THE EFFECT OF LIGHT ON MOVEMENT

THE control of the movements of living organisms, both plants and animals, by light is a fundamental function of great phylogenetic age, preceding the acquirement of vision and, indeed, leading directly to its development [1]; it will be remembered that the association of the functions of equilibration and orientation with the visual system of the higher animals is in every sense basic. This primitive control of movement by light is undoubtedly an adaptive process, directing the organism to regions in the environment which are favourable to it, and has originated and evolved in the same way as other biologically useful reactions.

Historical development

It was originally held that the orientation of primitive organisms in space depended on the exercise of those " vital forces " the presence of which were considered to differentiate living creatures from the inanimate world ; and it was not until the time of the Cambridge clergyman-journalist. John Ray (1693), that a mechanistic explanation was offered to account for this aspect of the behaviour of plants. This English botanist suggested that plants placed before a window turned towards the light because the side towards the window was cooler than that towards the room and consequently grew more slowly so that the plant became bent by the relatively greater growth on the warmer side. The Huguenot botanist. August de Candolle (1832), on the other hand, introduced the conception that light rather than heat was the responsible agent, a concept elaborated and rationalized by Sachs (1882), the botanist of Würzburg : he maintained that orientation was determined by the directional incidence of the light and so formulated the interpretation of these phenomena generally current today.

Meantime, similar reactions in the animal world were considered to be dominated by a vital force usually conceived as acting automatically and thoughtlessly, a view epitomized by the great French philosopher, René Descartes (1650). The publication of Darwin's *Origin of Species* in 1859, however, caused a revolution in biological thinking so that contemporaneous writers spent much ingenuity in interpreting the behaviour of the lower animals in an anthropomorphic [2] way, attributing their reactions to primitive psychic activities which

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[1] p. 105.
[2] ἄνθρωπος, man ; μορφή, form.

were held to be pre-human in the sense that they were the evolutionary forerunners of the mental attributes of man.[1] Emotions were thus attributed to the lowest animals so that their conduct could be equated to that of man who was their descendant. The rationalization of zoology thus lagged behind that of botany, the progress of which seems to have been unnoticed by those engaged in the study of animal life, possibly because the temptation to endow plants with anthropomorphic attributes was less compelling.

In extenuation of the general acceptance of what would be considered a shallow philosophy today, it must be remembered that the doctrine of " animal spirits " was of extreme antiquity [2]; as a basis of his philosophy man required the concept of an incorporeal essence to give meaning even to corporeal objects, a need still felt by such philosophers as Descartes (1650–64) and such scientists as Willis (1670) and Boerhaave (1708) ; and it was not until almost the middle of the 19th century that the physical discoveries of Galvani (1791), the anatomist of Bologna, and Volta (1796–1800), the physicist of Pavia, were applied to the reactions of living creatures by the two great founders of modern physiology, Johannes Müller (1834) and du Bois-Reymond (1843–49), who laboriously began to build up a physiological doctrine on a physical basis. Almost half a century was to pass, however, before these new concepts, already accepted by botanists and for long part of physiological teaching, were applied to the problems of the orientation of animals by light and other stimuli. The early experimenters in this field from Paul Bert (1869) to Graber (1883–84) interpreted these reactions in anthropomorphic terms : animals sought or avoided light because it was " agreeable " or " disagreeable " ; indeed, the experimental studies of Engelmann (1879–82) and Verworn (1889) were the first in which attempts were made to place a physiological interpretation upon these responses, attempts which rapidly fructified so that the doctrine soon became generally accepted by zoologists and physiologists.[3]

At the beginning of this period of activity and reorientation, a prophet arose in the person of the German biologist, JACQUES LOEB (1859–1924) (Fig. 11). Loeb's life-work was a study of the differentiation between the animate and the inanimate and his thesis the identity of the two, for to him all living things were chemical and mechanical

[1] Darwin (1872), Lubbock (1881–89) in England ; Paul Bert (1869), Plateau (1886), Binet (1894) in France ; Graber (1883–84) in Germany ; Romanes (1883) in America ; and others.

[2] This belief permeated the whole of ancient thought and mythology. Even although the philosophy of the Ionian Greeks became more impersonal than the bronze-age cosmologies, Thales of Miletus, c 625–545 B.C., the first of the Greek natural philosophers, ascribed a soul to the lodestone because it could move a piece of iron, a view generalized by Anaxagoras, c 488–428 B.C., who ascribed all motions of material or living things to the operation of a mind or a soul. Erasistratus of Chios, fl. c 300–260 B.C., believed that the inspired air was transferred into vital spirit in the heart, to be relayed as such all over the body by the arteries ; the small amount reaching the brain was again transformed into animal spirit (animus, a soul) which was distributed by the nerves and was responsible for sensitivity and movement. The same philosophy was further elaborated by Galen, A.D. c 130–200, and for centuries was an accepted doctrine.

[3] Loeb (1890–1913), Jennings (1904–6), Mast (1906–38), Bohn (1909), Patten (1919), and others.

machines the activities of which were explicable by the same physical laws.[1] As a young colleague of the botanist, Sachs, at Würzburg, he appreciated the immense strides his friend had made in the interpretation of the responses of plants and unicellular organisms to light, and applied the same techniques to the animal world. All voluntary and instinctive reactions of animals he considered to be determined by internal and external forces, the majority of their responses thereto depending upon their bilaterally symmetrical structure. Thus, in the simple reaction of an animal going towards or away from a light, if the velocity of the chemical reactions in one eye is increased, the equality of " tonus " in symmetrical muscles on the two sides of the body is altered so that the animal is compelled to change its direction of locomotion ; as soon as the plane of symmetry becomes directed through the source of light, muscular tone becomes equalized and the animal progresses straight ahead until some other asymmetrical disturbance changes its direction of motion. Any other form of energy, he claimed, acted in the same way as light, so that the animal, which may appear superficially to move purposively and of its own will, is in reality forced to go where it is carried by its legs or wings. Animal conduct was thus interpreted as consisting of forced movements, a conception very different indeed from the anthropomorphic and teleological views prevailing throughout the nineteenth century.

Loeb pursued his theories with immense activity and application, and defended them with unusual vigour and stubbornness. It soon became obvious, however, despite his warm advocacy, that the intricacies of animal behaviour could not be contained within a theory so simple. Moreover, its all-embracing character and its rigidity readily opened it to attack as observations on the complexity of the conduct of animals multiplied. Jennings (1904–6) first showed that the reactions even of Protozoa could not be explained in this deceptively simple way, and the automaticity of the reactions of animals was challenged and disproved by many workers,[2] but by none more conclusively and consistently than by SAMUEL O. MAST (1871–1947) who proved to be Loeb's most violent and successful opponent (Fig. 12). Undoubtedly Loeb had swung the pendulum too far. A considerable reconciliation between the two opposing views was put forward by Kühn (1919), but general accord has by no means yet been reached.

It is probably true that the mechanical evidences of organic activities ultimately conform to the rules of chemistry and physics ; *but these rules have yet to be formulated ;* nor—most fortunately—is it necessary to await a complete explanation in fundamental terms before

[1] See especially his *Mechanistic Conception of Life* (1912).
[2] v. Buddenbrock (1915), Bierens de Haan (1921), Alverdes (1932), Russell (1938), and others.

we attempt to analyse the behaviour of living things. Loeb's great contribution was the application of the experimental method to the reactions of animals, thus retrieving their interpretation from the vagueness and sterility of conjectural anthropomorphism and subjecting them to objective analysis. It must be admitted at once that any attempt to explain animal behaviour in terms of our present knowledge by one single embracing theory is premature ; and while more can be learned by studying reactions to stimuli and classifying the responses of animals on a mechanistic rather than on a teleological basis,[1] and although higher functions can never wisely be called upon to explain an action if lower functions can provide a rational and consistent interpretation, there are many aspects of the behaviour of animals wherein a mechanomorphic scheme based solely on forced and stereo-typed responses fails to meet the case and wherein the conceptions of motivation, incentive and learning can be more usefully and economic-ally invoked.[2]

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[1] The value of the objective approach in comparison with the teleological as a stimulus to progress is seen in comparing two textbooks published about the same time—War   Jenkins and Warner's *Introduction to Comparative Psychology* (N.Y., 1934) and   anthropomorphic *The Animal Mind : a Textbook of Comparative Psychology* b   shburn (N.Y., 1936).

[2] See fu   . 107.

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The Types of Motorial Responses

The behavioural responses of organisms to light are diverse and for three-quarters of a century workers in this field have made numerous attempts to rationalize them into a single system of classification. While terminology itself cannot claim to be an end of science—and, indeed, its apparent definiteness is often misleading—the labelling and classification of phenomena are of great value in the economy and clarification of thinking. Adequate classification, however, entails fundamental knowledge and it is not surprising in a subject which is still highly controversial and inadequately understood that agreement has not yet been reached.

In this connection several terms have been introduced into the literature. Strasburger (1878) in his revolutionary work on botany, wherein he made a fundamental study of the movements of plants, used the term PHOTOTROPISM ($\phi\hat{\omega}s$, $\phi\omega\tau\acute{o}s$, light ; $\tau\rho\sigma\pi\acute{\eta}$, a turning) to describe the movements of sedentary plants in contradistinction to PHOTOTAXIS ($\tau\acute{\alpha}\xi\iota s$, a precise arrangement) to describe the locomotor reactions of freely moving organisms to light.   Shortly thereafter, Engelmann (1883) introduced the term KINESIS ($\kappa\acute{\iota}\nu\eta\sigma\iota s$, a movement) to indicate reactions wherein the velocity of movement depended on the strength of the stimulus.   The next contribution to terminology was due to Pfeffer (1904) who introduced the useful differentiation of PHOBOTAXIS ($\phi\acute{o}\beta\sigma s$, fear) to describe random, trial-and-error avoiding movements, and TOPOTAXIS ($\tau\acute{o}\pi\sigma s$, a place) to indicate directional attraction movements, while Kühn (1919–32) subdivided the latter into four categories of increasing complexity in response, which we shall adopt—TROPOTAXIS, TELOTAXIS, MENOTAXIS, and MNEMOTAXIS.[1] To these, Gunn and his colleagues (1937) added the term KLINOKINESIS and KLINOTAXIS ($\kappa\lambda\acute{\iota}\nu\omega$, bend) to express changes in orientation determined by turning movements. The term SCOTOTAXIS ($\sigma\kappa\acute{o}\tau\sigma s$, dark) suggested by Alverdes (1930) and Dietrich (1931) is probably unnecessary since those movements which may be interpreted as the result of an attraction to darkness are probably best looked upon as a negative phototaxis.

It is true that against this urge for classification some have rebelled (Mast, 1938), but although the dangers of a system of classification in concealing ignorance are obvious, its advantages are so considerable that as a tentative measure we will base our terminology on the classical scheme of Kühn, introducing some modifications advanced by Fraenkel and Gunn (1940). It is to be remembered, however, that the types of response are by no means mutually exclusive and that in their activities many animals show a combination of reactions.

A somewhat revolutionary view has recently been advanced by Viaud (1948). He divided the reactions of animals to light into two types :

[1] p. 43.

(a) " *Dermatoptic sensitivity* ", a " primary " reaction of proto-plasm to light evident throughout the cell in Protozoa and particularly in the surface layer in Metazoa ; and (b) "*visual sensitivity* ", a characteristic of specific photoreceptor organs.

The first type of reaction is concerned with simple attraction towards (or repulsion from) light ; the second is concerned with orienta-tion. The first has two distinct and reciprocal phases : the essential reaction is attraction towards the light (phototropism), purposeful in nature, elicited most readily by short-waved light, the response varying as the logarithm of the intensity of the stimulus (the Weber-Fechner law). Repulsion from light (photophobism), on the other hand, is a negative reaction, a phase of adaptation and recuperation in which the animal flees from light at its own particular speed. Visual sen-sitivity, on the other hand, is confined to the eyes and, concerning itself solely with visual orientation, responds most readily to stimula-tion by the mid-region of the spectrum. The first type of reaction is prepotent in lowly forms (such as *Hydra*) but becomes masked in higher forms by the second, although it again determines the animal's conduct when it is blinded (Crustaceans such as *Daphnia*, Rotifers such as *Asplanchna*) ; it cannot be elicited in forms higher than Amphibians. The second type of reaction does not appear in the lowest forms and in the higher adds visual apperception to its original function of spatial orientation. This is an interesting although some-what speculative philosophy, and although all the complex story of orientation to light cannot be fitted into it as it stands, it may perhaps contain much truth.

In the scheme to be adopted here, the motorial responses of organisms to light will be divided into two main classes :

(a) PHOTOKINESES, *non-directional changes in random movements*. This implies merely a change of activity depending on the intensity of the stimulation, not on its direction ; for its initiation a mechanism is required sensitive only to changes in intensity ; there is no true orientation and the direction of the response is merely a matter of weighted chance.

(b) DIRECTIONAL ORIENTATIONS towards (*positive*) or away from (*negative*) the stimulating light. The term PHOTOTROPISM will be retained to indicate the directional orientation of parts of *sessile* plants and animals ; while the translatory movements of *motile* organisms will be described as PHOTOTAXES. It is obvious that these directional responses are more efficient and purposive than the more primitive changes in random activity, since they allow the organism to adapt itself more rapidly to the most favourable location in its environment.

To retain a sense of proportion it is well to remember that forms of stimulation other than light are operative on living organisms, although none shows the same interest and complexities in the responses elicited. The scientific conception of GEOTROPISM in plants to describe the effects of gravitational influences was introduced by Knight (1806) at a very early date, even before de Candolle (1832) formulated his theory of phototropism. Towards the end of the 19th century however, the study of the responses of organisms to various stimuli rapidly widened. In equally fundamental researches on the action of chemicals on the sperm of ferns and mosses, Pfeffer (1883–88) introduced the term CHEMOTAXIS, Stahl (1884) described HYDROTROPISM in fungi, Wortmann (1883) discovered THERMOTROPISM, and Verworn (1889) THIGMOTROPISM (contact stimulation ; $\theta i \gamma \mu \alpha$, touch) and GALVANOTROPISM. These, however, are not our present concern, and we shall proceed to exemplify shortly the various types of response to light.

It is also to be remembered that these various responses may be mutually additive ; thus some flatworms are photo-negative and at the same time swim towards a cathode. When the two stimuli are presented together the response depends upon the direction and strength of each. Thus when the light and the cathode are at right angles the worm will swim at an angle bisecting the direction of the stimuli when the density of the current is proportional to the logarithm of the intensity of the illumination.
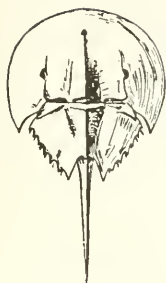
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PHOTOKINESIS

KINESES ($\kappa i \nu \eta \sigma \iota s$, movement) are the most simple responses of motile organisms to light—they are merely *the alteration*, either a quickening or a slowing, *of normal random movements without specific directional orientation* ; all that is required for their initiation is a mechanism of the simplest type which possesses the ability to react photochemically to variations in the intensity of illumination ; specific photoreceptors (eyes) are in no sense necessary. The phenomenon is essentially the same in character as the alterations in metabolic activity produced by light which we have lately considered. It must be remembered, however, that a motorial response of this type but frequently more dramatic in nature may result from other stimuli such as variations in temperature or moisture.

The response may involve a change of velocity (ORTHOKINESIS) (ὀρθός, straight) or a change in direction (KLINOKINESIS) (κλίνω, turn).

ORTHOKINESIS, wherein *random movements are accelerated or decelerated according to changes in the intensity of the illumination,* is seldom the sole mode of response of any organism to light but usually reinforces reactions of another type. In its most dramatic form the organisms move while the stimulus acts, that is, so long as an intensity gradient exists ; when the intensity becomes constant they come to rest. Viewed superficially this elementary response gives a false impression of orientation. Thus if the locomotor activity of an organism is increased by light and diminished in darkness, it aggregates preferentially in the shadowed region even if its movements continue to be random, just as the density of vehicular traffic increases as it is slowed in towns and decreases when speed is regained on the trunk roads ; an organism with this reaction of a *high kinesis* in the light thus appears to show a negative phototaxis but can be said to be negatively phototactic with as much logic as the average motorist may be assumed to delight in traffic-jams.

This response of activity in a light-gradient and rest in the shade giving rise to an apparently photophobic tendency to aggregation in the dark is relatively common ; it is seen typically in the *Bacterium photometricum* which, as its name implies, becomes active only under the influence of light, in many flat-worms,[1] in the maggot larvæ of various flies,[2] in certain Arthropods such as the king-crab[3] or the whip-tail scorpion,[4] in primitive Vertebrates such as the lamprey[5] and in the larvæ of certain fish such as the herring, *Clupea,* and plank-tonic animals as a means of depth-control.[6] The converse reaction is less common but is well exemplified by the inactivity of the cockroach in daylight and its activity in darkness.[7]

In higher forms these simple kinetic responses are less evident but stimulation of the eyes by light frequently has a dramatic effect on general activity. This is especially seen in Insects : thus in the cockroach, *Periplaneta,* exposure to light considerably reduces the threshold of response to other stimuli (Brecher, 1929), and as the intensity of light is increased the beetle, *Popillia,* walks more quickly (Moore and Cole, 1921).

KLINOKINESIS is of much wider application and interest ; in it a change of direction is involved, so that *turning movements, normally*

King-crab

Whip-tail scorpion

Lamprey

Cockroach

[1] *Planaria*—Pearl (1903), Walter (1907) ; *Leptoplana*—Hovey (1929) ; *Plagio-stomum*—Welsh (1933).
[2] Mast (1911), Herms (1911).
[3] *Limulus*—Cole (1923).
[4] *Mastigoproctus giganteus*—Patten (1917).
[5] *petra*—Young (1935).
[6] odhead and Woodhead (1955).
[7] *tta orientalis*—Szymanski (1914), Wille (1920).

haphazard, are influenced by the intensity of light so that avoiding reactions occur by trial-and-error with the result that a devious path is taken in a general direction away from the light ; in a favourable environment the animal pursues a straight course, but entering an unfavourable environment it turns away. This may be accomplished by creeping or oscillatory movements as in Algæ such as diatoms and desmids (Pfeffer, 1904), by amœboid movements as in slime-fungi (Stahl, 1884) or the amœba (Mast, 1911), or by free-swimming movements by cilia as in the swarm spores of Algæ and some Ciliates (Oltmanns, 1922). In some Ciliates, for example, the direction of movement in a uniform environment changes periodically for no apparent reason so that the animal does not travel long in a straight line ; when exposed to illumination the rate of change of direction is
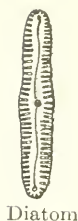
Diatom

Desmid
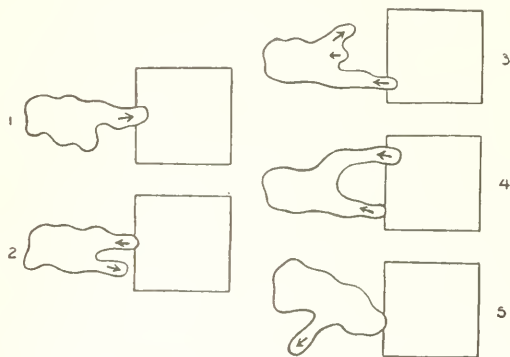
FIG. 13.—NEGATIVE KLINOKINESIS IN AMŒBA.
The organism is moving onto an illuminated cover-glass and eventually
its movement is reversed (after Mast).

increased although the speed remains constant, so that they appear to avoid the light and tend to aggregate in shadow (Ullyott, 1936). In comparison with orthokinesis whereby aggregation is reached entirely by chance, klinokinesis, although still haphazard, is obviously a more effective mechanism of orientation to attain an optimum environment either towards or away from the area of the highest concentration of the stimulus.

The simplest and most primitive response of this type is seen in the photo-negative kinesis of *Amœba proteus*, the reactions of which have received much study.[1] The reaction is extremely elementary. In a uniform environment this Rhizopod periodically throws out pseudopodia in an indiscriminate way and thereby effects movement. If, however, it is placed on a microscope slide with an illuminated

[1] Engelmann (1879), Davenport (1897), Mast (1910–32), Mast and Pusch (1924), Folger (1925–27), Luce (1926), Bovie (1926), Mast and Hulpieu (1930), and others.
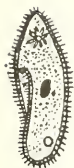
square, a pseudopod on entering the square will stop for a moment, then protoplasmic flow will commence in the reverse direction, the pseudopod being finally withdrawn from the area. After repeated experiences of trial-and-error, pseudopodia appear on the opposite side of the animal and its whole movement is reversed (Fig. 13).

Before the response occurs there is a latent period which varies with the intensity of the light [1] ; and if the stimulus be intensified by the use of ultra-violet light, a single stimulus may be sufficient to reverse the direction of locomotion at once. It is also interesting that modifications in behaviour due to experience occur even in organisms so lowly as the amœba, for the time-reactions of the response are accelerated as the number of consecutive tests is increased, so that the animal becomes *habituated* to the stimulus (Mast and Pusch, 1924 ; Grindley, 1937).

Amœba

As would be expected in this lowly organism, the receptor mechanism is undifferentiated and the response is primitive ; measurements of the elasticity of the plasmagel indicate that the change of movement is due to the gelating effect of radiation on the relatively fluid protoplasm [2] so that flow and the formation of pseudopodia are inhibited on the more highly illuminated parts but can occur readily in those parts of the organism on which the illumination is dim (Mast, 1932). The intimate nature of the mechanism whereby these changes are brought about is not known. It is noteworthy, however, that similar changes follow mechanical stimulation, and Folger (1926–27) concluded that since light and mechanical agitation produce the same changes and since the two are additive in the sense that the one stimulus can reinforce the other when both are subliminal, the response to the former is perhaps not specifically photo-chemical but of an even more primitive nature. It is also to be remembered that in some cases minute thermal increments are more effective than illumination, so that responses superficially accepted as photokinetic may in fact result from differential heating (differences as small as $0 \cdot 0005°$ C are effective in the slime-mould, *Dictyostelium discoideum*, Bonner *et al.*, 1950).

More mobile Protozoa appear to react with greater effect. Thus ciliated species such as *Paramœcium* swim about haphazardly but if they approach a noxious stimulus (light, heat, acids, etc.) they back and turn and start off in a different direction, a process which is repeated until, leaving the stimulus behind, they can swim freely forward.[3] A reaction which appears more complex is exemplified by the turbellarian flat-worm, *Dendrocœlum* (Ullyott, 1936) (Fig. 14). This ciliated flat-worm never travels far in a straight line even if its environment is uniform, but if the intensity of light is increased, although its velocity remains unaltered, the changes in direction occur more frequently, a

Paramœcium

Dendrocœlum
(ciliated on
ventral surface)

[1] *Pelomyxa*—Wilber and Franklin (1947).
[2] That the amœboid movements of pseudopodia were due essentially to a gel-sol transformation in which the propulsive force is derived from the contractility of the elastic plasmagel was suggested by Wallich in 1863 and the theory was confirmed by Hyman (1917), Pantin (1924–26) and Mast (1926–31).
[3] Ehrenberg (1838), Jennings (1906), Mast (1911), Rose (1929), and others.

response which decays with time as the organism becomes adapted. It follows that if travel in a certain direction exposes it to an increase in the intensity of light, the direction is changed by an increase in the rate of automatic turning and the worm eventually arrives in a

FIG. 14.—KLINOKINESIS IN A MOTILE ORGANISM.

Track of *Dendrocœlum*. At the upper part of the figure illumination was turned on ; turning movements are rapid. As their frequency decreases the path of the organism tends to straighten out so that it moves to an area of shadow. The velocity remains constant all the time ; the cross-lines mark half-minute intervals (after Ullyott, 1936).

haphazard way at the darker end of a gradient where a crowd tends to aggregate ; moreover, if it crosses from a dark region into an area of bright illumination, an immediate increase in the rapidity of turning renders it very probable that its re-entry into the dark is speedy. It is interesting and significant that the reactions of this organism seem to have a sensitivity to light resembling that of the human eye (Pirenne and Marriott, 1955).

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PHOTOTROPISM

Used in Strasburger's (1878) original sense, the term PHOTO-TROPISM connotes *the orientation of sessile organisms towards or away from light*. The phenomenon is a widespread and well-known characteristic of plant life and as a rule the stimulus is the sun (HELIOTROPISM ;
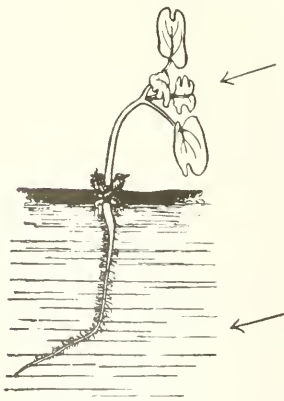

FIG. 15.—HELIOTROPISM.

Seedling of *Sinapsis alba* in water supported on a cork plate. It has been illuminated initially from all sides and then from one side only: the stem turns towards the light, the root away from it, and the leaf-blades at right angles to it (after Strasburger).

ἥλιος, the sun). Among the higher plants which are fixed in their habitat, heliotropic movements are limited to the component parts ; the aerial vegetative axes usually turn towards the light, thus exhibiting a POSITIVE HELIOTROPISM, the leaf-blades take up a position at right-angles to the rays of light in order to receive as much illumination as possible (TRANSVERSE or DIA-HELIOTROPISM), while tendrils and roots grow from the light (NEGATIVE HELIO-TROPISM) (Fig. 15). Occasionally these movements are remarkably delicate and rapid ; thus the Bengal plant, *Hedysarum girans*, nods to a passing cloud. Sometimes, however, the axes of the plant are photo-negative ; thus several grasses, corn and rice grow erect in darkness and tend to lie prostrate in bright illumination, becoming positively phototropic when shaded (Langham, 1941).

It is interesting that comparable non-translatory movements of the organs of animals may occur ; thus the hydroid, *Eudendrium*, and the marine polychæte worm, *Spirographis spallanzani*, show heliotropic bending movements (Loeb, 1890), some shell-fish open and others close their valves, clams retract their siphons (Hecht, 1919–20 ; Light, 1930), snails their tentacles (Grindley, 1937 ; and others) and sea-urchins, such as *Diadema antillarum*, move their spines if a light is flashed on them (P. and F. Sarasin, 1887 ; v. Uexküll, 1897 ; Millott, 1950), while many sedentary tubicolous polychæte worms, such as *Branchiomma*, withdraw into their tubes on a decrease in light intensity (Nicol, 1950).

Diadema antillarum

An interesting variant of this reaction is seen in certain sea-urchins such as the European *Strongylocentrotus* (Dubois, 1913) and the Caribbean *Lytechinus* (Millott, 1957), which normally withdraw their podia when illuminated. When lying in sunlit waters these echinoids gather small stones, the shells of bivalve molluscs, pieces of seaweed or whatever debris may be within reach of their tube-feet, and heap them upon themselves, using them as a parasol to protect themselves from light.

Branchiomma

The mechanism of the phototropic responses of plants is now relatively clear. They are due to the production of growth-regulating phytohormones [1] called AUXINS, a generic term applied to a number of related chemical substances of wide distribution formed by specialized parts of the plant—the tip of the coleoptile in seedlings and the leaves, particularly the young leaves, of mature plants. There these hormones are formed from precursors on stimulation by light and thence they are transported throughout the tissues of the plant at a rate more rapid than can be accounted for by simple diffusion (about 10 mm. per hour) ; as it travels through the tissues the freely-moving auxin regulates the varying rates of growth that account for such phenomena as photo- and geotropism, while some of it becomes bound in the tissues, there to regulate normal growth. In phototropic curvature the freely available hormone becomes unequally distributed in its passage along the two sides of a laterally illuminated plant, an increase of concentration on the shaded side of the stem leading to a bending of the organ. Its precise mode of action is unknown, but it would seem probable that, in addition to other activities such as the regulation of osmosis, it acts essentially as a co-enzyme in the respiratory activity of the cells, causing them to elongate and sometimes stimulating them to divide.

In these processes determining the phototropic movements of plants—and also of animals—carotenoid pigments act as sensitizers. These pigments are quite different in chemical structure and absorptive properties from the chlorophyll group of pigments which are primarily responsible for the photosynthesis concerned with metabolism in the vegetable kingdom [2] ; they will be more fully described at a later stage [3].

We have already seen that de Candolle (1832) first, and Sachs (1882–87) at a later date showed that light was responsible for the directional growth of
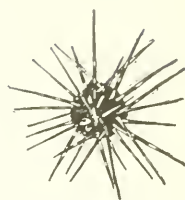
[1] p. 547. [2] p. 5. [3] p. 118.

plants, and since most plants bend towards the light, it was generally assumed
that it had a retarding influence upon growth, a view elaborated in great detail
by Blaauw (1909–18). That an explanation so simple could not account for the
facts, however, had already been shown in the classical researches of Darwin
(1880) on the behaviour of seedlings of grass (*Phalaris canariensis*) and the oat
(*Avena sativa*)—observations from which all modern views on the mechanism
of phototropism have directly descended. Darwin showed that the seedlings
only curved towards the light when the tip of the coleoptile was unilaterally

Figs. 16–20.—Phototropism in Seedlings.

(a)   (b)   (c)   (a)   (b)   (c)

Fig. 16.   Fig. 17.

(a) (b) (c)   (a)   (b)
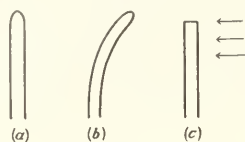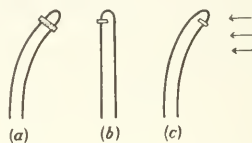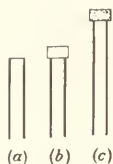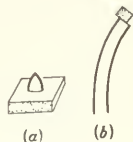
Fig. 18.   Fig. 19.   Fig. 20.

Fig. 16.—Darwin, 1880. The grass coleoptile exposed to lateral illumina-
tion (a) bends towards the light (b). When the tip is removed (c) the
phototropic response does not occur.

Fig. 17.—Boysen-Jensen, 1910–11. When a coleoptile tip is excised and
replaced with gelatin inserted between it and the stump (a), phototropic
curvature results normally ; a diffusible substance therefore passes across
the plate of gelatin. If, however, a plate of mica is inserted on the shaded
side (b), no response occurs. If the mica is inserted on the illuminated
side, the response is normal (c). It follows that the diffusible substance
passes down the shaded side.

Figs. 18–20. Went, 1928.

Fig. 18. When the tip of the coleoptile is removed, growth in length ceases (a).
An agar block placed on the stump has no effect (b). An agar block con-
taining juice extracted from the excised tip promotes normal growth (c).

Fig. 19. The coleoptile tip is placed upon an agar block (a), and a piece of the
block transferred unilaterally to a decapitated coleoptile (b). Unilateral
growth resembling phototropic curvature results due to the diffusion of the
hormone from the agar derived from the tip.

Fig. 20.—When unilateral light falls on an excised tip in contact with two agar
blocks separated by a razor blade, the greater part (65%) of the growth-
hormone is recovered from the agar on the shaded side.

illuminated and never when it was shaded by tinfoil even while the rest of the
plant was exposed, and that no curvature ever occurred in the stem or the root
if the growing tip were removed (Fig. 16). This localization of sensitivity to
the growing tip of the seedling was confirmed by subsequent workers. Rothert
(1892–96) incised the vascular bundles in various places and proved that the
phototropic stimulus travelled from the sensitive tip throughout the plant in
the parenchyma, while Fitting (1905–7) observed that the curvature was caused
by a difference in the rate of growth of the two sides, in positive phototropism
the darkened side growing more rapidly than the illuminated side. The next

fundamental step was due to Boysen-Jensen (1910–13) who showed that the stimulus could traverse a layer of gelatine but was arrested by a plate of mica, thus demonstrating that the curvature was due to the diffusion down the shaded side of the plant of a chemical substance stimulating growth (Fig. 17). These observations were confirmed by Paál (1914–18) who showed, moreover, that if an unstimulated tip were excised and replaced towards one side of the stump, growth was accelerated on that side, thus demonstrating that the stimulatory substance was continuously formed in the sensitive region. The final proof was effected by Stark (1921), Stark and Drechsel (1922), Cholodny (1927–35) and especially by the Dutch botanist, Went (1926–45), who trapped the diffusible growth-hormone descending from the coleoptile tip in a piece of gelatine or agar inserted into the plant and, transferring the jelly from the plant and placing it on the cut end of a non-illuminated plant from which the tip had been removed, demonstrated the occurrence of a typical phototropic response in the second even although light had been entirely excluded (Figs. 18–20). All that remained was to identify the chemical nature of the active agent.

A growth-hormone of this type was first extracted from fungi by Nielsen (1930) and Boysen-Jensen (1931), and shortly thereafter was chemically identified by Kögl (1932) and Kögl and Kostermans (1934) as 3,indole-acetic acid. Subsequent intensive research, particularly by Kögl and his colleagues (1931–35) in Germany, Zimmerman and Hitchcock and their colleagues (1935–48) in the Boyce Thompson Institute for Plant Research in New York, has shown that there are many such physiologically active substances (*auxins*) of wide distribution ; indeed, over 50 compounds, natural and synthetic, having this growth-producing property had been isolated by 1935. The most interesting historically are *auxin a* (a monocyclic trihydroxy-carboxylic acid, $C_{18}H_{32}O_5$), *auxin b* (a monocyclic hydroxy-keto-carboxylic acid, $C_{18}H_{30}O$), and *heterauxin* (3,indole-acetic acid, $C_{10}H_9O_2N$) (Kögl, 1935). Whether the first two or other allied substances are present in the living plant is not clear ; but the most popular hypothesis at present is that heterauxin is present in the tip of the stem initially as a precursor ; here it is activated into freely moving auxin by enzymic action ; and it would appear that its activity may be masked or reduced by anti-auxins. However that may be, it is clear that such substances applied to the intact plant or inserted into incisions or fed to the plant through the soil not only induce tropic curvatures but can modify the plant in size, shape, pattern and texture, can inhibit the formation of buds and perhaps of flowers,[1] and in supra-physiological concentrations can induce tumour-like growths.[2] It is puzzling why the same substances are found in human saliva (Seubert, 1925) and urine (Kögl and Smit, 1931).

It is interesting that an artificial end-organ to stimulate phototropic activity can be synthesized (Brauner, 1952). If capillary tubes filled with photo-sensitized indolylacetic acid are substituted for the cotyledons in *Helianthus* seedlings, illumination of one produces a marked curvature of the other hypocotyl.

This description may give the impression of over-simplification. It must not be thought that the whole story of the growth of plants is explained in terms of a single auxin. Research in progress as this book is being written is showing that the regulation of growth is based on a complex system of several auxins, kinetin-like hormones and gibberellin-like hormones, and possibly other related substances.

[1] p. 12.
[2] For general reviews, see Boysen-Jensen (1936), Went (1939), Zimmerman (1948), van Overbeek (1956), Bentley (1957).

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PHOTOTAXIS

A DIRECTED RESPONSE TO LIGHT is obviously a much more efficient orientating mechanism than the simple change in activity we have already discussed as photokinesis wherein a difference of intensity serves as the stimulus and aggregation is determined, as it were, merely by accident. The phototactic reaction is *purposive* ; for example, by suitable manipulation of the lighting system it is possible to make

certain photo-positive animals travel towards a light even although this movement brings them into a region of lower intensity of illumination,[1] or certain photo-negative animals to seek a dark shelter even although this entails moving towards a light.[2] It is a response, however, which requires one or more receptor organs specially designed to appreciate the direction of the incident light rather than merely changes in its intensity, and as the response becomes more and more efficient and therefore more and more complex, the receptor organs become progressively specialized until they eventually achieve the structural differentiation necessary to mediate the faculty of vision. The directional phototropic movements of sessile plants are slow and leisurely, essentially kinetic in nature, quantitative in type and chemical in execution ; but motile organisms require a more efficient mechanism capable of qualitative responses—a shock-reaction eventually mediated by nervous activity. The difference between the two types of response is well exemplified in the mutilation experiments of Viaud and Médioni (1949) on the flat-worm, *Planaria lugubris*, an animal in which both reactions are present ; they found that its positive photokinesis was entirely due to the action of light on the skin while positional orientation by phototaxis depended on the eyes.

As they evolved, these phototactic responses increased in complexity and efficiency ; the various stages may be classified as follows (Kühn, 1919–32 ; Gunn *et al.*. 1937).

(i) KLINOTAXIS (κλίνω, turn ; τάξις, a precise arrangement), wherein turning movements, normally alternating regularly, are directed towards or away from the light. One receptor organ only is necessary which responds by comparing the intensities of *successive* stimuli as the organism turns, and the directional path is consequently irregular and wavy.

(ii) TROPOTAXIS (τροπή. a turn), wherein orientation is effected by the *simultaneous* comparison of the intensities of the stimulation of two symmetrical receptors and the maintenance of a bilateral balance. The path is thus continuously corrected so that it is practically straight towards or away from the light, and it is obvious that greater accuracy and precision are obtained by a simultaneous comparison than by comparing present experiences with past.

(iii) TELOTAXIS (τέλος, a goal), a direct orientation towards or away from the light without the necessity of bilateral balance. A single receptor organ which can fixate the source of light is sufficient for its initiation. but it must possess a number of elements spatially distributed so that the stimulus can be localized on the sensory surface and the head and body can be orientated directly in line with the light.

[1] See the experiments of Richard (1948) on termite larvæ (*Calotermes flavicollis*).
[2] See Goustard (1948–50) experimenting on the cockroach, *Blatella* ; Bolwig (1954) experimenting on the stomatopod, *Gonodactylus*.

(iv) MENOTAXIS ($\mu\acute{\epsilon}\nu\epsilon\iota\nu$, to remain). Orientation is not directly towards or away from the light but at an angle to it ; the animal appreciates a definite distribution of the stimulus over its retina where it retains the impression, and having evolved beyond the ability to travel only in a straight line, it can orientate itself and accomplish separate reactions with reference to different parts of its field of vision. This activity is exemplified in the light-compass reactions of insects, or the dorsal (or ventral) light reaction of fishes.

(v) Kühn's final category, MNEMOTAXIS ($\mu\nu\acute{\eta}\mu\eta$, memory), wherein immediate orientation is aided by memory-images of past experience, is associated with other methods as an adjuvant mechanism of a higher type.

In these responses to light three stages emerge in the evolutionary process. In the simplest and most primitive response, the stimulus is appreciated in an indeterminate manner and orientating movements are corrective. In the next stage a more complicated but obviously more efficient reflex mechanism ensures a directed and purposeful orientation. The third and highest development involves the ability to retain the impression made upon the receptor organ, to adjust the response and utilize various means to gain the desired end should the most obvious fail ; it is a purposive rather than a reflex response. This more advanced development is exemplified in its simplest terms in the continued ability of some worms to orientate themselves to light when one eye has been removed, or in the compensatory modifications in the responses of certain insects when some of the legs on one side have been removed ; the same adaptability is seen in the complicated manœuvres of ants, backwards, sideways or forwards, to reach the desired goal, and reaches its highest forms in the reactions of Vertebrates among which its culmination is seen in the navigational ability of birds.

Drosophila

All these reactions, however, whether simple or complex, have certain features in common. In the first place, *they are all innate and show no evidence of being acquired* ; thus Payne (1910–11) bred the fruit-fly, *Drosophila*, in the dark and found that individuals of the 69th generation were normally photo-positive at the first trial ; while the young bird may set out on its first migration to a new land 2,000 miles away and follow by a light-compass reaction approximately the same route as its parents. It is true that the standard responses may become altered by use, being either accentuated by habituation (as we have seen even in *Amœba*, Mast and Pusch, 1924),[1] or diminished by adaptation (as we shall see in some insects, Clark, 1928–33) ; but these are physical processes. It is also true that their efficiency may be increased with training, as is seen in the migration or homing of birds (Rupp   and Schein, 1941 ; Matthews, 1953), or can be altered and even

[1] p. 36.

inhibited by associations established by conditioned reflexes ; thus the photo-negativity of the cockroach, *Blatella*, can be inhibited by training if a light is placed over its dark shelter (Goustard, 1948–50). It is also to be remembered that the removal of necessary effector organs may inhibit or invert a normal phototactic response even although these have no apparent connection with photoreceptors (the antennæ of the cockroach or the wings of the fruit-fly, *Drosophila*, Goustard, 1949).

In the second place, *these responses are all of biological value* and to attain this end they may vary with the strength of the stimulus or change their character if associated with a second stimulus of another nature ; moreover, they may alter in type and even reverse their nature during the life of the animal to meet the needs of a change in environment.

Balanus

Thus the usual photo-negative response (the *shadow-reflex*) seen in so many worms and molluscs is essentially an escape movement from the presence of predators, while the opposite response of the tentacle of the snail is the expression of the fact that a shadow usually signifies food. Some of these responses are very sensitive : thus the acorn-shell, *Balanus*, responds to a darkening of 5% (v. Buddenbrock, 1930). The simplest example of a variation in the response with the strength of stimulus is seen in the protozoon, *Euglena*, which is photo-positive in weak and negative in strong light so that it orientates itself to favourable mid-intensities (Mast, 1938), or in the fruit-fly, *Drosophila*, which is positively phototactic in illuminations below 9 lux and negatively over 79 lux (Médioni, 1954). A similar variation may occur with the nature of the light ; thus the flat-worm, *Planaria lugubris*, is said to be positively phototactic to red and negatively to blue light (Viaud, 1949). Again, other environmental circumstances may alter the response. *Paramœcium* is geo-positive in the light and negative in the dark (Fox, 1925) ; the normal negative phototaxis of the goldfish, *Carassius auratus*, disappears if the temperature is increased by 10° C (Andrews, 1952) ; the normal positive phototaxis of the tsetse-fly, *Glossina*, becomes negative if the temperature is raised above 40° C even if the temperature in the dark is so high that it drops down dead (Jack and Williams, 1937) ; exposure to dry air alters the phototactic reaction of the woodlouse, *Armadillidium*, from negative to positive (Henke, 1930) ; while the negative response of the oligo-chæte, *Perichæta*, when it is extended can be changed to a positive response when the worm is contracted (Harper, 1905).

Carassius

Glossina

An excellent example of a change in response with different combinations of stimuli is seen in the behaviour of *Littorina neritoides*, a tiny mollusc which inhabits the rocky shores of European seas. Fraenkel (1927) showed experimentally that it was always geo-negative, photo-negative always when out of the water and when normally orientated in the water, but photo-positive when
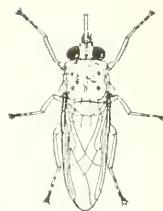
Littorina

Forficula

Two members of
Polyzoan colony

Caterpillar

Anguilla

in water and upside-down, one stimulus (the presence of water) thus modifying the influence of another (light). Its geo-negativity drives it to the surface of the sea and if it surfaces in bright light it returns to the water because of its photo-negativity ; if it surfaces beneath a submerged rock its positive photo-taxis makes it crawl beneath it in the upside-down position until, reaching the air, its negative phototaxis keeps it in a shaded cleft. Again, when the gardener traps an earwig in a flower-pot containing dry straw inverted on a cane, he is utilizing the fact that *Forficula* demonstrates photokinesis, thigmotaxis, hydro-kinesis and negative geotaxis.

A change in response during the development of the animal is well exemplified in the case of some marine worms ; these are usually photo-positive when they leave the egg so that they come to the surface and swim ; at a later stage they become photo-negative with the result that they burrow in the mud and crawl (Mast, 1911). The larvæ of the polyzoan sea-mat, *Bugula*, similarly disperse under a positive phototaxis, but after a few hours turn photo-negative so that they attach themselves to the bottom and undergo metamorphosis (Grave, 1930 ; Lynch, 1949).

These changes may be associated with stages in the development of the visual cells. Thus the larvæ of the cat-fish, *Ameiurus*, are initially unresponsive to light at a stage when the visual elements are not fully differentiated ; later they become photo-negative, a phase during which the rods and cones are contracted and show no retinomotor reactions ; finally the larvæ become photo-positive, a phase characterized by the commencement of retinomotor reactions (Armstrong, 1949).

A change in response may also accompany a change of habit. Thus young caterpillars of *Porthesia* are strongly photo-positive when they are hungry, a response which normally leads them upwards to the leaves of their food plant, but the response is lost after feeding ; while male and female ants become temporarily photo-positive at the time of their nuptial flight, a reaction lost when they shed their wings (Loeb, 1918).

Another interesting example of this type of change to suit a marked change in habit is the common eel, *Anguilla*. At the stage of sexual maturity in the autumn when it leaves fresh water to migrate downstream on its journey to its mating grounds in the Sargasso Sea, there is a great increase in the size of the eyes and the fish becomes photo-negative. This season coincides with the safety afforded by floods and moonless nights and the fish avoids the light to such purpose that its nuptial journey can be checked and the eels diverted into traps in large numbers by means of underwater lights shining upstream (Lowe, 1952).

A phototactic response of this type may be so prepotent that, although generally biologically useful, it may drive the animal to destruction. Thus the stimulus which leads the moth to fly towards the sun will drive it into the candle-flame ; the same response in the newly hatched larva of *Euproctis* which normally leads it upwards towards the leaves of its food plant will force it to

migrate downwards to starvation if illuminated from below (Loeb, 1918 ; Lammert, 1925 ; v. Buddenbrock, 1930) ; while, provided the stimulating light is sufficiently bright, the negative phototaxis of the larva of the bluebottle, *Calliphora*, will induce it to approach a source of ammonia of lethal concentration (Hurst, 1953).

Andrews. *Physiol. Zool.*, **25**, 240 (1952).

Armstrong. *Anat. Rec.*, **105**, 515 (1949).

Bolwig. *Brit. J. anim. Behav.*, **2**, 144 (1954).

v. Buddenbrock. *Z. vergl. Physiol.*, **13**, 164 (1930).

Clark. *J. exp. Zool.*, **51**, 37 (1928) ; **58**, 31 (1931) ; **66**, 311 (1933).

Fox. *Proc. Camb. philos. Soc. biol. Sci.*, **1**, 219 (1925).

Fraenkel. *Z. vergl. Physiol.*, **5**, 585 (1927).

Goustard. *C. R. Acad. Sci.* (Paris), **227**, 785 (1948) ; **228**, 864 (1949). *C. R. Soc. Biol.* (Paris), **144**, 485 (1950).

Grave. *J. Morph. Physiol.*, **49**, 355 (1930).

Gunn, Kennedy and Pielou. *Nature* (Lond.), **140**, 1064 (1937).

Harper. *Biol. Bull.*, **10**, 17 (1905).

Henke. *Z. vergl. Physiol.*, **13**, 534 (1930).

Hurst. *Nature* (Lond.), **171**, 1120 (1953).

Jack and Williams. *Bull. ent. Res.*, **28**, 499 (1937).

Kühn. *Die Orientierung der Tiere im Raum*, Jena (1919). Bethes *Hb. norm. path. Physiol.*, **12** (1), 17 (1929).

Claus, Grobben and Kühn's *Lhb. der Zool.*, Berlin (1932).

Lammert. *Z. vergl. Physiol.*, **3**, 225 (1925).

Loeb. *Forced Movements, Tropisms and Animal Conduct*, Phila. (1918).

Lowe. *J. Anim. Ecol.*, **21**, 275 (1952).

Lynch. *Biol. Bull.*, **97**, 302 (1949).

Mast. *Light and the Behavior of Organisms*, N.Y. (1911). *Biol. Rev.*, **13**, 186 (1938).

Mast and Pusch. *Biol. Bull.*, **46**, 55 (1924).

Matthews. *J. exp. Biol.*, **30**, 268 (1953).

Médioni. *C. R. Soc. Biol.* (Paris), **148**, 2071 (1954).

Payne. *Biol. Bull.*, **18**, 188 (1910) ; **21**, 297 (1911).

Richard. *C. R. Acad. Sci.* (Paris), **226**, 356 (1948).

Ruppell and Schein. *Vogelzug.*, **12**, 49 (1941).

Viaud. *C. R. Soc. Biol.* (Paris), **143**, 534 (1949).

Viaud and Médioni. *C. R. Soc. Biol.* (Paris), **143**, 1221 (1949).

The Types of Phototactic Response

We shall now proceed to exemplify the various types of phototactic responses ; but, as we have just seen, it is to be remembered that animals usually orientate themselves in more than one way depending on the circumstances prevailing. It is less correct to say, for example, that an animal is telotactic than that it may exhibit a telotactic reaction. Thus, as we shall see, some ciliated Protozoa or worms show an undifferentiated photokinetic response with one stimulus and a klinotactic or tropotactic response with another, while in its complex but very efficient mechanism of orientation, the honey-bee combines tropotaxis, telotaxis and menotaxis with mnemotaxis.

KLINOTAXIS

The most primitive directed orientation to light is by KLINOTAXIS whereby *turning movements, normally alternating regularly, are specifically orientated* with respect to the light. This is well exemplified in the behaviour of flagellated or ciliated Protozoa or the maggot larvæ of certain common flies. Each of these shows a different type of response. The Protozoa orientate themselves as a result of successive stimuli falling on a photosensitive organ periodically exposed as they rotate

longitudinally by means of cilia, maggots by muscular contraction as they crawl.

The Flagellates, protozoans which swim by means of a flagellum much after the manner of a gondolier, in reverse, with his single oar, are frequently photosensitive. Some of them retain a primitive photo-kinetic response whereby they become inactive in low illumination and resume activity if the light is increased. This simple kinetic response determining general activity is, however, supplemented by a shock-reaction which determines orientation ; for this purpose they have evolved a sensitized area specially modified for the reception of the stimulus. In a homogeneous environment they take a direct course undergoing continuous rotation on a longitudinal axis as they are propelled by the flagellum ; to variations of the intensity of light they respond by abrupt changes in the rate and direction of movement either towards or away from the light. Once orientated they are not held on a direct course by the continuing action of light, but if they diverge, the orientating stimulus changes and immediately recalls them automatically. The automaticity of the response is seen if the field contains two beams of light crossing at an angle, in which case these organisms orientate themselves and proceed in a direction between the two beams determined by their relative intensities and angles of incidence (Buder, 1917 ; Mast and Johnson, 1932). Their photic responses have been studied most fully in the typical species, *Euglena*, a transparent green Protozoon photo-positive in weak, photo-negative in strong light.[1]

Euglena

Euglena viridis, the flagellate infusorian which commonly forms the green scum on stagnant fresh water, has a photosensitive " eye-spot " or " stigma "[2] situated in the concavity of a pigmented shield[3] in close association with the root of the flagellum ; the arrangement is such that when the surface of the eye-spot is illuminated the photosensitive substance at the base of the flagellum is thrown into the shadow (Fig. 80). It follows that rotation of the transparent organism on its longitudinal axis produces an alternate shading and exposure of this substance unless it is orientated so as to proceed directly towards or away from a light (Fig. 21). If the direction of the rays is changed through 90° to illuminate the organism laterally, no reaction occurs until the rotation brings the eye-spot to face the light thus throwing the photosensitive area into the shade ; thereupon the organism suddenly bends away from the light, and, continuing rotation thus, gradually straightens, a response which is repeated on each rotation so that it is soon proceeding again directly away from the new direction of the light. Subsequent rotation in this position no longer produces changes in the intensity falling upon the two surfaces and the organism therefore proceeds uninterruptedly in this direction.

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[1] Verworn (1889), Jennings (1904), Mast (1911–38), Bancroft (1913), Buder (1917), Mast and Gover (1922), Mast and Johnson (1932), and others.
[2] p. 126.
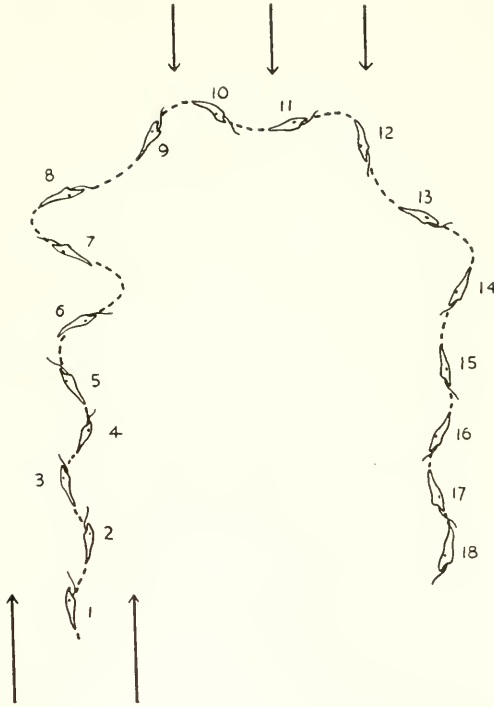[3] The pigment is *astaxanthin*, p. 120.

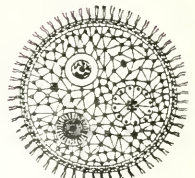FIG. 21.—KLINOTAXIS IN A SWIMMING ORGANISM.

The orientation of *Euglena viridis*. The orientation of the organism as it swims away from the light (coming from below) rotating in a wavy path (1 to 6). At 6 the direction of the light is reversed to come from above ; each time the receptor area is shielded by the pigment the organism swerves to the dorsal side. After an initial wavy course (7 to 8) it bends laterally across the path of the beam, and from 13 to 18 it again swims as before away from the light (after Jennings, 1906).

The Ciliates, which orientate themselves by means of cilia much as a rowing boat without a rudder, react phototactically in a similar manner (Fig. 22). Thus *Stentor cœruleus*, a trumpet-shaped [1] Protozoon, the bell of which is surrounded by cilia within which is an eccentrically placed mouth, exhibits the same reaction by virtue of the fact that the oral surface is more photosensitive than the aboral (Jennings, 1904 ; Mast, 1906–11).
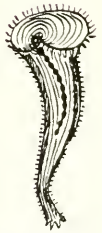
Stentor

A similar arrangement multiplied many-fold is seen in colonial forms, such as *Volvox globator*, a green organism found in fresh-water pools, formed of a hollow spherical colony of some 10,000 individual zooids each of which is equipped with two flagella and a stigma protected on one side by a pigmentary shield ; stimulation of the sensitive area results in the translation of the diagonal

Volvox

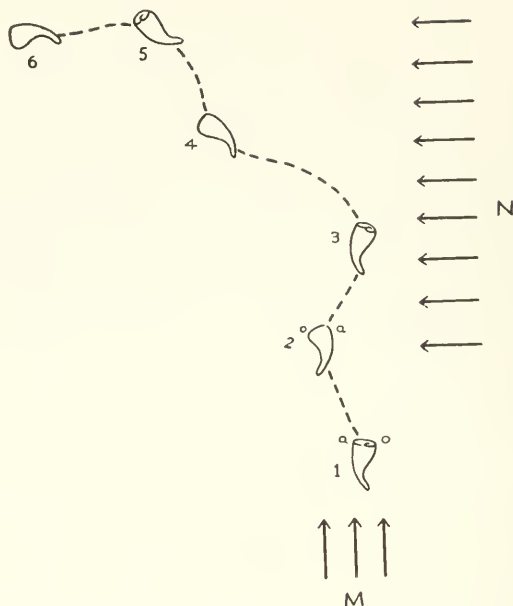[1] The name is from Stentor, the herald of the *Iliad* who had a loud trumpet-like voice.

FIG. 22.—KLINOTAXIS IN *STENTOR CŒRULEUS*.

In 1 and 2 the organism is seen swimming away from the light shining from behind it (indicated by the lower arrows, M). As it swims it rotates so that the oral side (*o*) and the aboral side (*a*) are equally stimulated. At 3 the original light is turned off and a lateral light (indicated by the side arrows, N) is turned on. As soon as the oral side faces the light the organism turns rapidly away to position 4 and continues in this sense until, at 6, the oral side is approximately equally exposed to light in all positions on the spiral course (after Mast, 1911).

stroke of the flagella into a backward sweep, the whole number beating in unison and thus orientating the colony in the required direction (Mast, 1906–27 ; Mast and Johnson, 1932).

Maggot of *Musca*

Maggot of *Calli-phora*

Crawling organisms such as the maggots of flies (the house-fly, *Musca domestica*, the bluebottle, *Calliphora erythrocephala*, etc.) were among the first organisms to be investigated in this way.[1] Their phototactic response is somewhat different from that of swimming Flagellates or Ciliates. Although the photosensitive structures are exceedingly primitive, the anterior end of the larva is negatively responsive to light. When crawling it raises its head in the air and alternately deviates to either side as if in exploratory movements ; on lateral illumination, the head is swung violently away from the light, a reaction which is repeated, turning the animal round until the head is equally illuminated at two successive deviations, whereupon it crawls directly

[1] Pouchet (1872), Holmes (1905), Loeb (1905–18), Mast (1911), Herms (1911), Patten (1914–16), Ellsworth (1933), Welsh (1937).
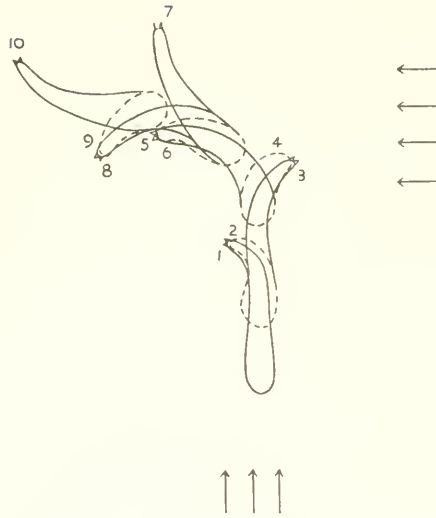
FIG. 23.—KLINOTAXIS IN A CRAWLING ORGANISM.

The maggot is photo-negative and crawls away from the light (below). From the initial position, 1, it contracts into 2, elongates into 3 and contracts again into 4, each time swinging its head across to one or other side. So long as the sides of the head are equally illuminated its path is straight. At 3, the lower light is switched off and the side light switched on ; the organism immediately swings violently into position 5. Thereafter it contracts to 6, and, having swung in the opposite direction to 7, again receives preferential illumination on the side. It therefore swings again violently to 8 and, having contracted to 9, proceeds again, as before, directly away from the light (10) (after Mast, 1911).

away from the light (Fig. 23). If a light is persistently flashed on the same side on each deviation of the head, a circus movement is produced, and if two directed lights are simultaneously employed the animal crawls away at a direction half-way between the two beams if they are equal, or proportionately more nearly in line with the brighter beam if they are unequal (Patten, 1914).

Bancroft. *J. exp. Zool.*, **15**, 383 (1913).
Buder. *Jb. wiss. Bot.*, **58**, 105 (1917).
Ellsworth. *Ann. entom. Soc. Amer.*, **26**, 203 (1933).
Herms. *J. exp. Zool.*, **10**, 167 (1911).
Holmes. *J. comp. Neurol.*, **15**, 98, 305 (1905).
Jennings. *Publ. Carnegie Inst.*, Wash., No. **16**, 256 (1904).
Loeb. *Studies in General Physiology*, Chicago (1905).
    The Dynamics of Living Matter, N.Y. (1906).
    Forces, Movements, Tropisms and Animal Conduct, Phila. (1918).
Mast. *J. exp. Zool.*, **3**, 359 (1906).
    Light and the Behavior of Organisms, N.Y. (1911).
    Biol. Zbl., **34**, 641 (1914).
    Z. vergl. Physiol., **5**, 730 (1927).
    Biol. Rev., **13**, 186 (1938).
Mast and Gover. *Biol. Bull.*, **43**, 203 (1922).
Mast and Johnson. *Z. vergl. Physiol.*, **16**, 252 (1932).
Patten. *J. exp. Zool.*, **17**, 213 (1914) ; **20**, 585 (1916).
Pouchet. *Rev. mag. Zool.*, **23**, 110, 129, 183, 225, 261, 312 (1872).
Verworn. *Psychophysiologische Protisten-studien*, Jena (1889).
Welsh. *Science*, **85**, 430 (1937).

TROPOTAXIS

In tropotaxis at least two symmetrical receptor organs are necessary, and instead of relying on successive exposures of a single receptor
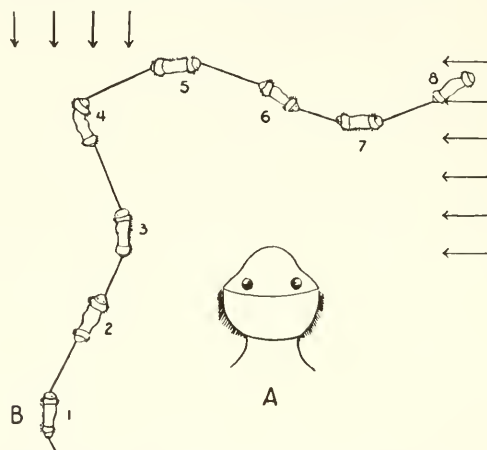

Fig. 24.—The Tropic Response of Larva of *Arenicola*.

A. The head of the larva with two symmetrical eyes.
B. The path of movement of the larva : in 1 to 4 the light remains stationary ; in 5 to 8 it is placed at right angles (after Mast).

by trial movements, *the animal orientates itself by the simultaneous comparison of the intensity of stimulation on the two sides.* In the simple
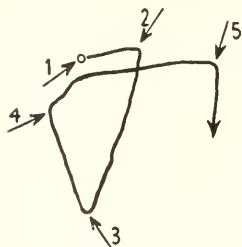

Fig. 25.—Negative Tropotaxis.

The path of the flour-moth larva, *Ephestia*, starting from the small circle with a light shown as indicated by the arrow, 1. Each successive number indicates the position of a new light turned on when the animal reached the corresponding point on its track ; its direction changed in a straight line directly from the light (after Brandt).

forms inequality of stimulation leads to orientation in the required direction by a reciprocal coordination of the muscles of either side of the animal controlled by the nervous system : if there is an excess of stimulation on one side, a turning movement occurs ; if equality, the stimuli cancel each other out and the animal progresses straight forwards ; and if it subsequently strays from its path a renewed inequality corrects the deviation. It follows that if two sources of light appear simultaneously the animal orientates itself directly between them in proportion to their relative intensities.

The larvæ of some marine worms provide the most simple type of this reaction ; they swim by the activity of cilia but orientation is the result of muscular contraction. Of these, the larvæ of the polychæte worm, *Arenicola*, have been most intensively studied (Mast, 1911 ; Garrey, 1918). These are minute creatures with two eyes anteriorly and a band of cilia at either end ; as they swim they rotate longi-

tudinally so that on lateral illumination each eye is alternately illuminated and shaded. As each eye becomes exposed to the light, the muscles of the illuminated side contract violently turning the head towards the light (Fig. 24). Since this occurs twice during each rotation, the larva is rapidly orientated towards the light until the two eyes are equally illuminated all the time, whereupon further muscular contraction and orientation cease.

A very similar and typical reaction is seen in the rotifer, *Branchionus* (Viaud, 1948), and in the photo-negative larvæ of the flour-moth, *Ephestia*, which are provided on either side of the head with an aggregate eye composed of six ocelli (Brandt, 1934) (Fig. 25).

A further evolutionary step is seen in earthworms. As is the general rule, impulses originating in the photoreceptors on one side of the body determine orientation by inducing a simple reflex contraction of the muscles on the opposite side, but it is obvious that if these impulses can be modified and integrated in the central nervous system, a more effective response is obtained.

Such responses have been fully studied in the earthworm, *Lumbricus terrestris*, and *Eisenia fœtida*.[1] In these animals the existence of photoreceptor organs associated with a subepidermal nerve-net was demonstrated by Richard Hesse (1896) and confirmed by W. N. Hess (1925)[2]; they are most numerous and receptive near the anterior extremity of the animal. The response to light is somewhat complicated and has given rise to some difference of opinion; but it would seem most likely that if the worm is sluggish and is exposed to dim light, it slowly extends, turns its anterior end away from the light, and continues to move thus. If, however, the worm is active when it is illuminated from the side, the anterior end is quickly raised and turned in the direction opposite to that in which it happens to be, whether it is directed to the light or not, and thereafter swung from side to side, a position and direction being eventually adopted in which the anterior end is least exposed to the light.

If now the cerebral ganglion is removed or destroyed or if it is inhibited by a reduction of temperature or the injection of depressant drugs such as cocaine or alcohol, the opposite reaction of a positive phototaxis results; in these circumstances lateral illumination of the more posterior photoreceptors produces a contraction of the muscles of the same side which causes the worm to turn towards the light, a reaction due to reflexes mediated through the ventral cord (Hess, 1924; Prosser, 1934). It would seem that normally this weak positive ipsilateral response mediated through the cord is overshadowed by the stronger negative contralateral response derived from the receptors in the highly sensitive anterior end and mediated by the cerebral ganglion, and that the final response of the animal is the resultant of the two antagonistic tendencies after integration and coordination in the central nervous system.

It is obvious that the bilateral balance of the tropotactic response will be upset if one eye is blinded, either by painting it over or by its removal, so that with lateral illumination the animal will tend con-

[1] Loeb (1894), R. Hesse (1896), Parker and Arkin (1901), Smith (1902), Adams (1903), Holmes (1905), Harper (1905), Mast (1911), W. N. Hess (1924), Nomura (1926–27), Prosser (1934), and others.
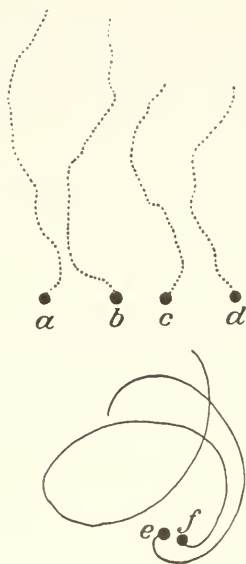[2] pp. 131, 518.

Fig. 26.—Positive
Tropotaxis.

The tracks taken by the
woodlouse, *Armadilli-
dium*, blinded on the
right side. *a, b, c, d*. The
tracks of the louse in
darkness. *e, f*. Circus
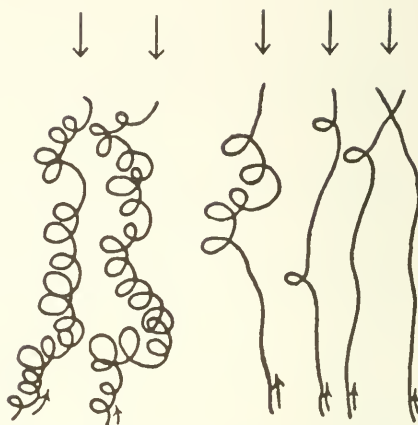movements with the light
overhead (after Henke).

Fig. 27.—Circus Movements in a
Unilaterally Blinded *Notonecta*.

The animal directs itself towards the light
above, indicated by arrows. The illustra-
tion shows the path taken in repeated trials.
From left to right, the tracks are the 1st, 3rd,
35th, 39th, 41st and 43rd attempts. It is
seen that the initial attempts are circus
movements which gradually straighten out
until eventually, after some trials, the track
is almost straight (after Clark, 1928).

Armadillidium

stantly to deviate towards one side, or in an overhead light to perform
circus movements. This deviation towards the seeing side after
unilateral blinding is well seen in the case of the woodlouse, *Armadilli-
dium*, a Crustacean which lives under stones or decaying wood
(Henke, 1930) (Fig. 26). In some instances these abnormal deviations
occur for an indefinite time,[1] but in others a process of adaptation sets
in so that the circus movements gradually cease and the path eventually
straightens out [2] (Fig. 27). An exception to this type of behaviour is
seen in the evolutionary development of the tropotactic response
whereby each eye becomes regionally differentiated so that each can
act as a symmetrical pair of organs. Thus the eyes of some worms and
insects possess two functionally different regions one of which initiates

[1] The snail, *Helix*—von Buddenbrock (1919) ; the millipede, *Julus*—Müller (1924) ;
the silver fish, *Lepisma*—Meyer (1932) ; the larva of the flour-moth, *Ephestia*—Brandt
(1934).
[2] The water-boatman, *Notonecta*—Holmes (1905), Clark (1928), Lüdtke (1935–42) ;
the robber-fly, *Proctacanthus*—Garrey (1918); the whirligig beetle, *Dineutus assimilis*—
Clark (1931–33), Raymont (1939).

turning towards one side and the other in the opposite direction ; although the responses are typically tropotactic in nature, the telotactic response is simulated since each eye exerts a symmetrical control.

Among worms, these reactions have been most closely studied in *Planaria maculata*, one of the turbellarian worms.[1] The normal individual orientates photo-negatively, illumination of one side producing a muscular contraction of the opposite side so that the worm proceeds directly away from the light. If, however, one eye is dissected out and the light is accurately directed or if different parts of the remaining eye are removed, it can be shown that stimulation of the elements of the anterior end of the eye makes the animal turn from the illuminated side, while stimulation of the posterior or ventral parts of the eye induces a turning towards the illuminated side. The boundary between these two constitutes the " line of fixation " (a functional fovea) stimulation of which evokes no turning movements (Lüdtke, 1942). A somewhat similar reaction is seen in the drone-fly, *Eristalis*, and related insects (Mast, 1923).
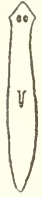
Turbellarian
worm

Adams. *Amer. J. Physiol.*, **9**, 26 (1903).
Boring. *J. anim. Behav.*, **2**, 229 (1912).
Brandt.   *Z. vergl. Physiol.*, **20**, 646 (1934).
von Buddenbrock. *Zool. Jb., Abt. Zool. Physiol.*, **37**, 315 (1919).
Clark. *J. exp. Zool.*, **51**, 37 (1928) ; **58**, 31 (1931) ; **66**, 311 (1933).
Garrey. *J. gen. Physiol.*, **1**, 101 (1918).
Harper. *Biol. Bull.*, **10**, 17 (1905).
Henke. *Z. vergl. Physiol.*, **13**, 534 (1930).
Hess, W. N. *J. Morph.*, **39**, 515 (1924) ; **41**, 63 (1925).
Hesse, R. *Z. wiss. Zool.*, **61**, 393 (1896).
Holmes. *J. comp. Neurol.*, **15**, 98, 305 (1905).
Loeb. *Pflügers Arch. ges. Physiol.*, **56**, 247 (1894).
Lüdtke. *Z. vergl. Physiol.*, **22**, 67 (1935) ; **26**, 162 (1938).
    Biol. Zbl., **62**, 220 (1942).

Mast.   *Yearbook Carnegie Inst.*, **9**, 131 (1910).
    Light and the Behavior of Organisms, N.Y. (1911).
    J. exp. Zool., **38**, 109 (1923).
Meyer. *Z. wiss. Zool.*. **142**, 254 (1932).
Müller. *Zool. Jb., Abt. Zool. Physiol.*, **40**, 399 (1924).
Nomura. *Tohoku Imp. Univ. Sci. Rep.*, Ser. iv, **1**, 294 (1926) ; **2**, 1 (1927).
Parker and Arkin. *Amer. J. Physiol.*, **5**, 151 (1901).
Pearl. *Quart. J. micr. Sci.*, **46**, 509 (1903).
Prosser. *J. Neurol. Psychopath.*, **59**, 61 (1934).
Raymont. *Biol. Bull.*, **77**, 354 (1939).
Smith. *Amer. J. Physiol.*, **6**, 459 (1902).
Steinmann and Bresslau. *Die Strudelwürmer*, Leipzig (1913).
Taliaferro. *J. exp. Zool.*, **31**, 59 (1920).
Viaud. *Le phototropisme animal*, Paris (1948).

TELOTAXIS

In TELOTAXIS *orientation is directly towards (or away from) the source of light* ; there is no question of bilateral balance, nor, indeed, are two eyes necessary ; but it is essential to have an eye with several receptor elements which are able to appreciate the direction of a single light or each of several sources simultaneously, and a central nervous organization which can inhibit all stimuli except one. It is this factor of *inhibition* which forms the essential evolutionary advance, for it provides a mechanism much more efficient than is available to the previous types which respond to the summation of all stimuli (Figs. 28 to 31).

[1] Pearl (1903), Mast (1910–11), Boring (1912), Steinmann and Bresslau (1913), and particularly Taliaferro (1920).

This type of response is characteristic of a large number of
Arthropods, particularly Insects, in laboratory conditions; most of
them react in a similar manner.[1] Whether flying or walking deprived
of their wings, they proceed directly towards a light ; if two lights are
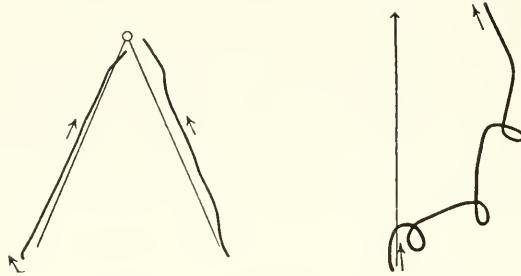
FIGS. 28–29.—TELOTAXIS IN THE BEE.

FIG. 28.   FIG. 29.

FIG. 28.—The tracks of two bees in a relatively straight line towards a light
(indicated by the circle).

FIG. 29.—The path taken by a bee in a directive light (indicated by the arrow),
when the left eye is blackened. There are some circus movements to the
right initially, whereafter the insect eventually walks directly towards the
light (Minnich, 1919).

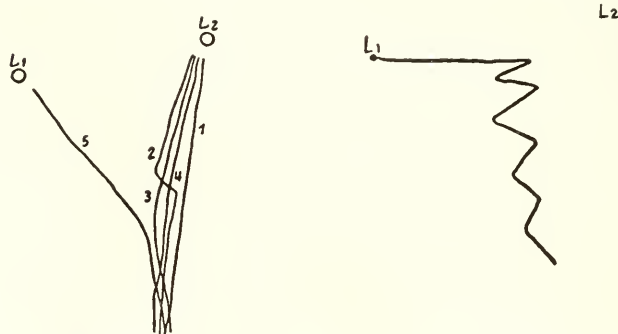FIGS. 30–31.—TELOTAXIS IN A TWO-LIGHT EXPERIMENT.

FIG. 30.   FIG. 31.

FIG. 30.—The tracks of 5 hermit crabs in their taxes towards two lights, L_1 and
L_2. Each part of the track is directed towards one light only. 1, 4 and 3
travel directly to L_2. 2 does so initially and after a short time directs
itself towards L_1 but rapidly resumes the path straight to L_2.′ 5, after
an initial start towards L_2, travels straight towards L_1 (after von Budden-
brock, 1922).

FIG. 31.—The track of an isopod, *Aega*. For a time it follows a zigzag course
alternating between L_1 and L_2 until it finally makes up its mind to travel
straight towards L_1 (after Fraenkel, 1931).

[1] The blow-fly, *Calliphora vomitoria*—Rádl (1903) ; the aquatic nepid, *Ranatra*
—Holmes (1905) ;   the fruit-fly, *Drosophila*—Carpenter (1908) ;   the butterfly,
Vanessa—Dolley (1916) ; the robber-fly, *Erax rufibarbis*—Garrey (1918) ; the honey-
bee, *Apis*—Minnich (1919), Clark (1928), Urban (1932) ; the drone-fly, *Eristalis*—Mast
(1923), Dolley and Wierda (1929) ; the flesh-fly, *Sarcophaga*—Wellington (1953) ; the
locust, *Locusta migratoria*, in the hopper stage—Chapman (1954) ; and others.

exposed they may take a zig-zig path initially, as if hesitating between the two, but soon the insect goes towards one, usually the stronger, neglecting the other (Figs. 30 and 31) ; and if it is unilaterally blinded, after some initial circus movements it again proceeds straight towards the light (Fig. 29). Experimenting with termite larvæ (*Calotermes*), Richard (1948) found that the direction of motion was determined by the direction of the rays rather than by the intensity gradient, but that the latter determined the straightness of the path. The
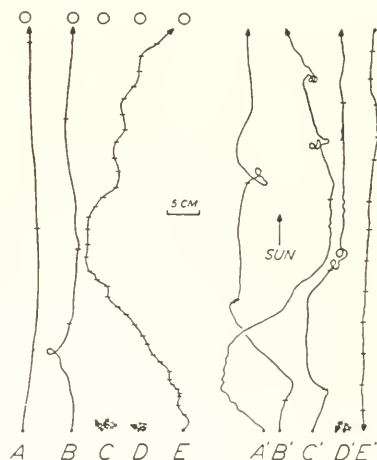
Fig. 32.—The Relative Role of the Ocelli and Compound Eyes
in Telotaxis.

A, B, C, D, the track of the flesh-fly, *Sarcophaga*, in a darkened room towards a light indoors (6-watt lamp, marked by the circle).

A, a fly with all its eyes uncovered ; B, only the compound eyes uncovered ; C, only the ocelli uncovered ; D, all the eyes covered. It is seen that in C and D the insect is completely at a loss.

A', B', C', D'. Movements of the same individuals over the ground outdoors towards the sun. It is seen that the fly with only its ocelli uncovered orientates itself well. The irregularities of the tracks were produced by responses to patches of cirrus cloud passing overhead and do not occur when the sky is clear.

E. The track of the larva of the sawfly, *Neodiprion*, indoors, and E' outdoors. It is seen that, in contradistinction to *Sarcophaga*, the track outdoors is straighter than that indoors.

The time-marks in all tracks show 10-second intervals (W. G. Wellington, *Nature*).

stemmata of larvæ generally mediate this activity, but in the adult as a rule the effective organ is the compound eye, the action of which is frequently supplemented by the ocelli which, however, may be quite ineffective by themselves.

Fig. 32, for example, taken from Wellington's (1953) work, shows the phototactic response of the common dipterous parasite, the flesh-fly, *Sarcophaga*, crawling with clipped wings towards an ordinary (non-polarized) light in the

Sarcophaga

Honey-bee

Mysid

Eupagurus

Photinus

laboratory ; its path towards the light with all its eyes uncovered is straight ; with only its compound eyes uncovered, relatively straight ; and with only its ocelli uncovered, quite indeterminate.

The compound eye of the average adult insect is well equipped to respond accurately to a telotactic stimulus of this type, and may be specifically differentiated for the purpose. In the honey-bee, for example, the rapidity and accuracy of the response are due to the functional arrangement of this organ wherein tropotactic as well as telotactic elements are found ; the anterior median units of the eye (ommatidia) initiate reflex turning movements to the contralateral side, the lateral ommatidia to the ipsilateral side, while the central ommatidia, which alone are used for fixation, initiate none (Fig. 33). The animal is thus provided with a very efficient mechanism of orientation, the peripheral parts of which can initiate turning in either direction so that the stimulus is rapidly directed to the important central area, a reflex mechanism which is analogous to the fixation reflexes in man.

A more plastic mechanism is seen in some aquatic Crustaceans such as the tiny mysids of aquarium tanks (*Hemimysis*—Franz, 1911 ; Fraenkel, 1931) or the hermit crab, *Eupagurus* (von Buddenbrock, 1922 ; Alverdes, 1930). The latter animal goes towards a single light, and even although it con-

FIG. 33.—THE TELOTACTIC TURN-ING RESPONSE IN THE COMPOUND EYE.

When *f* is the line of fixation the arrows show the direction of turning induced by illumination of different regions of the eye (after Kühn).

tinually changes its method of progression, now walking forwards, now sideways or at an angle, it invariably walks straight towards one light in the environment, a directness of path unaffected by the removal of one eye. It would seem that, unlike the bee, any part of the crab's retina can act as a fixation area, and that it must be endowed with a more plastic degree of visual coordination.

The orientation of the fire-fly, *Photinus pyralis*, is even more interesting (Mast, 1912 ; Buck, 1937). If a male glows [1] in the neighbourhood of a female, she raises and twists her abdomen so that its ventral surface is directed straight towards him no matter in which direction he may be, and produces a momentary glow ; he thereupon, no matter in which direction he is going, turns through any required angle between 0° and 180° towards the spot whence the glow came and proceeds in total darkness straight towards her. These responses, which
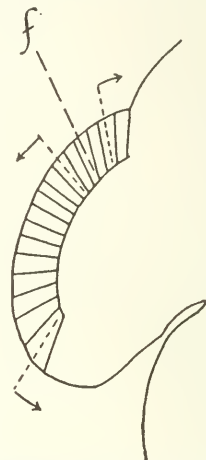
[1] p. 742.

frequently occur when one eye only is illuminated, are directionally very exact
and do not depend on the persistence of the stimulus—a primitive kind of
menotaxis.

The execution of these movements of orientation in insects is the
result of a complex series of coordinated reflexes in the wings or legs of
both sides, each of which is specifically correlated to the location of the

Figs. 34–36.—The Orientation of the Robber-fly, *Proctacanthus*, on a
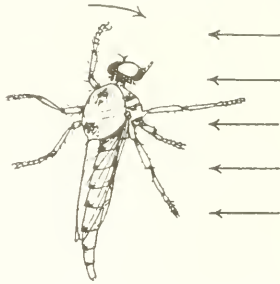White Background in a Horizontal Beam of Light.

Fig. 34.—The upper portion of the left eye and the lower portion of the right
eye are covered. The insect is leaning to the left and turning to the
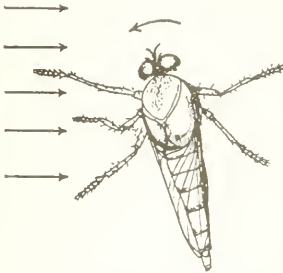right towards the light.

Fig. 35.—One leg has been removed on
the right side while the light comes
from the left. The insect is seen turn-
ing to the left towards the light guided
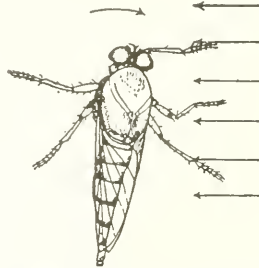largely by its left front leg.

Fig. 36.—When the light comes from the
right, in order to orientate itself in this
direction, the left front leg is thrown
over to the right side and is used to
pull the animal in this direction (after
Mast, 1924).

stimulus in the eyes. The excitation of a particular retinal area induces
a reaction which orientates the insect in a direction such that the
continuous turning allows successive retinal points to be stimulated
until the fixation ommatidia are reached ; once this orientation has
been attained, the reflexes become inoperative, and if any subsequent
deviation occurs further reflex re-orientation immediately corrects it.
These reflexes are somewhat analogous to the segmental scratch-
reflexes in higher mammals, and their effects have been explored
experimentally (as by rotatory experiments on a turn-table) in a large

Silver-fish

Mosquito
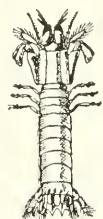
Gonodactylus

number of species by numerous observers.[1] If the insect is illuminated from in front, it steps forwards using all its legs ; if from the side, the front legs on both sides step towards that side even if one eye only or parts of the eye are functional (Fig. 34) ; and if the front leg on one side is removed, on lateral illumination the front leg of the other side is extended towards the light, pulling the animal round towards the normal or, if necessary, the mutilated side so that it can orientate nearly as precisely as a normal insect (Mast, 1923–24) (Figs. 35 and 36).

SCOTOTAXIS (σκότος, darkness) is a term sometimes employed to describe the habit of some organisms, particularly insects, to travel towards a dark object : thus insects such as the silver-fish, the caterpillar, the ant, the mosquito and the louse [2] will travel towards a dark screen ; if such a screen and a light are exposed, some will go directly away from the light (negative phototaxis) and some towards the dark screen (scototaxis).[3] The stomatopod, *Gonodactylus*, which becomes more active in darkness, will always seek a dark shelter rather than a bright object even although it has to swim towards the light to get there (Bolwig, 1954). It is probable, however, that in most cases such behaviour can be included within the concept of negative telotaxis, although occasionally the form of a dark object may be important in the orientation.

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MENOTAXIS

So far we have considered orientations either directly, or relatively directly, towards or away from a source of light ; it is obviously of greater biological importance if, in addition, *an animal can travel at an*

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[1] Rádl (1903), Santschi (1911), Wolf (1927–31), Fraenkel (1927), Schulz (1931), v. Buddenbrock and Schulz (1933), and others.

[2] *Lepisma*—Meyer (1932) ; *Vanessa*—Götz (1936) ; *Lasius*—Weyrauch (1936) ; *Aëdes*—Kennedy (1939) ; *Culex, Anopheles*—Rao (1947) ; *Pediculus*—Wigglesworth (1941).

[3] *Formula*—Klein (1934).

angle to the light, thereby putting itself in the position of the pilot of a ship who can steer otherwise than directly in line with the sun or the pole-star. In the simpler types of orientation, light acts as a stimulus attracting or repelling the animal into a more favourable environment ; in menotaxis light is merely used as a means to an end, guiding the animal to a place where it wishes to go whether favourable or not.

Four types of response which can be considered as menotactic (the term being used in its widest sense) require particular note—the light-compass reaction, orientation to polarized light, orientation to a visual pattern, and the dorsal (or ventral) light reaction.

The LIGHT-COMPASS REACTION, whereby *the animal travels at a fixed angle to a light* (the ORIENTATION ANGLE) either in a straight or a circular direction, was first described by Santschi (1911) in his observations on ants,[1] and was so named by von Buddenbrock (1917) (Lichtkompassbewegung) (Fig. 37). It is a response of considerable complexity and of wide distribution, occurring in some polychæte worms,[2] in some molluscs,[3] in the Amphipod, *Talitrus saltator*,[4] in spiders returning from a kill in the centre of their web,[5] in a large number of insects returning to their nests,[6] and in some birds as a means of navigation.[7] In general, light-compass reactions may be divided into two types. In the first (TROPO-MENOTAXIS, Ludwig, 1934), the reaction is essentially simple and tropic in type, being governed primarily by the intensity of the light, and if two lights appear, their effects are summated and the animal orientates itself balanced at an angle between them [8] ; but the more common reaction is one of TELO-MENOTAXIS wherein the receptor organ is sufficiently evolved to appreciate the direction of a light and is able to inhibit other stimuli so that it can orientate itself with reference to it alone.

There is no doubt that in laboratory conditions and with controlled artificial sources of light many Arthropods show a remarkably high degree of accuracy in maintaining an orientation angle by this means ;

Web spider

Geotrupe

●Light

α

FIG. 37.—
MENOTAXIS.

The orientation of the Mollusc, *Elysia viridis*, with respect to light. α is the orientation angle which the longitudinal axis of the Mollusc makes with the direction of the light (Fraenkel).
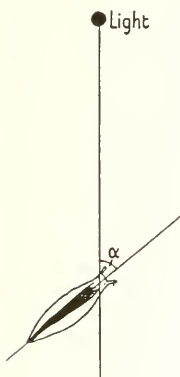
[1] p. 68.
[2] v. Buddenbrock (1937).
[3] The common snail, *Helix*—v. Buddenbrock (1919) ; the Mediterranean Gastropod, *Elysia*—Fraenkel (1927).
[4] Pardi and Papi (1953).
[5] Bartels and Baltzer (1928), Bartels (1929), v. Buddenbrock (1937).
[6] v. Buddenbrock (1931–37), v. Buddenbrock and Schulz (1933).
[7] Ruppell and Schein (1941), Lack (1943), Wilkinson (1949), Matthews (1951–53).
[8] The caterpillars of the gipsy moth, *Lymantria dispar*—Ludwig (1934) ; the dung beetle, *Geotrupes sylvaticus*—Honjo (1937).

the Amphipod, *Talitrus saltator*, for example, reacts in this way to the moon (Pardi and Papi, 1953). Until recently most writers agreed that this reaction was the essential factor in the orientation of insects out-of-doors. This is probably the case when fog or cirrostratus turns the sun into a small light source, but the lack of consistency in the behaviour of insects in natural conditions when the sun is bright does not substantiate that this is the main or even an effective mechanism, and the experiments of Wellington (1955) would seem to indicate that solar heat and the response to the plane of polarization of light[1] are the essential factors in determining their conduct in these circumstances.

The accuracy of the response of the light-compass reaction in insects is made possible by the structure of the compound eyes, for
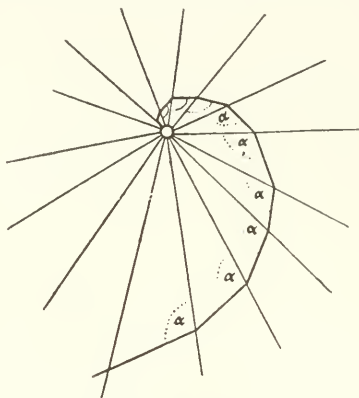

FIG. 38.—MENOTAXIS.

The insect moves so that its course makes a constant angle (α) with rays of light issuing from a source ; it therefore approaches the source along a logarithmic spiral (after von Buddenbrock).

they orientate themselves in such a way that the sun's rays stimulate one or at most a few ommatidia all the time.[2] The high degree of accuracy thus obtained may be gathered from the fact that insects sometimes correct their angle of orientation if the light merely passes from one ommatidium to its neighbour (von Buddenbrock and Schulz, 1933). When the guiding light is sufficiently far away this type of response is effective in orientating the insect in a straight line, but if the stimulus is close an entirely different result is seen. If the insect were to pursue a straight path, the incidence of such a light on the retina would constantly change ; and if the angle of incidence is to be kept constant, the insect must perforce turn along a logarithmic spiral which ends in the light itself (Fig. 38) (von Buddenbrock, 1937). Caterpillars crawl to a light in this type of spiral path (Ludwig, 1933–34) and it is for this reason that the moth, applying a mechanism adapted

[1] p. 73.   [2] p. 174.

for reference to a distant source of light, flies to its death in the nearby flame.

This behaviour is not constant in moths. If a number of these insects is introduced into a room where a candle is situated on a table they will take up positions on the table around the light with their heads turned towards it. As a rule, one by one they take wing ; the first may fly around the flame in diminishing circles until it passes through it to fall in flames into the molten mass of wax beneath ; the next will similarly follow to commit deliberate suicide ; and so on the procession goes, some perishing in the flame itself, others escaping with singed wings to fall on the table when, with wings too charred to use, they may crawl with difficulty up the candle and walk straight into the base of the flame to die. While most fly around the flame in decreasing circles, some may fly straight into it ; others remain upon the table apparently worshipping from afar, while others again wander aimlessly about the room paying no attention to the light. The cause of this variation in conduct is quite unknown ; it seems to indicate that the phototactic response is not entirely determined on a mechanistic level.

The navigational sense in birds is an astonishing example of the accuracy of a modification of the light-compass reaction. It has long been known that young birds will undertake their initial migration from one continent to another unaccompanied by their parents and arrive in the correct habitat with extreme precision, and that homing birds such as the pigeon or the gull, released in an unknown area in random directions, will rapidly head straight for home in a direct line of flight (Matthews, 1951–55 ; Kramer and St. Paul, 1952 ; Kramer, 1953). The Manx shearwater, *Puffinus*, for example, transported to America, has homed 3,050 miles across the Atlantic wastes to arrive after $12\frac{1}{2}$ days in its own particular burrow on an island off the west coast of England (Matthews, 1953). It is obvious that in navigational feats of this type visual orientation is quite inadequate and a bi-coordinate orientating mechanism of great accuracy must exist. It is true that many birds show a relatively simple positive phototactic response, flying towards an illuminated patch or the lighted end of a long dark tunnel—a primitive reaction still carried out after ablation of the cerebral hemispheres (pigeons, Viaud and Marx, 1948) ; but it is equally true that they are capable of executing the most complex type of orientation.

Puffinus

For years this navigational ability of some birds has excited the curiosity of naturalists. Several explanations have been explored such as an acceleration-displacement recording mechanism or an ability to exploit the earth's magnetic field, but they have all been discredited by experiment [1] ; nor do the structural arrangements apparently exist in the eyes of birds as in the compound eyes of insects to appreciate the

[1] Gordon (1948), Matthews (1951–55), Yeagley (1951), van Riper and Kalmbach (1952).

polarization pattern of the sky (Montgomery and Heinemann, 1952). The evidence would seem incontrovertible that these birds can orientate themselves by an innate ability to estimate the sun's arc by observation of its movement over a small distance and, by extrapolation, to navigate automatically over great distances with extreme accuracy even when flying is continued during the night. Flight throughout the journey is governed by a number of factors developed by individual experience in respect of which considerable variations exist, but the fundamental basis of the method of orientation is an innate form of sun-navigation depending on an appreciation and memory of the angle of incident light and an ability to make appropriate corrections according to the 24-hour rhythm of a reference system (an internal clock) operating in the brain (Ruppell and Schein, 1941 ; Lack, 1943 ; Saint Paul, 1953 ; Matthews, 1953–55 ; Kalmus, 1954 ; Pratt and Thouless, 1955).

Homing pigeon

This theory had its origin in the observations of Ising (1945), Varian (1948), Davis (1948) and Wilkinson (1949), but the most satisfying evidence came from the experiments of Matthews (1951–55) on homing pigeons, gulls and Manx shearwaters. He found (as have others) that birds released in a strange or clueless environment (such as over the sea) rapidly orientated themselves in the correct direction for home as they soared to fly, and maintained their direction over long, direct flights over unknown country ; but they were able to find the correct direction only when the sun was up and their initial accuracy in flight depended on a clear sky ; in cloudy or overcast weather they were helpless

FIGS. 39–40.—NAVIGATION BY BIRDS.

To illustrate the initial orientation of the Manx shearwater when released in a strange environment. The home direction is vertically upwards. The length and breadth of the rays is proportional to the number of birds that orientated in the direction indicated.
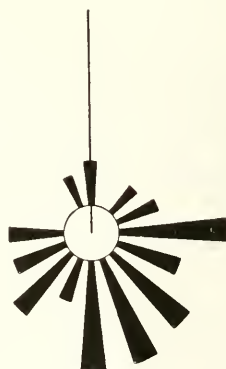

FIG. 39.   FIG. 40.

FIG. 39.—Orientation under a cloudless sky. It is seen that the great majority of the birds orientated themselves initially in approximately the right direction.
FIG. 40.—Orientation under heavily clouded skies. The ability to orientate correctly has been lost (G. V. T. Matthews).

(Figs. 39 and 40). By keeping the birds in conditions wherein the sun and sky were excluded for a number of days before release, consistent errors were made which could only be explained on the supposition that the birds were failing to correct for the seasonal variation in the sun's altitude from which they derived their measurement of latitude. By de-synchronizing the day–night rhythm before release by arranging an artificial day beginning and ending a few hours earlier or later than normal, errors in longitude were made which could be explained on the basis of a disturbance of an inherent time-sense based on
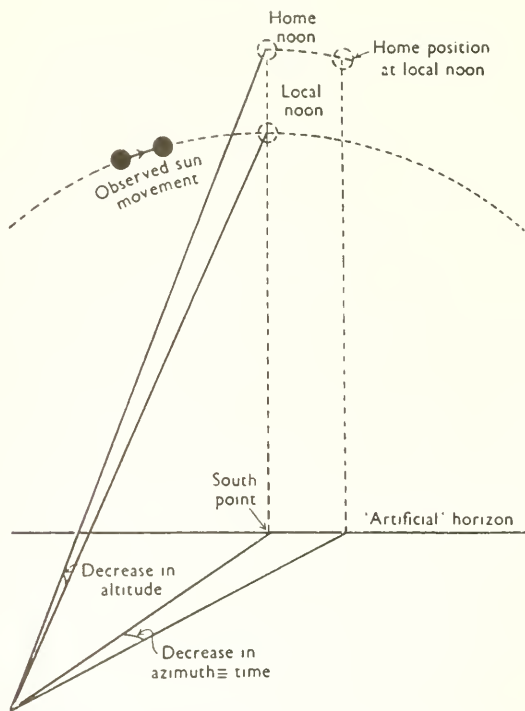

FIG. 41.—DIAGRAM ILLUSTRATING THE HYPOTHESIS OF SUN NAVIGATION.
Released to north and west of home. See text. (The diagram is not to scale.) (After G. V. T. Matthews.)

regular light-dark sequences ; they flew in a false direction—too far east after an advanced day, too far west after a retarded day. That the direction is determined by the incident light was strikingly shown in Kramer's (1952) experiments with migrating starlings : when the light was deflected by 90° by mirrors, the birds' flight was equally deflected and in the same direction.

Wilkinson's hypothesis is illustrated in Fig. 41. Briefly, the sun's arc is observed over a small excursion and from this its position at local noon and the geographical south are extrapolated ; the latitude is determined by the difference between the observed noon altitude and the remembered noon altitude at home. The difference in longitude is derived partly by comparison with the home position in azimuth at local noon combined with an estimation of time in the diurnal night–day cycle. This, although it is not yet experimentally

proven, appears at present to be the most probable explanation of the observed facts ; it may well seem so complicated an automatic calculation by a creature with a proverbially small brain as to appear fantastic ; but the ability of a bird released in America to orientate itself immediately for its flight to a particular and very precise locality in Europe is fantastic—it occurs within 40 seconds of viewing the sun. It would seem that on the basis of its structural potentialities, the avian retina should be capable of such a feat.[1] It has also been suggested (again without proof) that the pecten [2] may play some part in the analysis by acting as a fixed point when taking observations (Menner, 1938 ; see also Crozier and Wolf, 1943 ; Griffin, 1952).

ORIENTATION TO POLARIZED LIGHT. Arthropods as widely different as the king-crab, the sand-hopper, the ant and the honey-bee possess the ability to respond to the plane of polarization of light, and by this means may orientate themselves in skylight out-of-doors. This faculty can be investigated experimentally by observing the response to the rotation of the axis of a sheet of " Polaroid " glass. Sensitivity of this type was first demonstrated in bees by von Frisch (1949) and has since been confirmed in behavioural experiments involving a number of Arthropods, both larvæ and adults,[3] and has also been proved by electroretinographic responses.[4]

Light from the blue sky (not directly from the sun) has been scattered from particles in the atmosphere which also partly polarize it, that is, more of the light-waves vibrate in one transverse direction than in others. The plane of maximum polarization is different for each patch of blue sky, and the proportion of light polarized also varies, being greatest at 90° from the sun. Thus each patch of blue sky has its own plane and intensity of polarization, differing from every other patch. A " Polaroid " glass is a submicroscopic crystalline grid transmitting chiefly light vibrating in one particular direction ; it can be used to analyse the plane and intensity of polarization of light since, on rotation, light polarized in other planes is cut off.

We shall see presently [5] that insect larvæ have simple eyes (stemmata) while adults, in addition to simple eyes (ocelli) are usually equipped also with two large compound eyes. The stemmata of the larvæ respond both to direct light and alterations in the plane of polarization, while in adults the ocelli sometimes show little or no phototactic response to non-polarized light, but aid the compound eyes in their response to polarized light. In these cases the former are thus supplementary in function so that the intact animal reacts more quickly and accurately than one deprived of its ocelli.

[1] p. 417.   [2] p. 416.
[3] Larvæ of the sawfly, *Neodiprion*—Wellington *et al.* (1951) ; mosquito larvæ— Baylor and Smith (1953) ; adult insects—Vowles (1950–54), Menzer and Stockhammer (1951), Carthy (1951), Stephens *et al.* (1952–53), Wellington (1953), de Vries *et al.* (1953) ; other Arthropods—Waterman (1950), Kerz (1950), Pardi and Papi (1952), Baylor and Smith (1953), and others.
[4] Autrum and Stumpf (1950). Waterman (1950–51).
[5] p. 222.

The interesting experiments of Wellington (1953) will make the matter clear. Fig. 42 shows the abrupt changes of direction associated with rotation of the axis of a sheet of " Polaroid " held over larvæ crawling over the ground ; the intact animal responds most markedly, but an adequate response is obtained if either the ocelli or the compound eyes are functioning alone.
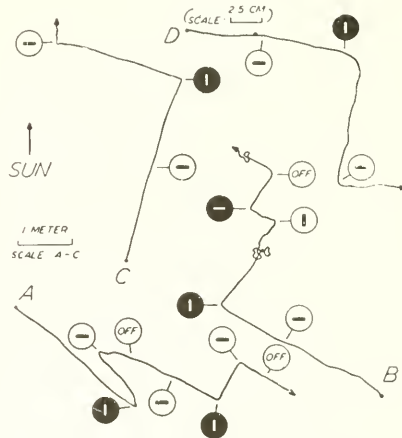

Fig. 42.—The Effects of Alterations in the Plane of Polarization
on the Orientation of Insects.

The plane of polarization was changed by rotation of the axis of a sheet of " Polaroid " held between the insect and the sun as it crawled over the ground. The circles show the point at which the sheet of Polaroid was placed over the moving insect or rotated or withdrawn. The bar inside the circles shows the orientation of the axis with respect to the sun, and the shading of the circle indicates whether or not the sky was appreciably darkened when viewed through the " Polaroid " with the axis set as shown.

A, B, C. The path of a fly : A, with all its eyes functioning ; B, with only its compound eyes uncovered ; C, with only its ocelli uncovered.

D. A fourth-instar larva of *Neodiprion* (drawn on a different scale).

The marked convolutions in the path of B show the response to alterations in the polarization of the skylight when a patch of cirrus cloud passed overhead (W. G. Wellington, *Nature*).

The Orientation of Insects out-of-doors

It would thus appear that the orientation of insects in natural conditions in daylight is a very complicated matter. When these questions first received attention in the classical observations of Santschi (1911) and Brun (1914) on the behaviour of the ant,[1] its conduct was interpreted as being regulated by a light-compass reaction alone. At a later date the experiments initiated by von Frisch (1949–51) introduced the complicating factor of a response to the plane of polarization of light. Finally, the experiments of Wellington and his co-workers (1953–55) have stressed the importance of a thermal response. There is complete agreement that the light-compass

[1] p. 68.

reaction is the essential determinant of behaviour in laboratory conditions with artificial light, in natural surroundings at night and in circumstances during the day when the sun is largely obscured, but these latter workers believe that on a clear day the sun acts primarily as a source of heat. Wellington (1955) concluded that in full sunlight, insects in open places orientate themselves primarily by solar heat when it is available and maintain their orientation to the sun or their straight-line travel in its absence by polarized light from the overhead sky ; if as may happen when smoke or cirrus cloud of varying densities passes overhead, the plane of polarization changes rapidly, the response may completely break down and the insect remains stationary even although the sun remains exposed (see Fig. 32). This sometimes makes its behaviour appear irregular and difficult to interpret, particularly in the neighbourhood of industrial centres where haze and smoke are plentiful. Wellington considered that during overcast weather travel is probably also aided by light gradients (tropo-menotaxis). In general, when an insect is cool it is thermo-positive and travels towards the sun ; when it is warm it is thermo-negative and orientates itself away from the sun, and if it becomes overheated and the plane of polarization changes rapidly the insect becomes disorientated and is incapable of travelling so that it often circles aimlessly until it succumbs to heat-stroke (Wellington *et al.*, 1951–54 ; Sullivan and Wellington, 1953 ; Wellington, 1955). The same complex interaction between thermal and visual stimuli is seen in the locust which postures at right angles or parallel to the sun's rays depending on the temperature (Volkonsky, 1939). Occasionally, as in the ant, the evidence suggests that other stimuli such as gravity are also effective in orientation in such a way that the geotropic and phototactic elements are correlated in a single central mechanism of taxis (Vowles, 1954).

From the historical point of view, the *homing of the ant* provided the classical example of this type of activity. The purposive behaviour of these insects, particularly when returning to the nest laden with
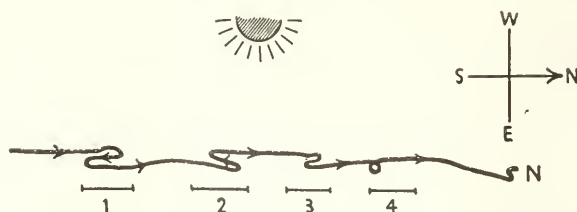
Ant

FIG. 43.—MENOTAXIS.

The ant was returning to its nest, N, with the sun on its left side. On four consecutive places, 1, 2, 3 and 4, it was shaded from the direct light of the sun and the image from the sun was projected from the animal's right by means of a mirror. On each occasion the animal preserved its initial orientation relative to the sun or its image by turning round (Santschi).

food, in spite of an immense load between their mandibles and in face of all obstacles, has excited admiration and conjecture for centuries. Nevertheless, although considerable intelligence is suggested, the response is largely automatic. Cornetz (1911) observed that if such an insect were lifted up and set down in another place, it set off in the same direction as before whether or not this led to the nest. That the directing influence was the sun was shown by Santschi (1911) who shaded the ant from the sun and deflected its rays by a mirror so that they reached the insect from the opposite side ; each time this was done the ant immediately changed its path so that it maintained the same direction with regard to the reflected rays as it had previously to
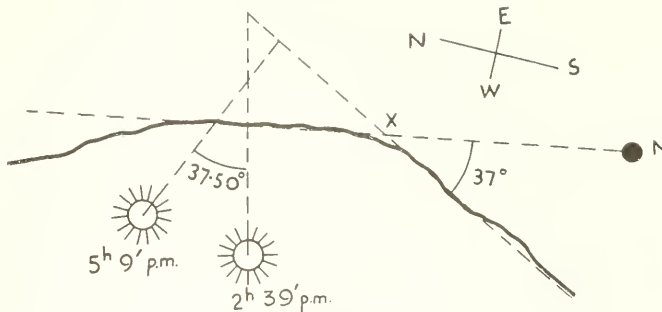

FIG. 44.—MENOTAXIS.

The orientation of the ant, *Lasius niger*. The dark line indicates the route taken by the ant towards its nest, X. The initial part of its journey was orientated at an angle of about 90° to the sun. At X, the ant was imprisoned in a box for 2½ hours, from 2.39 p.m. to 5.9 p.m. During this time the sun had traversed an angle of 37·5°. On its release, the ant resumed its path again at right angles to the late afternoon sun, deviating from its former path by an angle of 37° (after Brun).

the direct rays (Fig. 43). The same reaction was demonstrated in locusts by Kennedy (1945–51), who found that the direction of the marching desert hoppers could readily be changed and that of flying adults momentarily changed by reflecting sunlight onto them with a mirror. At first this response was assumed to be a typical example of the light-compass reaction, but Wellington (1955) brought forward evidence that it was more probable that radiant heat associated with the reflected light was the more effective stimulus.

A still more elaborate response was demonstrated in the classical experiment of Brun (1914) who confined an ant in a box for some hours in the middle of its homeward journey to its nest ; on releasing the insect it set out on a new track, not now towards its nest but deviating from its original route by an angle corresponding to that through which the sun had moved in the interval so that its rays were still received at the same angle as before (Fig. 44). Again, this was initially

taken to be an example of the light-compass reaction, but the response could be equally explained by orientation by the pattern of polarization which also shifts with the sun (Griffin, 1953 ; Wellington, 1955). The homing of the honey-bee when deprived of other optical clues such as conspicuous landmarks[1] is determined by the same mechanism (Wolf, 1927 ; von Frisch, 1931). Behavioural experiments have demonstrated that certain insects are not only able to analyse the polarization of light but can retain its pattern in their memory to take account of the alteration in the position of the sun with the time of day (von Frisch, 1950 ; Vowles, 1950 ; Griffin, 1950 ; Stephens *et al.*, 1952) ; by this type of mnemotaxis it is probable that homing remains accurate for long journeys despite the changing position of the sun.

It is not to be thought, however, that the homing of the ant need be an entirely visual process. Bonnet (1779–83) first showed that odour trails may be an effective aid (Carthy, 1950 ; Vowles, 1955), and the ability of this insect to improve its path-finding and avoid detours is exemplified in its extraordinary capacity to learn quite complex mazes (Turner, 1907 ; Schneirla, 1929–33 ; etc.).

It is interesting that *the " dancing " of bees*, the ballet by which they communicate to other foraging bees the direction, the distance and the richness of a discovery of nectar, is also largely determined by the
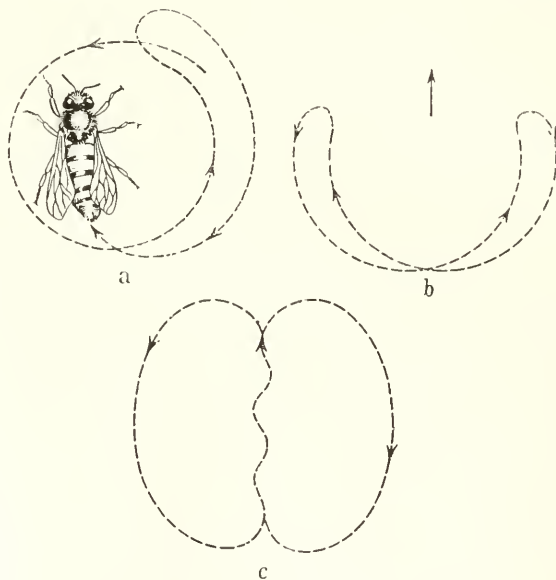

FIG. 45.—THE DANCE-FIGURES OF BEES.

(a) The round dance for short distances performed by German and Austrian bees. (b) The " sickle dance " for short distances performed by Dutch and Swiss bees. (c) The figure-of-eight dance for long distances, with the " waggle-run " forming the central component of the figure (von Frisch).

[1] p. 78.

polarization pattern reflected from the sky. The coordinated dance which a returned forager performs on the surface of the comb within the hive was described by Aristotle,[1] and in recent times has been most closely studied by von Frisch,[2] the Austrian naturalist (1949–54), using slow-motion cinematography and specially marked bees attracted to rich diets placed at different distances in different directions from the hive. For distances closer than 10 metres the returned bee communicated its news to the rest of the hive by performing a simple circular dance ; for distances greater than this the direction of the food is indicated by using the vertical direction on the surface of the
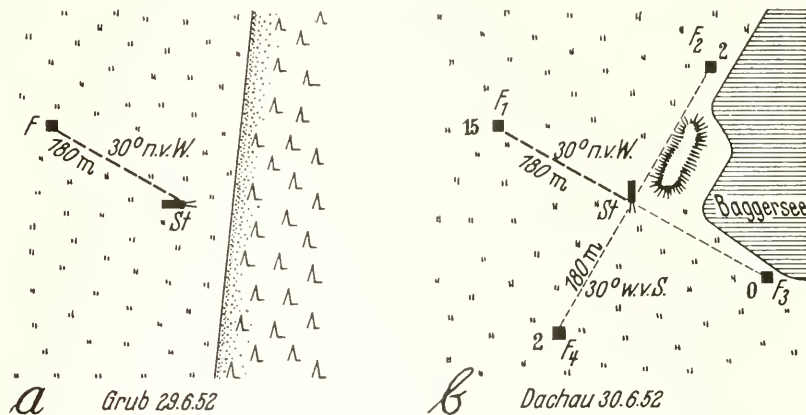

Fig. 46.—The " Displacement Test " in the Orientation of the Bee.

    This test indicates the ability of the honey-bee to allow for a change in the position of the sun. In (a), marked bees from a hive, *St.*, were allowed to feed on the afternoon of June 29th, 1952, from a feeding place, *F*, 180 m. away in the direction 30° north of west. The following morning the hive was transported to another entirely unknown landscape of a completely different type. The vast majority of the bees (15 out of 19), without any help from familiar landmarks, went to one of 4 alternative feeding places 180 m. away from the hive and 30° north of west, ignoring other symmetrically placed feeding places. On the first afternoon the sun had been in the west ; on the second morning the sun stood in the east ; so that in order to retain the same orientation the bees must have been able to calculate and allow for the solar movements (von Frisch).

comb (the direction of gravity) to represent the direction of the sun's rays outside the hive, the distance of the source of food by the speed of the dance, and the richness of the find by its vigour. The dance takes the form of a squat figure-of-eight, the straight transverse run of which is marked by the bee actively waggling its body with an enthusiasm depending on the richness of the nectar (Fig. 45) ; the direction of this run bears the same relation to the vertical as does the position of the

[1] *Hist. Animal.*, 18, 624b. 8. See Haldane, *Behaviour*, **6**, 256 (1954).
[2] See Fig. 728.

source of food to the position of the sun at the time, while the speed of the dance varies inversely as the distance (about 10 revolutions in 15 secs. to indicate a distance of 100 metres, 2–5 revolutions to indicate 3,000 metres). The indications of direction attain an accuracy of 3° in good conditions, of distance of up to 100 metres. Moreover, unlike the ant, bees possess an innate time-keeping mechanism whereby they can make compensation for the movements of the sun or changes in the pattern of polarization in the sky as the day progresses, making the appropriate correction in their direction (Fig. 46).

It is interesting that there is no component in the dance for a vertical distance, presumably because such is rarely required in natural surroundings ; and when von Frisch et al. (1953) fed bees on a feeding-table perched on a radio beacon directly above the hive, new foragers were unable to find it. As performed in the hive the waggle-run serves to indicate the direction of the food as related to the sun by reference to the vertical as determined by gravity ; occasionally the dance is performed on the horizontal alighting board in front of the hive and in this case the waggle-run points to the actual direction of the feeding place without reference to the sun. Moreover, in different localities different " dialects " are used. Thus, while von Frisch (1950) found that Austrian and German bees dance in a circle to indicate food near at hand without giving any indication of its direction, Tschumi (1950) and Baltzer (1952) found that Swiss bees, and Hein (1950) that Dutch bees perform a "sickle dance", dancing in a semi-circle the axis of which denotes the appropriate direction to be followed exactly in the same way as the straight part of the figure-of-eight dance indicates this for far distances (Fig. 45b).

This extremely complex and highly ritualized pattern of behaviour is an astonishing performance, particularly when it is recalled that the brain of the bee is about one-tenth of an inch in diameter ; it is apparently inborn and instinctive, but its precise implications have to be learnt through experience by the young workers (Lindauer, 1952). The response is disorientated in shadow, resumes its rhythm as soon as a patch of blue sky becomes visible, and can be artificially changed by the interposition of a polarizing film between the insects and the sun. Moreover, when trained bees are transported from the northern to the southern hemisphere where the direction of the sun's movement to an observer is anti-clockwise instead of clockwise, their foraging movements tend to be reversed (Kalmus, 1956). A somewhat similar or even more complicated " language " is used by scout bees to indicate the position or direction for a suitable new home or swarm.

It is clear, therefore, that the orientation of insects out-of-doors, although determined by automatic responses, is an extremely complex affair influenced by many stimuli acting sometimes singly, sometimes in combination ; and it is equally clear that much work will require to be done before their behaviour is fully elucidated.

Aquatic Arthropods also make use of polarized light to orientate themselves while swimming, in some cases reacting to the polarized

light of the sky, as do Amphipods when seeking their return to the sea (Pardi and Papi, 1952–53), or making use of the polarization patterns which exist between the air-water interface (Waterman, 1954). Such reactions have been demonstrated in 12 species of Cladocera, water-mites and caddis-fly larvæ, which tend to swim so that their direction of movement is at right angles to the plane of polarization (Baylor and Smith, 1953). The crab, *Eupagurus*, shows a definite response to a change in the direction of polarization (Kerz, 1950) as also do mosquito larvæ.
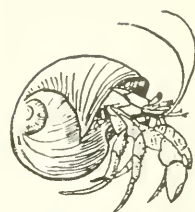
Eupagurus

The navigation of the small crustacean, *Talitrus saltator*, as recorded by Pardi and Papi (1952–53) is a fascinating story. These Amphipods normally live in the intertidal zone. Transferred inland, they move towards the coastline whence they came, taking their direction from the angle of the sun ; as with insects and birds their course can be deflected by changing the direction of the incident light by a mirror. If direct sunlight is not available they can orientate themselves by polarized light from patches of blue sky and can be similarly deflected by the interposition of a polarizing sheet ; under a completely overcast sky they are disorientated. As with bees there is also an innate mechanism which allows them to compensate for movements of the sun throughout the day, but, unlike the reactions of the bee, it would seem that the whole mechanism is established by heredity or acquired in early youth and is set in each individual for ever and cannot be changed. Thus specimens on the west coast of Italy move westwards towards the sea, and even when brought to the seaside of the east coast will automatically attempt to travel westward right across country away from the nearby water. The most extraordinary thing about these creatures is that travelling through the night they appear to be able to navigate with reference to the moon. This is the only instance where this has been established and in view of the complication and rapid change of the lunar path across the sky, it would seem to be an extraordinary feat.

Talitrus saltator

ORIENTATION TO A VISUAL PATTERN so that its reception on the retina remains constant corresponds closely in its mechanism to orientation with respect to a source of light. Thus insects placed on a turn-table facing a window will move round when the table rotates (Rádl, 1902) and if a striped drum is rotated in front of them they will endeavour to keep in line with a given stripe (an " optomotor response") (Schlieper, 1927 ; Schulz, 1931 : Zeiser, 1934)[1]. Gregariousness in locusts depends on the same reaction ; moving so that it nullifies the movement of images across its retina, each swarming insect travels precisely with its neighbour (" gregarian inertia "), the whole host being guided by a light-compass reaction to the incidence of the sun's rays (Kennedy, 1939–45). Orientation when swimming against a current of water (" rheotaxis ") is in fact a visual response of the same type : the water-boatman, *Notonecta*, for example, turns upstream and swims with sufficient strength to maintain a constant impression of the nearby bank ; if the landmarks on the bank are moved, the water-

Locust

Notonecta

[1] This reaction has been used to measure the visual acuity of insects, see p. 588.

Gyrinid beetle

Dragon-fly

Daphnia

boatman moves with them, and if they are obliterated as when swimming in the dark or between plain white boards, the insect allows itself to be carried passively downstream (Schulz, 1931). Gyrinid beetles are similarly disorientated when swimming in the dark or if a sudden change is made in the landmarks on the banks (Brown and Hatch, 1929).

THE DORSAL (VENTRAL) LIGHT REACTION. The orientation of animals which progress on the earth's surface can be treated as if movement on one plane only need be considered ; but those that swim or fly have three available planes of movement—they can turn as do land animals on a vertical axis, but they can also roll on a longitudinal axis or they can pitch, turning somersaults about a transverse axis (Fig. 48). They must therefore possess a complex means of orientation to maintain the body in a desired position as it travels towards a goal. Because of its relatively greater specific gravity the stability of an animal body in air is greater than in water, and since the attachments of wings are comparatively high making the centre of gravity relatively low, the equilibrium of balance in birds raises no serious difficulties. This does not apply with the same force to insects although some, such as the dragon-fly, *Anax*, demonstrate a dorsal light response during flight, the effective organ being mainly the compound eye (Mittelstaedt, 1950) ; but aquatic animals require to perform constant and active balancing movements to maintain their normal orientation. Many fishes maintain their position optically by keeping one surface (usually the dorsal) perpendicular to the light, using their eyes as receptor organs ; others have evolved a specific statocyst organ to maintain equilibrium, but although this development has assumed the greater importance eventually, the eyes still participate in the orientating reflexes, a collaboration between the senses which survives in the elaborate reflex connections which continue to yoke the visual with the vestibular system in Man.

The dorsal light reaction was initially recognized in the crustacean, *Daphnia*, by Rádl (1901), and its wide distribution was first appreciated by von Buddenbrock (1914–37) ; it has since been observed in many groups of aquatic animals of a wide variety.[1] In its essentials the DORSAL LIGHT REACTION ensures that when the light is above, the animal swims with the dorsal surface upwards, maintaining itself symmetrically to it and moving (if it does move) in a plane at right

[1] In Medusæ—Fraenkel (1931) ; polychæte worms—Fraenkel (1931), v. Buddenbrock (1937) ; in a large number of Crustaceans—v. Buddenbrock (1914), Alverdes (1926–3) Schulz (1928), Seifert (1930–32) ; among Insects in nymphs and larvæ—v. Buddenbrock (1915), Wojtusiak (1929) ; in the dragon-fly, *Anax*, during flight—Mittelsta t (1949) ; perhaps in the desert locust, *Schistocerca gregaria*—Rainey and Ashall (1   ) ; and particularly in Fishes—v. Holst (1935).

angles to it ; if the light is placed horizontally the animal rotates correspondingly, and if the light is placed below, it either rolls or somersaults over to swim belly-upwards (Fig. 47). In the VENTRAL LIGHT REACTION an animal which normally swims belly-upwards behaves analogously (Fig. 48). Occasionally, however, if the normal direction of the incidence of the light is changed, the animal does not
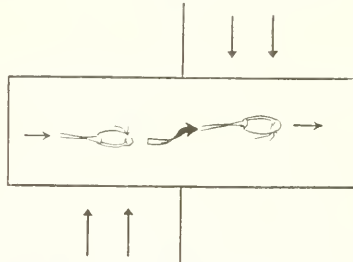

FIG. 47.—THE DORSAL LIGHT REACTION.

On the left half of the aquarium the Crustacean, *Apus*, is illuminated from its right side; on the right half of the aquarium, from its left side. As it swims between the two, it orientates itself by rolling on its longitudinal axis (after Seifert).
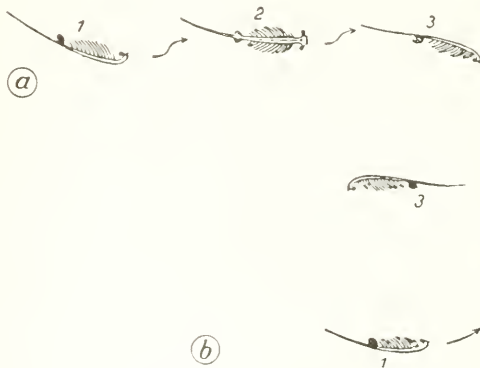

FIG. 48.—THE VENTRAL LIGHT REACTION.

The change of orientation in the Crustacean, *Artemia salina*, when the light is changed from above to below. Fig. 48*a*, by a rolling movement ; Fig. 48*b*, by a back somersault or pitching movement (in a photo-positive individual) (after Seifert).

act reflexly but becomes completely disorientated and swims aimlessly, a reaction seen, for example, in the nemertine worm, *Lineus ruber*, which in normal circumstances is negatively phototactic (Goutcharoff, 1952).

The visual mechanism involved varies in different species. In some larvæ the response is mediated by the dermal light sense and persists after total blinding (Schöne, 1951) but as a rule the eyes are

Lineus ruber
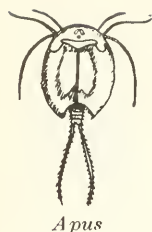
Apus

implicated.   The water-flea, *Daphnia*, orientates itself in the typical manner by means of a single dorsal median eye ; while the fresh-water crustacean, *Apus*, has two compound eyes and a median eye on the dorsal surface.   Other crustaceans have two eyes ; when one is removed or painted over, rolling and circling movements occur towards the seeing side, and if both are thrown out of action the light reaction disappears (the brine-shrimp, *Artemia*, Seifert, 1930–32).

The relation between the statocyst and the eyes in those animals which possess the dual mechanism was prettily shown by von Holst
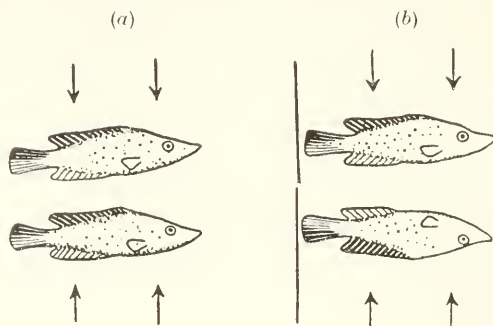

Fig. 49.—The Dorsal Light Reaction.

In the fish, *Crenilabrus rostratus.*
Upper two fish.   The light comes from above ; (a) in the intact animal, (b) in the labyrinthectomized animal.   Orientation is normal.
Lower two fish.   The light comes from below ; (a) the normal posture is retained owing to the influence of the labyrinth ; (b) the labyrinthec-tomized animal swims in an upside-down posture (after von Holst).

(1935) in the fish, *Crenilabrus rostratus*.   Normally the balance is maintained essentially by the static reactions of the labyrinth which are supplemented by the light reaction.   If, however, a light is placed horizontally, a compromise orientation is assumed with the body slightly tilted towards the light, the inclination varying directly with the strength of the illumination ; when the light is placed underneath, the static reactions control the animal and the light is without effect (Fig. 49).   When, however, the labyrinths are put out of action, the optical reaction functions in the pure form, the movements of the trunk, the fins and the tail, hitherto controlled by the labyrinth, now being entirely coordinated by the eyes so that with a transverse light the fish swims on its side ; with a light below, upside-down; finally, when one eye is put out of action, the fish rolls towards the seeing side for a time until an adaptive reaction asserts itself.

This reaction, of course, is often combined with other types of phototaxis. Thus the water-flea, *Daphnia*, is usually positively tropotactic and also exhibits a compass reaction (von Frisch and Kupelwieser, 1913 ; Eckert, 1938), the brine-shrimp, *Artemia*, may be positively or negatively phototactic, and so on.

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MNEMOTAXIS

MNEMOTAXIS is the most complicated method of orientation and *allows the animal to deal with all the elements of a complex situation in the light of experience gained in the past* (Kühn, 1919–39). In the previous reactions we have studied, the response is made to one stimulus only or the synthesis of several, and it may be either direct as in tropotaxis or indirect as in menotaxis, a simple mechanism which becomes effective by the inhibition of all stimuli but the dominant one. These more primitive taxes determine the reactions of lower species, and although they enter into the total response of the higher animals and can be studied separately in experimental conditions, the normal activities of the latter are rarely based on so simple a pattern of behaviour. It is true that the homing honey-bee can orientate itself with regard to the sun and that this is the only mechanism available to the soaring bird as it rises in strange surroundings, but both also make use of other clues in ordinary life as soon as they can appreciate objects in a known environment. In this more elaborate type of orientation two new capacities are added to one or other of the simpler methods— (1) the ability to integrate a number of stimuli simultaneously instead of inhibiting all but one, and (2) the modification of a direct automatic response by the factor of memory through a process of conditioning. By a synthesis of these factors the animal is thus able to deal with a complex situation as a whole (Adlerz, 1903–9 ; v. Buttel-Reepen, 1907 ; Turner, 1908 ; Rabaud, 1924–26 ; Wolf, 1926–27 ; Hertz, 1929–31 ; Friedländer, 1931 ; Tinbergen, 1932–51 ; Tinbergen and Kruyt, 1938 ; Baerends, 1941 ; and others).

In its simplest form this is illustrated by the experiments of van Beusekom (1948) with the homing digger wasp, *Philanthus* (Fig. 50). The initial training situation to which the wasp was conditioned was a square block set at right angles close to the nest and a model of a tree 1 metre from the nest. In the test experiment the block was turned through 45° and the tree displaced first to one side and then the other ; the wasp approached the corner opposite to that

in which the tree was located as if up to the last moment she used both the tree and the block as landmarks.

The pretty experiment of Tinbergen and Kruyt (1938) shows the astonishing rapidity and precision with which the wasp learns to relate its nest to neighbouring landmarks and to appreciate a situation as a whole. A ring of 20 pine-cones was placed around the nest while she was inside ; on leaving she made a study of the locality for 6 seconds only (Fig. 51) ; the pine-cones were then arranged similarly one foot away from the nest ; returning after 90 minutes with a captured bee, she alighted in the middle of the ring of cones, a choice repeated
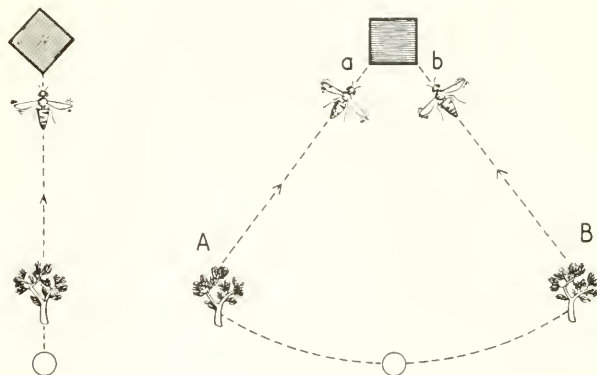

Fig. 50.—The Path of the Digger Wasp, *Philanthus triangulum*.

On the left, the training situation. The path of the wasp (starting from the circle) is directly to its nest at the angle of the block past the tree.

On the right, the test situation. The block is rotated through 45° and the tree moved first to A and then to B. The wasp alights alternately at *a* and *b* (simplified from van Beusekom).

13 times, and only found the nest after the original situation had been restored (Fig. 52). A still more extraordinary ability is seen in the wasp, *Ammophila*, which hunts caterpillars too heavy to be brought back on the wing ; as it laboriously drags its prey to the nest it is apparently able, apart from occasional exploratory flights, to utilize the memories of aerial observation, probably aided by light-compass orientation (Thorpe, 1943–56).

Behaviour of this type is obviously determined by the utilization of a number of stimuli and experiment has shown that in making its decision the insect does not condition itself to every available landmark but exercises some degree of choice on principles which would differ from that of a human being. Moreover, the stimuli need not be simultaneous for visual memories may be retained for some considerable time ; thus the bumble-bee, *Bombus*, will fly regularly round a number of fixed landmarks in the same sequence for weeks on end (Frank, 1941). Such studies are of unusual interest but our knowledge of the problems they raise is yet very imperfect ; indeed, experiment has just

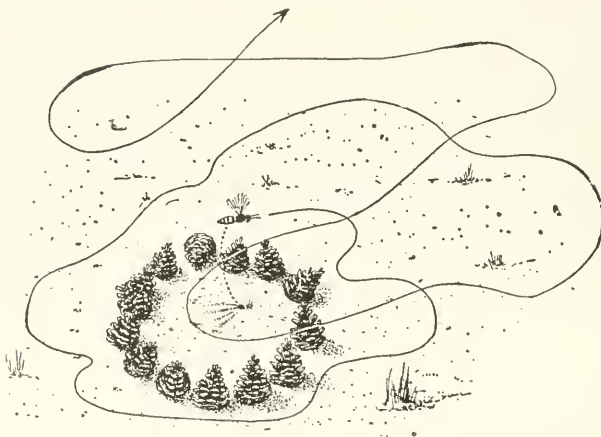*Bombus*

FIGS. 51 AND 52.—THE REACTIONS OF THE DIGGER WASP.

FIG. 51.—The wasp, *Philanthus triangulum*, on leaving the nest in the centre of the ring of pine cones, makes a locality-study lasting 6 seconds and then leaves.
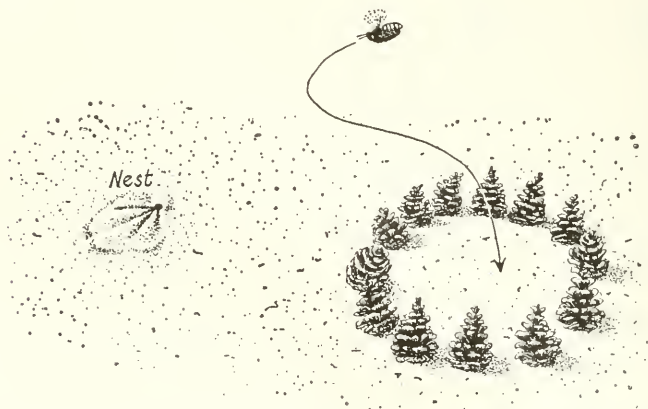

FIG. 52.—The ring of pine cones is then displaced from the nest and on her return the wasp alights in the centre of the ring and will only find the nest after the original situation has been restored (Tinbergen, *Study of Instinct*; Clarendon Press).

begun to elucidate the more complex aspects of animal psychology in which the basic instinctive reactions are modified by experience of the past.

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