CHAPTER V

THE EMERGENCE OF VISION

In the varying reactions of living organisms to light that we have now studied, in some cases vision does not—or need not—co-exist, in others an associated sensory impression is conjectural and unimportant while in others it seems to be a necessary accompaniment ; indeed, it is no easy matter to decide where its origin lay or when the sense of vision first became a factor in conscious behaviour. There are many creatures which have no eyes (as we understand the term) and yet " see " (using the word in its widest sense) ; and equally reasonably it may be said that there are many which have what we may well call " eyes " and yet see not.

To a considerable extent the matter is one of definition ; on the one hand, few would acquiesce with Max Schultze (1868) who spoke of the transformation of luminous into nervous energy as vision ; more would agree with Hesse (1908) who contended that the *light-sensitiveness* of primitive creatures did not imply the possession of a *light sense.* On the other hand, there are those who would ascribe to all animals which react to light a sentiency, no matter how vague (McDougall, 1933). To many this may seem gratuitously anthropocentric ; for if such an awareness, tinged with affective tone, is ascribed to the amœba as it flees from a bright light and expands in mid-intensities of illumination, is it to be ascribed also to the speedwell which opens its petals to the mid-morning sun? The question is disputable ; but whichever attitude we adopt the most illegitimate premise from which we can reason is the assumption that an organism has the same appreciation of light and patterns of shade or hue as ourselves, whether it reacts diffusely without specific end-organs or whether it is possessed of eyes more highly differentiated for the resolution of visual images than the relatively simple eyes of man.[1]

It must be remembered, however, that vision is one of the latest senses to be evolved and that in its phylogenetic development it lingered long behind those depending on mechano-receptors and chemo-receptors. Even when a considerable stage of complexity had been reached there was little attempt at discrimination ; for this purpose reliance was placed upon those senses which are more fully developed in primitive life—the tactile sense, the chemical sense, and the olfactory sense. The great majority of animals are non-visual

[1] The few sign-stimuli to which the vision even of birds is limited are striking examples (p. 66

creatures depending essentially in their behaviour on non-visual stimuli.

For example, the scallop has numerous visual cells around the edge of its mantle, and if these are stimulated by the "sight" of its enemy, the starfish, no response except the awareness of the presence of something is elicited, and no attempt at flight is made ; but whenever some extract of starfish is added to the water in which the animal lies, the scallop immediately runs away (Dakin, 1909 ; von Uexküll, 1921). Moreover, in *Pecten*, no response is called forth until the object moves, and any movement of any object excites the same response, a protrusion of the tentacles ; these are endowed with organs of

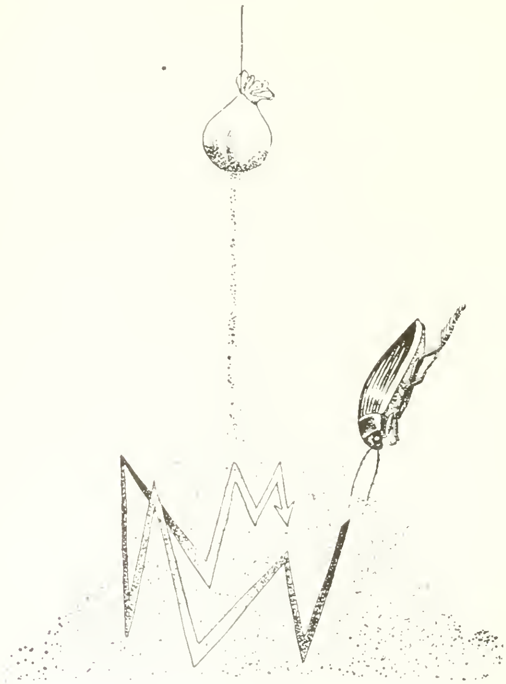

Fig. 74.—The Sensory Reactions of the Water Beetle.

A watery meat extract is contained in the bag. The feeding responses of *Dytiscus marginalis* show its dependence on chemical stimuli rather than visual (Tinbergen, *Study of Instinct* ; Clarendon Press).

chemical and tactile sensitivity which explore the object "intelligently", and on the results of their findings the animal either eats or flees (Dakin, 1910). The purpose of this response is obviously to secure further information in a form in which it is analysable. Even in man the olfactory sense organs are relatively more fully developed than the visual at birth ; a fish with its olfactory nerves severed ceases to feed spontaneously (Steiner, 1888) ; and the lately-born rabbit will die of starvation if deprived of the sense of smell because it cannot find the teats of its mother, even although it has been allowed to make use of its eyes before it has suffered the loss of the more fundamental sense.

It must also be remembered that even although vision is well developed it may not be used in many innate reactions for the efficient execution of which it would appear to us to be of value. The feeding response of the carnivorous water-beetle, *Dytiscus marginalis,* is a good example of this (Tinbergen, 1936) (Fig. 74). This beetle has elaborately developed compound eyes and can be trained to respond to visual stimuli. Its feeding response, however, is released only by chemical and tactile stimuli, and visual impressions, even those of a moving prey, never release this reaction. Thus in the presence of a watery meat extract it neglects the source but, going to the region of highest concentration, it attacks any solid object it touches.

Of the three fundamental effects of light on living organisms—the stimulation (or occasionally the depression) of metabolic activity, the orientation of movement, and the control of pigment and colour—it would be reasonable to assume that the first, equally shared between plants and animals, does not necessarily involve vision as a conscious experience, occurring as it does in Protozoa and eyeless types.[1] In its more primitive form this activity may conjecturally be accompanied by a vague sentiency, but this can be little more than an awareness of light, and even in its most advanced forms it is essentially a chemical or hormonal function for the implementation of which eyes are effective but not unique receptors. The last—the control of colour—is a late evolutionary development, and although poikilochromic reactions would appear to occur without conscious accompaniment, in their higher developments they would seem to imply the existence of a visual sense in the organism for whose benefit (or confusion) they are intended. The economy would seem unnatural and contrary to all biological trends that at one time urged all plants except the modest Cryptogams, in their struggle for existence in a cooling world, to luxuriate so shamelessly in the blatant sexual exhibitionism of flowering if the pollinating insects could not both see and appreciate their charms ; their appreciation, however, has probably no resemblance to the interpretation of the same imagery by the human brain. Equally uneconomic would be the scandalously attractive dress put on by many fishes and birds for their love-making. Clearly, if they are endowed with biological usefulness and survival-values, allæsthetic characters—and without these endowments they would not persist—must be appreciated by other organisms.

Although the eyes serve as the receptors for many adaptive colour changes, this function need not imply that the animal itself has any conscious appreciation excited by shifting visual patterns. Even when the responses are mediated nervously and are rapid and complex, as in teleostean fishes, they show no parallelism with what is known of the visual functions of the animals concerned, for reflex alterations of the chromatophores may occur to suit differences in shade of the back-

[1] Such, for example, as the white cave crayfish, *Cambarus ayersii* (Wells, 1952).

ground too small to excite visual discrimination in training experiments. Many of the reactions, as we have seen, are hormonal ; some may occur in eyeless animals ; and indeed, in species wherein these organs are necessary for their occurrence the chromatophores may still respond if the eyes are transplanted to a new location in the body (as was demonstrated in the adult fish, *Fitzroya lineata*, by Szepsenwol, 1938). Temperature and humidity, as seen in Amphibians and Reptiles, may be equally or more effective stimulants in comparison with light, and although heat and light usually coincide in natural surroundings, the paling of the desert lizard in the heat of noon so that it blends with the sand is fortuitous so far as its own vision is concerned. Tactile organs are sometimes adequate receptors as is seen in the control of chromatophores by the suckers of Cephalopods (Steinach, 1901) ; while the adoption of a brown colour by the European tree-frog, *Hyla arborea*, when it steps on a rough surface and of a green colour on a smooth surface brings about an environmental adaptation to a background of tree-bark or leaves respectively as adequate as any photic response. Indeed, many of these colour reactions are fortuitous so far as adaptation to a background is concerned ; thus the iguanid lizard, *Anolis*, turns green in the shade and brown when exposed to light, and it is merely coincidental that in its natural haunts it usually becomes invisible on a background of shady foliage in the first event or of soil in the second, since, if it is removed from the shade upon a green leaf and placed in the sun still sitting on the leaf, it promptly changes its colour into a vividly contrasting brown (Wilson, 1939).

It is essentially from the primitive motor response to light that vision almost certainly developed. In natural circumstances these tropisms and taxes are invariably of biological utility, and it would appear that *the essential and primary function of vision was the control of movement in order to attain an optimum environment as efficiently as possible*, a function which is eventually employed for the avoidance of obstacles, the pursuit of prey and flight from enemies, and survives in man in the close relationship between the eyes and the vestibular apparatus and in their importance in the control of posture. It follows that visual organs are found almost solely in actively moving animals, while in such as assume a sedentary phase they tend to degenerate and disappear.[1]

The stage at which these motorial responses to light evolved beyond purely reflex acts below the level of consciousness and became endowed with awareness is impossible to conjecture. This question has given rise to a controversy which is still unsettled.

In the simple philosophy of Aristotle [2] and for 2,000 years thereafter no argument arose ; plants had a vegetative soul responsible for growth and repro-

[1] p. 721. [2] p. 28.

duction, to animals was added a sensitive soul governing movement and sensation, and to man a rational soul. But doubts occupied men's minds particularly in the seventeenth and eighteenth centuries in the long disputation between the materialistic French Cartesians who followed Descartes (1596–1650) and the English Newtonians who were inspired by Newton (1642–1727) on the one hand, and the mystic German Nature-philosophers on the other, the disciples of Paracelsus in the classical tradition, who found philosophical expression in Leibnitz (1646–1716) and Goethe (1749–1832). To the first the universe was essentially mechanical ; to the second not only living creatures but minerals and chemical compounds were permeated by a directive vital force. A middle view was represented by Lamarck (1744–1829) who claimed that the lowest organisms were insensitive and that their conduct was completely governed by external factors, driving forces derived from the environment ; but as the evolutionary scale was ascended and a centralized nervous system was acquired, organisms generated their own " sentient intérieur " to a progressivly greater degree, thus attaining an ever-increasing measure of self-determination until Vertebrates were reached, at which stage intelligence became possible and ultimately found its fullest expression in Man. Each of these views has been maintained in recent times—the simple reflexology represented by Loeb (1918) and the Russian school (Sechenov, 1863 ; Bekhterev, 1913 ; Pavlov, 1926–27) on the one hand, and the purposive or " directive " psychology represented by Whitehead (1929), McDougall (1933) and Russell (1934–45) on the other, wherein vital force has been replaced by the " general drive " of modern biologists, a state of tension or action-energy which activates living organisms. Each view would find its advocates today.

The mechanistic view would place the emergence of visual reflexes into the plane of consciousness as a late development. This attitude found its apostle in Jacques Loeb (1906–18) [1] who considered that all the orientating and instinctive reactions of the lower animals to light or other stimuli were mechanically determined ; although in many cases it seems to respond voluntarily and often purposively, the movements of the phototactic animal are those of a robot ; it is forced to go where it is taken by its reflexly-driven cilia, legs or wings, an activity in which consciousness or vision has no place. Even an ant with all its proverbial intelligence orientates its journey to light unthinkingly as does a sleep-walker or an automaton [2] and in this respect is as unteachable as a machine, completely totalitarian and incapable of individual adjustment.

It must be remembered that the new science of cybernetics has demonstrated that similar reactions, sometimes of astonishing complexity, can be carried out by non-vital mechanisms, those curious electro-mechanical first cousins of computing machines, which by a combination of photo-cells, amplifiers, motors and automatic governing devices, can simulate many of the reactions of living things, not in appearance but in behaviour, as they navigate themselves around the play-room of the electronic engineer (see Ashby, 1952 ; Walter, 1953 ; and others). Such mock-biological robots, goal-seeking and self-regulatory, capable of the storage of information and possessed of a rudimentary type of memory

[1] p. 28. [2] p. 68.

maintained by electrical oscillations, have been constructed so that they can explore their environment with an apparent purpose. A photo-cell can serve as a receptor and amplifiers and motors can be interconnected in such a way that a positive taxis (for example) to a moderate light and a negative taxis to bright light (or to material obstacles, gradients, etc.) can endow it with the faculty to discriminate between effective and ineffective behaviour, to seek actively an environment with moderate and optimal conditions, to acquire conditioned reflexes, and even to perpetuate its activity and " feed " itself with electricity by being optically attracted to a charging circuit when its batteries begin to fail.

On the other hand, there are those who consider that such automata have little resemblance to even the simplest living things ; their behaviour has only a superficial appearance of being dominated by taxes and kineses, by memory, habituation or trial-and-error learning. The school of biological philosophy formalized by Whitehead (1929), amplified by McDougall (1933) and pursued by such recent writers as Agar (1943) and Thorpe (1956) argues that every vital event is an act of perception, a mental as opposed to a material process ; a living organism is essentially something which perceives ; its behaviour is not an automatic response to sensory impressions but includes an element of purpose building up primary perceptions into unitary systems in which the whole is different from and greater than the sum of its constituent parts. Such a view, as we have already hinted, tends to pan-psychism, or even to pan-theism ; according to it a purely objective biology is sterile ; like the warp and woof, mechanism must be interwoven with teleology.[1] While mechanisms may eventually become explicable in physico-mathematical terms, there is no suggestion yet that the subjective concepts of conscious purpose ever will be (Sommerhoff, 1950). But, even although this is agreed, it is to be remembered that there are no grounds for supposing that any well-defined mental content is associated with the reactions of the lower animals comparable to the perceptual experiences of the higher animals.

On the whole it would seem that the matter is not so simple as the more materialistic outlook might suggest. It is true that many of these primitive tropic activities of the animal world can be interpreted as reflexes without motivation, incentive or appreciation ; but because there are no discernible conscious accompaniments to many purely reflex acts in man whose apperceptive powers have been translated from the level of ganglia to the cerebral cortex, it by no means follows that there are none in those lowlier organisms the nervous system of which consists only of ganglia and nerve-fibres—or even of an uncentralized nerve-net or nothing at all. It must be remembered that the transference of sensory appreciation to the neopallium occurred late in evolutionary history,[2] and that although the lower centres in man have

[1] See D'Arcy Thompson (1942). [2] p. 542.

become merely relay-stations in this respect, they used to subserve much more important functions. Indeed, in the higher animals—and to some extent also in man—much of mental and most of visual activity, especially those aspects associated with primitive responses and endowed with emotional tone, remain closely associated with the vegetative activities which are integrated in the thalamus. Even in Fishes and Amphibians, vision is entirely unrepresented in the cortex.

Thus although ablation of his occipital lobes deprives man permanently and completely of all sensations of light, the higher mammals are by no means so incapacitated.[1] Most decerebrate Vertebrates will react and exhibit emotions to visual stimuli and even perform complex instinctive reactions without difficulty. So will the headless bee sting with accuracy on irritation (Bethe, 1897) and the clover-fly clean its wings with its legs after decapitation (Sherrington, 1920). A brain, or even a head-ganglion, is thus not a necessary residence for apparently " intelligent " reactions.

Phototactic reactions are " instincts", that is, adapted reactions of a purposive nature handed down from the previous experience of ancestors ; and, as with all instincts, the component afferent impulses have become associated in consciousness and synthesized into a meaningful pattern, a process which necessarily connotes some degree of perception.[2] As instincts, their usual stereotyped uniformity can be modified by experience provided the modification tends to the well-being of the individual—or the race. The reactions of even the lowly earthworm are amenable to training [3] ; many molluscs are readily trainable ; many insects eminently so. Thus the photo-negative cockroach, *Blatella germanica*, can be conditioned to advance towards a light provided it has been taught that a dark and comfortable shelter is placed beneath it (Goustard, 1948). Similarly, as we have seen,[4] after interference with its receptors or effectors either by partial blinding or by removing some of its legs, the mutilated insect will rapidly modify its reactions and after several trials will learn to orientate itself to light with almost the same accuracy as before. It is thus impossible to say where in the animal scale reactions to light were first associated with conscious awareness ; nor can we guess the form such consciousness may take, for like a solid to an inhabitant of Flatland, it exists in a form which cannot be assessed by the measuring instruments at our disposal ; we can only reason by inference from an analysis of our own peculiar form of consciousness of which alone we have immediate knowledge. From a study of the sensory capacities of animals few things emerge more certainly than that each species has its own perceptual world (the *Merkwelt* of v. Uexküll, 1921), and that

[1] p. 545.

[2] See Lloyd Morgan (1896–1912), Jennings (1906), Sherrington (1920), Parsons (1927), and many others.

[3] p. 573. [4] p. 59.

each of this multitude of worlds bears little resemblance to the environment of the animal as we see it or interpret it in terms of our own *Merkwelt*.

It seems reasonable to assume that the development of vision as a facet of consciousness evolved in three stages. We may surmise that the first conscious appreciation was a mere sentiency, crudely vague and undifferentiated, characterized perhaps by a minimum of cognition endowed with a rudimentary affective tone ; it was limited perhaps to an awareness of the existence of light as a change in the environment, tinged perhaps with sufficient affective tone to allow it to be appreciated as pleasant or unpleasant, and endowed with meaning in so far as the organism responded appropriately by motor activity in which initially there was offered the choice only of two alternatives, towards or away from the source of stimulation. We may even surmise, as indeed experimental evidence on the amœba would suggest,[1] that the most primitive sensation was a co-æsthesis without constituent modalities in which the several senses as we know them were merged into a vague and indiscriminate unity, and the stimuli (photic, chemical, tactile, etc.) which to us are distinct and unrelated were co-equal and additive. Some such concept as the emergence of a consciousness of a lowly type at an early but unknown stage, on the reflex plane or even below, would seem a possible hypothesis, a consciousness at first indefinable and vague but at the same time sufficiently plastic to contain the germ of the elaborate emotional behaviour of the higher animals—so long as we remember that the latter with all its undoubted richness and complexity bears little resemblance to the consciousness of man.

For such a surmise, however, there is no direct evidence; at this level the motor response to stimulation is all we can directly assess. From morphological and behavioural observations, however, we can be more certain that a primitive perception of light emerged with the development of a centralized nervous system in worms[2]; at this stage in evolution it would seem reasonable to suppose that a mechanism became available for the creation of perceptual symbolism; and at this stage vision undoubtedly became a perceptual process forming part of the conscious life of the animal and capable, at first in a minor degree, of determining its conduct. As we ascend the animal scale the primitive light-sense evolved into a sense of appreciation of the directional incidence of light, of movement, of form, and eventually of colour, until in the Primates the capacity to analyse complex visual patterns became the chief determinant of conduct. In its final development, the first elements of which have been detected in the chimpanzee,[3] the sense of vision passed beyond the stage of passively

[1] p. 36. Compare also the integration of phototaxis and galvanotropism seen in certain worms (p. 33). [2] p. 572. [3] p. 602.

recording objective appearances in the outside world and emerged as an imaginative and creative sense. This æsthetic quality was certainly a late acquisition acquiring maturity only in man.[1]

The extent to which in the animal scale an appreciation of these three progressive stages became a factor in the customary activities of the life of living organisms is a question which must await the acquisition of a much more profound knowledge of their natural history than we at present possess. And—whatever the future may bring forth—the manner of its becoming so is inexplicable by any physico-mathematical techniques we have at our disposal today or will have tomorrow.

Agar. *The Theory of the Living Organism*, Melbourne (1943).
Ashby. *Design for a Brain*, London (1952).
Bekhterev. *La Psychologie objective*, Paris (1913).
Bethe. *Arch. mikr. Anat.*, **50**, 589, 629 (1897).
Dakin. *Pecten*, London (1909).
Quart. J. micr. Sci., **55**, 49 (1910).
Goustard. *C. R. Acad. Sci.* (Paris), **227**, 785 (1948).
Hesse, R. *Das Sehen d. niederen Tiere* (1908).
Handb. norm. path. Physiol., **12** (1), 61 (1929).
Jennings. *The Behavior of Lower Organisms*, N.Y. (1906).
Lloyd Morgan. *Habit and Instinct*, London (1896).
Instinct and Experience, London (1912).
Loeb. *The Dynamics of Living Matter*, N.Y. (1906).
The Mechanistic Conception of Life, Chicago (1912).
Forced Movements, Tropisms and Animal Conduct, Phila. (1918).
McDougall. *An Outline of Psychology*, 6th Ed. (1933).
Parsons. *Intro. to the Theory of Perception*, Cantab. (1927).
Pavlov. *Die höchste Nerventätigkeit (das Verhalten) von Tieren*, München (1926).
Conditioned Reflexes, Oxon. (1927).
Russell. *The Behaviour of Animals*, London (1934).
The Directiveness of Organic Activities, Cantab. (1945).
Schultze. *Untersuch. ü. das Zusam. Auge der Krebse u. Insekten*, Bonn (1868).
Sechenov. *The Reflexes of the Brain* (1863) : Trans. in *Selected Works*, Moscow (1935).
Sherrington. *The Integrative Action of the Nervous System*, Yale (1920).
Sommerhoff. *Analytical Biology*, Oxon. (1950).
Steinach. *Pflügers Arch. ges. Physiol.*, **81**, 1 (1901).
Steiner. *Die Functionen des Centralnervensystem*, **2** (1888).
Szepsenwol. *C. R. Soc. Biol.* (Paris), **129**, 1265 (1938).
Thompson, D'Arcy. *On Growth and Form*, Cantab. (1942).
Thorpe. *Learning and Instinct in Animals*, London (1956).
Tinbergen. *De Levende Natuur*, **41**, 225 (1936).
von Uexküll. *Umwelt u. Innenwelt der Tiere*, Berlin (1921).
Walter. *The Living Brain*, London (1953).
Wells. *Anat. Rec.*, **113**, 613 (1952).
Whitehead. *Process and Reality*, Cantab. (1929).
Wilson. *Amer. Nat.*, **73**, 190 (1939).

[1] p. 753.