally in the yellow-green and ultra-violet, particularly the latter (Fig. 733).[3] The spectral location of the first region corresponds closely to the peak of the luminosity-curve in man, the variation in some insects resembling the human dark-adapted state (*Apis*) and

[1] Such as butterflies (*Pieris, Vanessa*—Ilse, 1928), fire-flies (*Photinus*—Buck, 1937) and locust hoppers (*Locusta*—Chapman, 1954).
[2] The honey-bee, *Apis*—v. Frisch (1914), Kühn (1927) : the wasp, *Vespa*—Schremmer (1941).
[3] 553 mμ in the yellow-green and 365 mμ in the ultra-violet for the bee, *Apis*, (Bertholf, 1931–32 ; Sander, 1933 ; Weiss *et al.*, 1941–43 ; and others). 540 mμ for the equal energy spectrum in *Drosophila* (Médioni, 1956). The same applies roughly to Crustaceans (p. 578).

in others the human light-adapted state (*Pieris*) (Schlieper, 1927–28 ; Ilse, 1932). The electroretinogram obtained on stimulating the retina with different wave-lengths also shows a curve resembling the absorption-curve of visual purple in Vertebrates (the grasshopper, *Melanoplus*—Jahn, 1946). The occurrence of a Purkinje shift towards shorter wave-lengths in decreasing intensity of light in some insects suggests the presence of two receptor mechanisms (*Drosophila*— Fingerman and Brown, 1952–53) ; in this connection the presence of twin-peak sensitivities in electroretinograms is also of interest (at 630 and 540 mμ in *Calliphora*—Autrum and Stumpf, 1953). These, of course, are measurements of the threshold of physiological response, not of sensation.

Calliphora

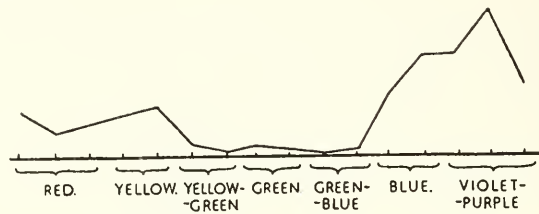| RED. | YELLOW. | YELLOW-GREEN | GREEN | GREEN-BLUE | BLUE. | VIOLET-PURPLE |

Fig. 733.—Colour Vision in Insects.

A chart showing the relative number of visits of *Gonepteryx rhamni* to papers of different colours during the feeding phase (after Ilse).

The capacity for *colour vision* in insects has given rise to some controversy. It would seem reasonable to suppose that the brilliant colours of flowers would be œcologically linked with the insect visitors on which so many plants depend for their propagation. Such a suggestion demands that flower-visiting insects, which reciprocally depend on the flowers for their food, should appreciate and differentiate the variegated riot of colour evolved for the mutual benefit of both. It must not be thought, however, that colour vision in insects is confined to those that visit flowers or that its function has been evolved specifically for this purpose and none other ; the flower-visiting beetle, *Cetonia*, for example, is colour-blind, whereas the dung-beetle, *Geotrupes*, is endowed with a well-developed colour sense. However that may be, it has long been accepted for this reason that most insects are possessed of colour vision. The first to extricate this problem from the vagueness of speculation and subject it to scientific analysis was Sir John Lubbock (1885) who applied the relatively simple but somewhat inconclusive technique of " preferential choice." [1] On exposing honey on coloured cards and recording the frequency with which each was visited, he found that the honey-bee exhibited a substantial degree of colour differentiation with a marked preference for blue. At a considerably

Cetonia

Geotrupes

[1] p. 568.

later date, however, Carl von Hess (1913) concluded on the basis of similar experiments that this insect moved towards different lights depending on their relative intensity and that it was colour-blind ; but von Frisch (1914–50), in a long series of well-controlled experiments wherein other factors were excluded, confirmed Lubbock's original conclusion and demonstrated that, after training, the bee reacted selectively when presented with sugar-water associated with differently coloured squares on a checkerboard, preferring blue and yellow to other hues. These results were corroborated in the bee by Kühn and Pohl (1921) and Kühn (1927), who used pure spectral colours, and by various techniques in other species (Fig. 733).[1]

The results of the earlier investigators gave the impression that the bee was only able to distinguish between two groups of colours, the yellow group and the blue-violet group ; but although this applies in a general way to their reaction to the colours of flowers in nectar-hunting, it was later demonstrated that this insect was able to distinguish several colours within each group if trained to show differential responses (Lotmar, 1933). Thus after training to bands of spectral light, bees have been found to distinguish four regions : 650–500 mμ (red-green), 500–480 mμ (green-blue), 480–400 mμ (blue-violet), and 400–310 mμ (ultra-violet), the last being probably perceived as a colour (Kühn, 1927 ; Hertz, 1939). At a later date Daumer (1956) interpreted the reactions of bees as mediated through 3 types of receptors—yellow, blue, and ultra-violet. Red flowers seem to be distinguished because of their reflection of ultra-violet. The colour system of the bee is therefore widely different from that of man.[2] Moreover, on testing optomotor reactions, von Buddenbrock and Moller-Racke (1952) concluded that butterflies have three receptors—an orange-red, a yellow and a green-blue. It would thus appear that different species have different types of colour vision (Ilse, 1928–49 ; Schlegtendal, 1934), while some may be colour-blind.[3] Finally, various regions of the compound eye may react differently : thus the antero-ventral portion of the eye of the water-boatman, *Notonecta*, is equally sensitive to all colours while the dorso-posterior part shows preferential differences in colour-sensitivity (Lüdtke, 1938–54 ; Rokohl, 1942 ; Resch, 1954).

It is interesting that different mechanisms are applied in different activities since innate reactions show a selective responsiveness to very different stimuli ; one reaction may be released by the intensity of light, another by its wave-

Bombylius

Dixippus

Notonecta

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[1] The bee-fly, *Bombylius*, and the hawk-moth, *Macroglossa*—Knoll (1925–26) ; butterflies, *Pieris, Gonepteryx* and *Vanessa*—Ilse (1928), Tinbergen *et al.* (1942); the aphid, *Myzus*—Möricke (1950) ; the fruit-fly, *Drosophila*—Fingerman and Brown (1952–53).

[2] And also different from that of birds which are attracted preferentially to red flowers (p. 630).

[3] Such as the nocturnal stick-insect, *Dixippus*, and the bug, *Troilus* (Hundertmark, 1936–37; Schlegtendal, 1934).

length ; in one response the bee may act as if colour-blind, in another as if
partially so, and in a third it may show a wide discrimination of hues. In the
same way the hawk-moth, *Macroglossa*, selects yellow and blue objects when
hungry, yellow-green backgrounds for oviposition, and dark surroundings of
any colour for hibernation (Knoll, 1925–26). This restriction of a specific
response to a few " sign-stimuli " rather than to all possible environmental clues
is of wide application ; it is well exemplified in the apparent blindness of the
water-beetle, *Dytiscus*, in its hunting reactions [1] and is by no means confined
to Insects.[2]

Musca

The perception of form in insects appears to be rudimentary. The
visual acuity as measured by responses to revolving striped drums is
relatively low (Hertz, 1929–39 ; Hecht, 1931)—about 1/100 that of
man in the bee, 1/1,000 in *Drosophila* (Baumgärtner, 1928 ; Hecht and
Wolf, 1929 ; Hecht and Wald, 1934 ; Gavel, 1939 ; Roeder, 1953),
while in the house-fly, *Musca*, the narrowest stripe that can be
perceived subtends an angle of 5° (Gaffron, 1934) (in man, 1'). These
results of behavioural experiments correspond with the theoretical
acuity deduced from the structure of the eye (Pütter, 1908 ; Best,
1911).[3]

Butterfly, *Vanessa*

As would be expected from their low standard of visual acuity,
the capacity of insects to analyse a pattern is relatively poor. It is
true that experiments have shown that bees and butterflies can be
attracted by broken or checkered figures and divided contours to
which they have been trained, a response which confirms the biological
value of " honey guides " on flowers (Zerrahn, 1933 ; Hertz, 1935 ;
Bolwig, 1938).[4] It is also true that the honey-bee can be trained to
seek a sugar-container associated with a black disc and avoid one
associated with a black cross or can differentiate four parallel lines
from a black circle ; but it cannot be conditioned to distinguish
between a black cross and four parallel lines on a white surface (von
Buddenbrock, 1952). In order to allow the discrimination of patterns,
therefore, the differences must be gross. It is probable, indeed,
particularly in so far as the " fast " type of eye is concerned, that the
response is less to the recognition of the configuration of objects than
to the frequency of change of retinal stimulation (Wolf, 1933–37) and
that fast-flying diurnal insects resolve the spatial display of a pattern
into a temporal display of sequential stimuli. The method of interpreta-
tion of slow-moving, nocturnal or aquatic insects is not yet known.

From these characteristics it follows that moving objects excite

[1] p. 103, Fig. 74.   [2] p. 664.   [3] p. 171.
[4] It must not be thought that all the adult bee's activities in visiting flowers
for honey are determined by vision. At relatively close quarters the sense of
smell is important. Bees can be trained to react to scent alone. Moreover, when the
insect lands on the flower, taste-organs which occur not only on the mouth but on
the antennæ, labial palps and feet, come into play. In the search for honey, therefore,
the eyes are the distance-receptors, the organs of smell the intermediate, and of taste
the contact-receptors. See Bolwig (1954) and others.

attention and stationary objects tend to be neglected. This tendency is borne out, as we have already seen [1] in behavioural experiments involving the optomotor response to a striped drum which shows a high flicker-threshold up to 200 per sec. in the bee,[2] the corresponding figures in man as measured by the fusion frequency of flicker being 50 to 100 depending on the intensity of illumination and the size of the field stimulated (Collins and Hopkinson, 1954); similarly, the fusion-frequency as measured by the changes in the electrical potential of the retina in many insects, particularly of the rapidly flying diurnal type, may reach very high values,[3] a capacity doubtless correlated with the need to resolve succeeding impressions during flight. It would thus seem that in their activities insects depend much more on the primitive faculty of the appreciation of movement than of form. The widely over-lapping visual fields of the compound eyes allow *perception of distance*, a power of judgment which is impaired if one eye is obscured (Homann, 1924): and behavioural experiments show that a high degree of *spatial appreciation and localization* is possible (Tinbergen, 1932–38 ; Wiechert, 1938). The extraordinary capacity of some insects for memorizing and recognizing landmarks in their territory has already been discussed at length.[4]

Fig. 734.—The Praying Mantis, *Mantis religiosa*

Sitting on a leaf. Note the large and prominent eyes and the " praying " position of the front legs. The terminal part of the bent fore-leg with its powerful joint resembles a pen-knife, normally held half open ready to snap shut against its " sheath " with the prey trapped between (photograph by Michael Soley).

The dependence of insects on visual stimulation by moving objects is seen in the every-day behaviour of the ordinary house-fly which neglects stationary objects but immediately absconds on the first suggestion of movement. It is also exemplified in a striking way by the habits of the praying mantis (Fig. 734) ;

[1] p. 583.
[2] 60 stimuli per sec. in *Aeschna* nymphs, Sälzle (1932), and in *Anax* nymphs, Crozier *et al.* (1937) ; see also Autrum and Stöcker (1952), Autrum (1954).
[3] 95 per sec. in the ocellus of the bee (Ruck, 1954) and of the order of 165–300 stimuli per sec. in the compound eye of this insect, or 265 per sec. in the blue-bottle *Calliphora* (Autrum and Stöcker, 1950 ; Autrum, 1952). Corresponding measurements in man with the electroretinogram are 25–30 for the scotopic and 70 for the photopic fusion frequency (Wadensten, 1956).
[4] p. 78.

the adjective, incidentally, applies not to the habits of the insect but to its characteristic stance with its front legs raised as if in an attitude of prayer. The female is a particularly anti-social creature who will eat anything in sight, including her mate. Since she can only see moving objects, the male approaches her with staccato movements, standing motionless whenever she looks in his direction, exactly in the manner of the children's game, Grandmother's Footsteps. Fortunately, the male has better vision than the female and usually manages to approach her in this cautious manner until he can leap upon her ; but the end is usually the same because he is generally eaten either while mating is in progress or after it is finished.

ACCOMMODATION IN INVERTEBRATES

The relative simplicity of the eyes of Invertebrates would not lead us to expect elaborate accommodative facilities ; from the functional point of view, of course, the degree of visual acuity of most types would not merit a complicated mechanism of this nature. In rare cases a muscular apparatus provides an active method of accommodation somewhat analogous to that characteristic of Vertebrates. An exceptional device is a forward movement of the lens by increasing the contents of the globe by secretory activity. More often, however, any accommodation that is present is static in nature and depends on the provision of different optical systems in the same eye or in different eyes, one being adapted for distant vision and the other for near.

Cephalopod,
Loligo

An active muscular apparatus to produce an accommodative change of focus is seen in its most elaborate form mainly among Molluscs ; it acts primarily by compressing the globe, that is, altering the position of the lens secondarily, a method of accommodation, incidentally, adopted by snakes.[1] Such an accommodative mechanism is seen in its highest form in the eyes of Cephalopods (Figs. 113, 114). Beer (1897), Heine (1908) and Pflugk (1910) considered the eyes of Cephalopods to be normally myopic (— 2 to —10D), but v. Hess (1909) found them to be emmetropic or slightly hypermetropic. This author concluded that a considerable degree of amplitude of accommodation is effected by the forward displacement—not the deformation—of the lens, the mechanism being the relatively simple one of compression of the globe by the contraction of the ciliary muscle, an action which raises the intra-ocular pressure so that the vitreous pushes the lens forwards passively, thus producing a positive accommodation of 10 to 14 dioptres (v. Hess, 1909; Alexandrowicz, 1927); this effect can be abolished by atropine (v. Hess, 1909–12) and augmented by electrical stimulation of the cerebral ganglion (Magnus, 1902).

A somewhat similar method is seen in the Heteropod, *Pterotrachea* (v. Hess and Gerwerzhagen, 1914). The accommodation of the pulmonate, *Onchidium*, is closely allied : a muscular collar surrounds the distal part of the eye which, on contraction, alters the shape of the globe in an analogous manner. In the cockle, *Cardium*, the whole globe is invested with muscular fibres the contraction of which may serve as a similar and very primitive accommodative device.

[1] p. 648.

A different type of muscular mechanism appears to occur in the Copepod, *Copilia* (Fig. 139) ; the long slender muscle running along the side of the elongated eye may not only move this organ in different directions but also act by altering the distance between the lens and the receptor elements and thus provide an accommodative adjustment. This is reminiscent of the way in which Cyclostomes accommodate.[1]

A unique method appears to be present in the elaborate eyes of certain Polychætes such as *Alciopa* (Fig. 112). It is said that stimulation of the secretory cell increases the volume of the " distal vitreous " lying immediately behind the lens, and it has been suggested that this pushes the lens forwards to accommodate the eye for near vision. In this eye there is in addition an accommodative muscle similar to that in Cephalopods the contraction of which should also be effective (Demoll, 1909 ; v. Hess, 1914).

These active mechanisms, however, are exceptional. More usually, accommodation is achieved by the static device of the presence of two optical systems in different parts of the eye. The simplest example of this is seen in the ocelli insects. In the grasshopper, for example, there is a double curvature on the proximal surface of the corneal lens which thus acts after the manner of a bifocal spectacle lens and seems to be capable of producing two images at different distances (Tümpel, 1914).

By its nature the optical arrangements of the compound eye do not admit accommodative adjustment, but this is rendered unimportant in the mosaic type of vision. It would seem, however, that the different optical configurations seen in different segments of certain compound eyes which are so arranged that in one region there are short ommatidia and powerful lenses and in another region long ommatidia and weak lenses, may provide alternative focusing mechanisms. This is seen in its most dramatic degree in composite compound eyes such as those of some Ephemeroptera and Diptera (Dietrich, 1919) and some Hemiptera (Weber, 1934) (Fig. 140), and of certain pelagic Schizopods wherein one part is adapted for near and the other for distant vision (Fig. 141) (Hesse, 1908).

Finally, two separate eyes may exist, one optically adapted for distant objects and the other for near. This is exemplified in the median and lateral ocelli of spiders,[2] while the same expedient is also adopted in the dorsal and ventral compound eyes of the whirligig beetle, the former being adapted for aerial and the latter for aquatic vision (Fig. 231).
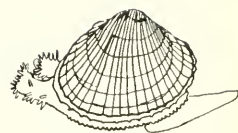
Cardium

Copilia

Grasshopper

Whirligig beetle

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