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ON THE SENSES OF INSECTS

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by

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When, a year ago, I had the honour of addressing this Society, I endeavoured to deal with our Science in somewhat general terms, briefly summarising the academic interest and the practical applications of Entomology. My remarks on that occasion were intended quite as much for the layman as for the expert, and judging by some of the kindly appreciations I have received, my efforts were not altogether unsuccessful. To attempt a second address on similar lines would scarcely be possible even if it were expedient, and I have therefore been faced with the problem of selecting a subject which, though less generalised, might yet prove of interest to as large a proportion as possible of my audience. It occurred to me that the Senses of Insects might prove an acceptable theme, the more so, if interest and experiment in a subject concerning which so much still remains to be discovered, might thereby be stimulated.

The study is one to be approached with considerable care. In the earlier days of Entomological study, many workers seemed unable to dissociate the supposed senses of insects, not merely from human psychology, but also from human, or at least vertebrate, morphology. As Forel has pointed out, when authors maintain that a damp mucous membrane is necessary to an olfactory sense, they merely assert, without any supporting evidence, that the structure of a vertebrate organ is the only possible one for that particular function. As well maintain that because an insect has no lungs, therefore it cannot breathe.

Whilst we may feel satisfied that we have readjusted our mental attitude sufficiently to avoid the limitations of the morphological obsession, we find it less easy to control those of our psychological outlook. We try to find in insects the equivalents of the senses we ourselves possess. There seems to be no fundamental error in taking this as our starting-point, provided we use it as a comparative rather than an absolute conception. Our own senses enable us to regulate our mental and physical communications with the outside world. Like other animals, the insects must have similar or at least equivalent faculties, limited, and to some extent controlled though they may be, by the requirements of a sequence of stereotyped activities, and responding to external influences, almost entirely by subconscious reaction rather than by intelligent reason and conscious purpose.

We usually ascribe to ourselves the five senses of sight, hearing, taste, touch, and smell, and most of our conscious impressions can be roughly assigned to the five categories mentioned. One might with reason argue that hearing and a sense of musical tone are not necessarily the same, and since Beethoven wrote music after he became totally deaf, the former seems not to be a necessary basis of the latter. Nor does sight, as such, necessarily imply the faculty of correct colour vision, or even any colour vision at all, though purely monochromatic vision in human beings is of the greatest rarity. A very important sense, though limited in scope, is that of equilibrium. Although this sense happens in our own case to be associated with the inner mechanism of the ear, it is not part of our hearing faculty, and the apparent coexistence of static control and an auditory apparatus in an insect need not imply that both faculties are to be attributed to the same organ or position. Furthermore, we must remember that the nervous system of an insect differs widely from that of a vertebrate. In ourselves the brain is the central exchange which receives and answers the infinitely complex messages with which it has to deal. An electric telegraph which receives and transmits a number of separate messages simultaneously along the same conductor is a human invention at which we may well marvel, but the response by our central nervous system to minute and multiple stimuli can perhaps best be appreciated when we contemplate the performances of a Paderewski, a Cinquevalli, or a Lindrum.

Certainly the insect has a brain, but it is not fully comparable with that of the vertebrate. Its responsibility is partly delegated to a series of ganglia, or substations, roughly corresponding with the segments of the creature's body. Even a vertebrate animal such as a frog will perform coördinated and purposeful movements after the brain is no longer in spinal communication with the rest of the body. The removal of the entire head of an insect neither kills it immediately, nor inhibits many of its thoracic and abdominal activities. In conjunction with the suboesophageal ganglion the insect's brain has some influence over the coördination of the body movements. According to Loeb, removal of one side of the brain causes circular movements. The suboesophageal ganglion seems of importance in the maintenance of life, since, provided this is intact, the insect may live for months without the rest of the brain. Packard observes that a decapitated insect will continue to clean its legs and wings. The thoracic ganglia control the movements of their respective segments, and there is good evidence that in all the somatic ganglia the dorsal lobe is motor, and the ventral sensory, in function. Plateau found that each ganglion of the ventral nerve cord is a respiratory centre for its own segment.

In searching for some common basis from which to compare insect senses with our own we should, I think, guard against the assumption that our own actions are always the result of reason and conscious purpose. Subconscious actions are more frequent in ourselves than is generally recognised. They play an all-important rôle in any activity which implies skill. Proficiency in any mental or physical performance is acquired only through the training of many actions, both mental and physical, which grow in efficiency in proportion as they become subconscious, and while the insect inherits its subconscious ability to perform the few, if sometimes highly complicated, activities necessary for its survival, we have to learn individually. All that we inherit, if we are fortunate enough to do so, is the mental and physical equipment which enables us to acquire our varied accomplishments.

Bearing these considerations in mind we may approach the subject of insect senses, and attempt to estimate at least their analogies with our own. We may say that an insect can see, without committing ourselves to any positive assertion as to what it can perceive. It may hear in the sense of being affected by aerial vibrations without our claiming that it analyses sounds or derives any conscious impression from them. It may have a chemical sense, either through a gaseous or fluid medium, corresponding with our senses of smell and taste, without having any aesthetic appreciation of the agreeableness or otherwise of the odours or tastes involved. Its tactile sense may arouse automatic responses without any psychic accompaniment.

For myself I am inclined to favour a slightly higher conception of insect senses than that of pure automatism. Many insects are so highly organised that I feel compelled to credit them with faculties at least in some degree more advanced than mere unconscious responses to unperceived stimuli. Though the insect seems almost insensible to pain in any sense in which we understand the word, there is, I think, ample evidence that it is not entirely unconscious of the two most primitive stimuli of living organisms, sex and food. Sexual excitement is quite obvious in many insects, and whilst food may be quite secondary, since many imaginal insects do not feed at all, I cannot persuade myself that the butterflies in the general assembly on the *Buddleia* in my garden are not deriving, from the taste and scent of the nectar, something more than the mere unconscious satisfaction of an unperceived but stimulating appetite. Let us then proceed to consider in more coldly anatomic fashion the forms and apparent functions of some organs to which we may with certainty or probability attribute sensory functions.

Perhaps the only insect sense organs whose functions we can regard quite certainly as analogous if not homologous with our own are the eyes, though these organs vary slightly in number and very considerably in structure and efficiency. Simple eyes have one lens and to that extent are similar to the eyes of vertebrates. They may occur either with or without the accompaniment of compound eyes in the same individual. The simple eye usually consists of a comparatively large plano-convex or double convex lens, by which such rays of light as fall within its range are concentrated on to a rather primitive retina composed of a comparatively small number of nervous elements. Speculation on the degree of usefulness of such an eye has been as extensive as its conclusions have been indecisive. In larval forms such eyes are commonly found in groups, as in the usual set of six on each side of the head of a Lepidopterous larva. Their cerebral connections are branches of a single nerve. The form of lens provided must give a small inverted image, but the value of six small inverted images of scattered portions of a diverse field of view seems so problematical that we must conclude that the organ is a mere light-perceptor, and the behaviour of insects having this arrangement of eyes would seem to confirm that view.

The lateral ocelli of Neuropterous, Coleopterous, and Lepidopterous larvae have a lenticular thickening of the cuticle, beneath which there lies a crystalline body, consisting of three cells joined in the central axis. The visual cells are usually arranged in two crowns, the distal crown having three cells and the proximal four.

In Chironomid and Culicid larvae the ocelli are of the simplest possible form, being composed of a few sense cells of which the distal ends lie in a pigmented cup of the cuticle. In many adult insects, however, we find these simple eyes large and highly developed. A wasp with its three ocelli, two lateral and one median, must have some use for such organs. The two ocelli of the Gamma Moth lie adjacent to the compound eyes, and each consists externally of a brilliant lens, surrounded by a fringe of radially placed setae whose function is quite evidently to prevent obstruction of the view by the long scales with which the head is so plentifully adorned.

Still further complexity is found in the ocellus of the Dragon-fly (*Agrion*). The lens is a laminated structure lying in a cup of pigmented cells, and this layer is continued round the sides and proximal parts of the visual cells. These visual cells are unpigmented and are arranged in two layers. Those of the outer layer are distally expanded into cone-shaped extremities, bearing a marked resemblance to the cones of compound eyes. Those of the proximal layer are more or less blunt and flattened externally. Each cone of the distal layer is formed of three cells joined in the central axis where they form a small rhabdom or stiffening rod. The proximal layer of visual cells is embedded in a refractive mass forming a tapetum to which I shall refer later. This curious arrangement of a double layer of visual cells occurs in simple and intermediate forms of eye. Hesse suggests that they form what may be termed a double retina, the outer perceiving distant, and the inner nearer objects, though it is difficult to understand how this could occur in an eye of such a pattern. However that may be, the ocellus of *Agrion* must be something much more than a mere light perceptor, and may well be credited with true, if somewhat coarse visual powers. Interesting and varied as are the ocelli we must pass on to those extremely complex organs, the compound or faceted eyes. Of these there are four principal types.

The eucone eye, in which there lies beneath each corneal lens a transparent highly refractive body, the crystalline cone.

The pseudocone eye, in which there is a cone-shaped body, of little refractive power and of a fluid or semi-fluid consistency.

The exocone eye, in which there is a cone-like formation of high refractive power, but which, instead of being a structure of independent origin, is really a proximally directed process of the corneal lens itself, and,

The acone eye, in which there is no cone at all.

Eucone eyes may be further divided into two sub-types. Those in which the retinulae or visual cells extend outwards to, or almost to, the apices of the cones, and those in which they stop short at some distance from the cones, the intervening space being occupied by a transparent medium.

I propose briefly to describe the structure of these forms of compound eye and afterwards to discuss their function. Of the first sub-type of eucone eye, that of a butterfly is a good example. Each element of the eye consists, first, of the corneal lens or facet. Beneath this there is a layer of transparent substance separating the lens from the cone. It contains four nuclei representing the so-called Semper cells. True cones are supposed to be secreted by the Semper cells, but in exocone eyes these cells are modified for a quite different purpose.

The cone is a hard transparent body formed of four cells, joined in the central axis, and reduced almost to a point proximally, where it is extended into the depth of the eye as a long transparent rod, the rhabdom. Packed round this rod is a bundle of visual cells, the retinulae. The number of these is rather variable. There is reason to suppose that the primitive number is eight, though in many species we can count only six. Each visual cell tapers off proximally into a fine nerve fibre, and all the nerve fibres pass through a basal membrane into the external optic ganglion. The transparent rod, or rhabdom, in the centre of the bundle stops short of the basal membrane and rests on a funnel-shaped chitinous cup, the tracheal distributor, from the edge of which there arise fine tracheae, supplying the visual nerves. The cone lies in a kind of sleeve or cup formed of pigment cells. These isolate each cone from its neighbours, and absorb all light rays not falling nearly perpendicularly on the corneal facet. In this type of eye the light entering a particular facet cannot affect any of the visual nerves except those immediately beneath it. The whole element, lens, cone, rhabdom, and retinulae, is known as an ommatidium. Of these independent elements or ommatidia there may be 5000 or more in each eye of a butterfly.

In the second sub-type of eucone eye the retinulae do not reach the apices of the cones. There is a considerable intervening space occupied by a transparent medium. Moreover, the pigment cells surrounding the cone are capable of expansion and contraction. A section of such an eye made from an insect which has been kept for some time in darkness shows the pigment sleeve contracted forwards and exposing an appreciable part of the apical area of the cone, whereas if the insect has been killed in a bright light, the pigment extends backwards almost to the apex. Evidently we have here an adjustable apparatus somewhat analogous with that of the iris of the vertebrate eye.

The pseudocone eye is, so far as I am aware, always of the type in which the retinulae extend outwards to the cone apices, and there is good reason on optical grounds for supposing that this must always be so. So far as concerns the structure the only difference is in the nature of the cones, which are of a soft consistency and poor refractive power. This difference, however, involves a profound modification of the method of image formation.

The exocone eye appears at first, in section, to be very similar to a eucone eye with the retinulae not extending to the cone apices. As Kirchhoffer has pointed out, however, there is no true cone, in the sense of a structure independent of the corneal lens, but the corneal lens is itself produced inwardly to form a cylindro-conical refractive body, not produced into a rhabdom. The visual cells end some distance beneath it and the intervening space is occupied partly by a great extension of the Semper cells.

In the acone eye, such as that of *Tipula*, there is neither cone nor pseudocone. The position usually occupied by these bodies is filled by a group of small transparent cells surrounded by a collar of pigment.

With such a variety of visual organs, how does an insect see? The classical demonstration of the image formation in a compound eye was given by Exner. He experimented first with the eye of *Hydrophilus piceus*, a eucone eye, and found that the cone is possessed of very peculiar optical properties. He was able to show that the refractive index decreases from the centre to the periphery, and described it as virtually a lens cylinder. He pointed out that a lens cylinder of which the length is equal to its focal length would give an inverted image like that of an ordinary lens, but that the more central rays entering it would leave it, not divergent, as with an ordinary lens, but parallel. If the length were twice its focal length the inverted image would be in the middle of the lens cylinder, and would be reinverted, and so erected at its base. On the assumption that the lens and cone of the eucone eye together act as a lens cylinder of twice its own focal length, he prophesied the appearance of an erect image at the apex of the cone. Still using the Water-beetle's eye he failed to demonstrate this image, since he was unable to remove the retinulae and other soft parts, without at the same time detaching the cones from the corneal lenses. He could not dissect the camera without damaging its optical equipment. Perseverance was, however, ultimately rewarded by the discovery that the cones and corneal lenses in the eye of the Glow-worm adhered so firmly together that he could dissect out, without damage, the purely optical part of the eye. This he mounted with a drop of dilute glycerine of the same refractive index as that of beetle blood, and, focussing down with a medium power objective, towards the apices of the cones, he saw a perfect erect image of objects in front of the cornea. It was not a multiple image but a single erect picture made up of all the elements of the whole field of view in their proper order and position. Not only did he see it, but he photographed it. I have several times repeated Exner's experiments and a photograph taken by using the Glow-worm's eye as a lens will be found, rather defectively reproduced, in our Transactions for 1919.

Now comes a curious discovery. Exner regarded the Glow-worm's eye as a eucone eye. The fact that its cones and corneal lenses adhered so firmly together does not seem to have suggested to him anything but a fortunate peculiarity. Kirchhoffer published his work on the eyes of beetles in 1908. It has taken us 24 years to recognise that the only type of compound eye in which the image has been completely and satisfactorily demonstrated is not a eucone eye at all, but an exocone eye. The Glow-worm's eye has no cones in the true sense, what appears to be a cone being merely a process of the corneal lens. From Kirchhoffer's drawings it seems to have several other peculiarities which we have not time to discuss here. The discovery is perhaps no longer of more than academic interest, since there is now good reason to suppose that the image formation in the true eucone eye is of much the same nature, meanwhile we must return for a moment to Exner. The iris-like movement of the pigment remained to be accounted for, and he showed that in a bright light the expansion of the pigment sleeves round the cones would cut off all but the most centrally placed rays, so that each set of visual cells would be stimulated only by the light transmitted through its own corneal facet. This he called the apposition image. In reduced light, however, some of the less parallel rays would, owing to the receding of the pigment, be able to stimulate visual cells adjacent to those of their own facet. There would thus be an overlapping of the light rays, and the insect would use a larger amount of the available light. This he called the superposition image. It would be difficult to devise an experiment to prove this action, but the whole structure of the eye in crepuscular and nocturnal insects supports the theory. We have then, in the exocone eye, a dioptric apparatus capable of producing a good erect image. We can only suppose that so complete an equipment has not been developed without a corresponding efficiency in the nervous mechanism provided for its reception.

Whilst the image formation in the eucone eye cannot be demonstrated so completely as in the exocone form, there is good reason to suppose that it is of a similar kind. In my paper on Butterfly vision, published in our Transactions for 1919, I showed that by suitable methods a small erect image could be seen at the apex of each cone in the eye of a butterfly, and I suggested a theory of the image formation and reception, for which perhaps the most that can be said is that it has not yet been disproved. The presence of the image implies that the lens and cone together act in the same way as the dioptric apparatus of the exocone eye, but the transmission of the image to the retinal elements seems to be of a different kind. The cone is continued into the depth of the eye as a transparent rod or rhabdom, and in this eye the rhabdom would appear to be an essential part of the dioptric apparatus. It is in physiological continuity with the visual cells, and the rays forming the image can pass down it, and can stimulate the retinulae throughout their entire length, instead of merely on the distal ends as in the Glow-worm. There should also be a more perfect analysis of the image by the six or more retinulae clustered round the rhabdom. Eucone eyes in which the retinulae extend to the cone apices are characteristic of diurnal insects. There is no iris-like adjustment to the intensity of the light, and there can be no superposition image. In the eucone eyes of crepuscular insects there is always a space between the cone apices and the distal ends of the retinulae, and the pigment is movable, thus providing for the formation of a superposition image. It may be pointed out that the more central rays from each facet will stimulate the whole length of the retinulae, whilst the superposed rays from other facets can only stimulate their distal ends. This is probably true, but as the central rays only come from one facet and the superposed rays from several, the stimulation is probably fairly equally balanced.

Vision with the faceted eye may be quite good at close quarters, but its acuity depends on the number of facets within whose field the object lies, and as this varies inversely as the square of the distance, insects must be very short-sighted. I calculated, and, in the paper referred to, endeavoured to illustrate, the distance at which one butterfly should be recognisably visible to another, and the results agreed well with their observed behaviour in nature.

Let us now consider the pseudocone eye. Here the cone has little refractive power. It cannot reinvert the image or even pass it on unaltered. The image formed by the corneal lens is therefore useless as such, and all that appears at the cone apex is a spot of light of the average value of that part of the field of view covered by the lens. How then can an image be formed?

We have only to look at a half-tone illustration to see that a picture can be formed of black dots, so large as almost to touch in the shadows, and so small as to leave considerable spaces in the high lights. If a picture can be formed of different-sized dots it can also be formed, even more perfectly, by dots of differing intensity, and this seems to be the nature of the image in the pseudocone eye. It must obviously be an apposition image, since superposition would destroy it, and I know of no pseudocone eye in which there is a clear space between the cone-apices and the retinulae.

An interesting feature of this method of image formation is the obvious fact that it requires no focal mechanism, the clarity of the image being entirely dependent on the number of facets engaged. Vigier in 1914 published a description, without illustrations, of a supposed focal apparatus in a compound eye. He claimed to have found, between the retinulae, striated muscle-fibres, so arranged as to provide for variations in the length of the retinulae, combined with an adjustment of the curvature of the corneal surface. Apart from the fact that modifications of the curvature of the corneal surface would not affect the focus of a compound eye, though it might alter the extent of the visual field, he was unfortunate in using for his research the eye of a Dragon-fly. Since this is a pseudocone eye, producing what we may call the " half-tone " type of image, a focal apparatus would be of no use to it, and we can only conclude that the author must have been mistaken in his interpretation of the sections at his disposal.

The absence of any focal adjustment in the eucone eye is more difficult to account for. Even if a focal apparatus were present it could only be of use at a certain optimum distance the clarity of the image being mainly dependent on the number of facets engaged.

Of the acone eye I have little to say. The group of transparent, or crystal-cells, which occupy the position of the cones in other eyes may serve to concentrate the light and the eye may work on a principle very similar to that of the pseudocone eye. In the Tipulid eye, each retinula has a small rhabdom of its own, but this would appear to be more in the nature of a supporting structure than a part of the dioptric apparatus.

The great majority of compound eyes can be referred to one or other of the types described, but there are exceptions. The eyes of *Lepisma saccharina* seem almost intermediate between simple and compound eyes. There are twelve on each side and the bi-convex lenses have convergent axes. Beneath each lens is a transparent body formed of four cells, and considered to be homologous with the cones of the higher forms. There are two layers of visual cells, four above and three below.

A very remarkable form of eye is that of *Scarabaeus variculosus*, apparently a eucone eye, but the "cone" is of the shape of an hour-glass. It is difficult to estimate the refractive action of so curious a dioptric apparatus.

Apart from the peculiarities of the internal structure of the compound eye, there are certain interesting modifications of its external form, one of the most curious being that of *Cloëon*, which has an anterior eye elevated on a pillar-like outgrowth of the head, and a posterior eye normally placed. Moreover, the anterior eye is of the form in which the distal ends of the retinulae do not reach the cone apices, thus resembling the eye of a moth, whilst in the posterior eye they extend right up to the cones and thus resemble the eye of a butterfly.

A peculiar feature of the eyes of many nocturnal and crepuscular insects is the tapetum, a structure which also occurs in some ocelli. I have already mentioned the tracheal supply to the retinulae, but in the eyes of many moths the mass of tracheae surrounding the visual cells seems out of all proportion to the requirements of respiration. If we project a strong light on to the head of a moth which has previously been in darkness, its eyes are seen to shine with a golden or reddish glow. This is caused by the reflection of the light from the air-filled tracheal tubes in which the visual cells are embedded. If the external illumination be continued the glow rapidly disappears, and the cause of this is the expansion of the pigment cells under the influence of the light. The apices of the cones are quickly covered and the admission and reflection of the light reduced. It has been suggested that this reflecting apparatus is of service to a creature which has to make the most of a rather poor light, by throwing the light back again through the eye and so stimulating the visual cells twice over. It is difficult to imagine how this can occur without blurring or destroying the image, and yet the explanation is not without support from the analogy of some vertebrate eyes. Those of nocturnal mammals and some birds reflect light from the *tapetum lucidum*, which is a reflecting layer at the back of the eye, owing its properties to the presence of minute crystals of guanin. Curiously enough some fish scales owe their glitter to the same substance. Though the reflection in insect eyes is generally caused by air-filled tracheae, Hesse claims to have observed minute crystals in the tapetum of the ocellus of *Cloëon*.

From the foregoing brief summary we may conclude that the eucone eye of an insect, such as a butterfly or moth, is, for its size, the most efficient type of compound eye. It is true that the power of sight seems to be greatest in the large Dragonflies, which have pseudocone eyes, but in these the greater size and far more numerous facets would account for their superiority. The relative size of eyes is a consideration which has scarcely received the attention it deserves. As Professor J. B. S. Haldane has pointed out, in reference to vertebrate eyes, these organs are rather inefficient until they reach an optimum size. The nervous elements have a diameter of little more than a length of an average light wave. With fewer but larger nerve-membrane cell. It would seem that these three cells are the origin of the sense-cell, enveloping cell and cap-cell so typical of the peculiar organ known as a scolopale and found in chordotonal organs. Many modifications of these comparatively simple sensillae are known, and it is almost impossible to draw a dividing line between those which are purely tactile and others which may have assumed, partially or completely, some other function. Sometimes the walls of the hair are very thin and the nerve extends to the outer extremity. This form is generally considered to be chemo-receptive rather than tactile. Freiling has described Lepidopterous scales having nerve connections, and Vogel has also observed them, usually on the veins. On the cerci of the mole-cricket there are claviform sensory hairs, each being set in a ridged alveolus of the chitin.

If we cannot, as yet, clearly define the organs of touch there can be no doubt of the great importance of that sense in insects. The complex constructional and domestic activities of the social insects, usually performed in darkness, must be largely dependent upon it. The same faculty is observed in caterpillars both when feeding and in the construction of their cocoons, in the arrangement of the perfectly ordered clusters of eggs of such insects as the Lackey moth or of some Mosquitoes. In flying, tactile impressions may have static, orientating, or even barometric functions.

The larvae of some Limacodid moths furnish a curious example of the tactile sense associated with a special form of defence. On the near approach of a possible enemy they move in such a way as to turn their batteries of poison spines in the direction of the expected attack. There is, however, in these clusters of spines a delicate hair or hairs of considerable length and so fine as to be almost invisible. Contact with the extremity of this induces the appropriate movement of the creature's body.

Amongst the many forms of sensillae those known as scolophores and containing scolopales, or sense-rods, are specially interesting. A typical scolophore consists of a cap-cell, often extended to form a strand, or ligament, attaching the sensilla to the cuticle. In the proximal part of the cap-cell is embedded the distal end of a second structure known as the enveloping cell. Embedded in this again is the nerve-cell. The end of the nerve-cell here forms a delicate tube, often expanded into a small vacuole, and then again reduced to form a little chamber, whose sides are supported by stiffening ribs. In this chamber there is an exceedingly delicate thread, usually with a small expansion at its distal end, called the apical body. The thread and its apical body seem free to vibrate in the ribbed chamber. This type of nerve-ending is the scolopale or sense-rod. Sense-rods of either a primitive or elaborate kind are found in many forms of sensillae and also in internal situations. Organs containing groups of sense-rods are commonly called chordotonal organs, and the term has become so general that it is convenient to retain it. At the same time the name suggests an auditory function, which cannot by any means be ascribed to all chordotonal organs.

Organs to which auditory functions can with reasonable probability be ascribed, consist of chordotonal sensillae associated with a membrane or tympanum. The best known and most elaborate are those in the fore-tibiae of TETTIGONIIDAE, and Schwabe's beautiful illustration is known to most Entomologists. Two large tympanal cavities open through slits in the exterior of the tibia, and the large central trachea beneath the membrane bears sub-genual, intermediate, and tympanal organs, all provided with a large number of chordotonal sensillae. They are supplied partly by the crural nerve and partly by a special tympanal nerve, both arising from the ventral ganglion of the first thoracic segment. If auditory organs exist at all we should certainly expect to find them in insects which themselves produce sounds, a condition amply fulfilled in the Tettigoniids. The Cicada, however, one of the noisiest of insects, for long proved something of a problem till Vogel showed that both sexes have tympanal organs, what was formerly supposed to be a resonator of the sound organ being provided with some 1500 chordotonal sensillae.

It is less easy to account for the presence of tympanal organs in insects which, so far as we are able to perceive, do not themselves produce sounds. Such organs are present in many moths, and in our Transactions for 1923 I described the structure in the beautiful Madagascar moth, *Chrysiridia ripheus*. It lies in the second abdominal segment and is not quite the same in the two sexes. There is a tympanum supplied by a delicate nerve containing two scolophores. For one curious feature of these organs there is no explanation at present forthcoming. One end of the scolopales stains more darkly than the other, and this dark portion is distal in the male and proximal in the female, as though their respective positions were reversed. The tympanal organ is in the thorax of Noctuid moths and in the abdomen of Geometrids. If we examine a Geometrid under a moderate power, there may be seen a small opening on the side of the abdomen close to its junction with the thorax. On dissecting out the parts we find that there are two hemispherical vesicles, rather like kettle-drums, symmetrically placed with the drum or tympanum facing forwards and slightly outwards. Each has a piece cut off the edge, leaving an opening bounded partly by the drum and partly by the " kettle," and this forms the external orifice already referred to. What, for descriptive purposes, may be called the cut edge of the drum, is bounded by a chitinised margin, from the middle of which arises a chitinised arch, forming a little curved bridge, the other end of which is attached to the opposite edge of the drum. From the centre of this bridge there depends a nerve, attached to the drum and containing two scolopales. The straight chitinous margin or chord of the drum has upon it fine muscle fibres, apparently for regulating the tension. We must suppose an apparatus of this kind to be capable in some way of detecting aerial vibrations, but with only two sensitive nerve-endings its power must be very restricted. In Noctuid moths, extensively studied and beautifully illustrated by Eggers, there are two drums in each thoracic organ. A horizontal section shows the cavity to be roughly semicircular, the outer end closed by the true tympanum, to the inner surface of which is attached the tympanal nerve with two scolopales. The inner end of the cavity is closed by a secondary tympanum, regarded by Eggers as a resonator and unprovided with any nerve supply.

Nerve-endings of the scolopale type are found in many insects and in various positions without any accompanying tympanum, and there is no satisfactory evidence that they are auditory in function. They occur in the halteres of Diptera, in the legs of Ants, in an antennal structure known as the organ of Johnston, and in segmental series in many larvae, notably those of Cerambycid beetles.

As to the evidence of auditory powers in insects, Baier's experiments with Field Crickets and other Orthoptera are of considerable interest. In order to eliminate factors of scent and sight, he connected, by telephone, cages containing males and females respectively. The females responded to the sounds made by the males, by orientating themselves towards, and approaching the receiver. Direct vibrations were eliminated by careful insulation of the cages, and in a subsequent experiment by putting the insects in receptacles carried by balanced balloons. Females whose tympana had been excised failed to respond, as did those which had been locally anaesthetised with ethyl-chloride. Phonographic records of the male notes have a similar effect. Eggers experimented with moths and found that they responded to sounds, by movements of the wings or by flying, but failed to give any response when the tympanum was destroyed. Of the functions of chordotonal organs unprovided with tympana we know even less. Fielde and Parker found that ants gave no reaction to sounds ranging from 27,000 to 60,000 vibrations per second. They reacted to vibrations reaching them through wood, glass, sponge, or nest earth, and such reaction was not dependent on the antennae, head, abdomen, or any one pair of legs. Generally their behaviour could as well be ascribed to touch as to hearing.

On the other hand, Baier found that *Myrmica rubida* responded to high staccato notes from a violin, the formicarium being suspended from the ceiling. The ants ran violently about and hid themselves. The same author showed that some Ephemerids and Coleoptera were sensitive to sounds.

Eggers favours a rhythmic function for the chordotonal organs, pointing out that most of the movements of insects result in rhythms, and there must be organs for controlling and regulating them. Unless chordotonal organs or their equivalent can be found in other animals I confess to some difficulty in perceiving their special necessity in insects. Larvae of *V. antiopa* were shown by Minnich to react to sound, of pitches from 32 to 1024, but he also found that the reaction was due to the tactile sense of certain hairs on the anterior part of the body. So far as we know at present there seems little evidence that insects, other than some Orthoptera and Hemiptera, can hear in any sense comparable with that faculty in vertebrates. Nothing approaching the delicate and discriminative sense which we associate with hearing can be attributed to the most elaborate of such organs in insects. The human ear possesses some 10,000 nerve-rods, 15,000 hair cells, and about 24,000 basilar membrane fibres. It can distinguish differences of less than one vibration per second between 32 and 2048. The nerve supply to the tympanal organs of insects does not warrant any comparison with vertebrate ears.

As we pass from the consideration of the sense of sight, through those of touch and hearing to the remaining senses, the difficulty of locating them is progressively increased. In insects the olfactory sense is probably more highly specialised than any other, nevertheless not only is that sense difficult to define, but it seems in many species to be combined with touch and taste. Distributed over the body of an insect are sensillae of many forms. Several different types occur together in the antennae and it is manifestly impossible to devise experiments which will inhibit the action of one form without interfering with that of others. Of the existence of an olfactory sense there can be no doubt whatever. So far as we are able to compare the reactions of insects with those of other animals, scents of various kinds play a rôle in their economy, the delicacy and importance of which transcend anything in our own experience. Apart from their appreciation of odours associated with their habits of feeding and oviposition, many of them produce scents as secretions of specialised glands and complex distributive mechanisms. I need not dwell on the phenomenon of assembling, well known to all Entomologists. That the directive agent is a scent diffused by the female seems to be generally admitted, since a receptacle which has recently contained one, proves as attractive as the female herself. Kellogg's remarkable experiments with silk-worm moths showed that the seat of the secretion is in the terminal segments of the abdomen, and that these segments, when amputated, are just as attractive as the whole moth, whilst the mutilated female ceases to have any effect. I have prepared sections from the females of *Ocneria dispar* and *Saturnia pyri*, and can find no special glands in this position. The volatile substance, whatever its nature, must be a secretion of the hypoderm cells, which in this region are much enlarged. Not only must the scent be specific but its perception by the male must be specialised, since the presence of other odours in the neighbourhood does not confuse or inhibit the male reaction. Curiously enough these directive odours are rarely if ever perceptible to our senses. It might naturally be supposed that they would be by far the most important for the continuance of the species, but judging by the widespread occurrence and great complexity of organs peculiar to the male, and apparently having for their function the production of what may be termed aphrodisiac perfumes, the male scent organs would seem to be even more important than those of the female. I need not devote any time to the discussion of male scent organs. Many of their forms in several orders of insects have been described in our Transactions in recent years. Though not sense-organs I refer to them here since their existence is additional evidence of the existence of an olfactory sense. It is an interesting fact that whilst the attractive and directive odours of the female are usually, if not always, imperceptible to our senses, the perfumes produced by male insects are frequently perceptible and almost invariably agreeable. A well-known example is that given off by the scent scales of *Pieris napi*, which resembles that of lemon verbena.

Amongst the most conclusive experiments on the olfactory sense are those of Von Frisch, who trained bees to find a sugar solution in a porcelain box scented with an essential oil having a flowery odour. Three similar but empty and unscented boxes were provided. The bees soon found the sugar box and returned to it with precision, in whatever position it was placed relatively to the other three. Amputation of the four terminal segments of the antennae inhibited the faculty altogether, and the bees then entered the empty boxes as often as that containing the sugar. That the inhibition was not the result of shock was ingeniously proved by putting the sugar in a blue box whilst the empty ones were coloured yellow. The antennaless bees soon learnt to select the blue box, thus showing that they could make use of their colour sense when the olfactory power had been destroyed.

So far as concerns the bee, the olfactory sense is evidently in the last four segments of the antenna. Other experiments have shown, however, that though the antennae are usually the principal seat of this sense, it is not entirely confined to these organs, and Abbott has found that certain carrion beetles could discover decaying meat, buried in sand, after their antennae and wings had been removed, and their leg bases covered with shellac.

If, as we know, our own senses of smell and taste are sometimes liable to be confused, what we call flavours being mainly perfumes, it is even more difficult to separate in insects those senses which most nearly represent olfactory and gustatory powers. It is easy to demonstrate that a butterfly can taste, in the sense of discriminating between substances on which it may be feeding. It will contentedly suck up a solution of sugar, but if a drop of some alien substance such as methylene blue, or picric acid, be added it will at once withdraw its proboscis. We may say that it likes sugar, and dislikes methylene blue. I am not prepared to say that we are wrong in using such terms, though we cannot know whether the insect has conscious preferences associated with taste as we understand it. If, however, we find that it can distinguish between substances merely by touching them with its *feet,* we realise that chemo-tactile is a more appropriate term for a sense which has no exact parallel in our experience. This remarkable tarsal sensitivity has been demonstrated by Minnich and provides an interesting contribution to our knowledge of insect senses. It would take too long to describe in detail the experimental methods used, but certain butterflies were shown to have the power, through tarsal contact, of detecting and distinguishing between such substances as apple-juice, quinine sulphate, hydrochloric acid, sodium chloride, and distilled water. Not only does the insect respond, by extension of the proboscis, to tarsal contact with various fluids, but after long periods of abstention it shows a sensitiveness to sugar solutions some 256 times more delicate than that of the human tongue. Certain Muscid flies were also used for experiment with similar results. I have for some time been investigating the histology of the chemo-receptive sensillae of the tarsi and hope shortly to be able to give some account of them. Meanwhile we are justified in asserting that insects possess a distance chemical sensitivity comparable with the olfactory sense of other animals, and that they also have a chemo-tactile sense, which though not always associated with the mouth-parts can be reasonably termed a sense of taste. Though probably extremely specialised, both these faculties may be associated with a sensitivity immensely greater than we ourselves possess. Having established the existence of such senses it is a much more difficult task to assign them to their appropriate sensillae. Though sense-cells of various forms are concentrated in immense numbers on the antennae, they are by no means confined to those complex organs, and may be found in almost every position all over the body. Numerous attempts have been made to classify the forms of sense-cells, but they are not always clearly differentiated and many intermediates occur. The following classification is based on that of Snodgrass. The supposed function of each type is only suggestive and not fully established by experiment.

I. Trichoid.
  1. Trichoid proper. Setiform, but varying in length, thickness and density of the hair walls.
    a. Hair long and stiff. Nerve reaching only to base. (Tactile.)
    b. Hair short and thin-walled. Nerve often reaching apex. (Chemo-receptive.)
  2. Squamiform.
    Resembling a scale set in the usual scale socket, but supplied with a nerve. (Tactile.)

3. Basiconic.
   Resembling pegs or cones.
   - *a.* Pegs thick-walled and innervated by a single nerve. (Tactile.)
   - *b.* Pegs thin-walled and innervated by a group of sense cells. (Chemo-receptive.)

4. Coeloconic.
   Resembling Basiconic, but the pegs are sunk in cavities of the cuticle.
   - *a.* Thick-walled, with a single sense cell. (Function doubtful but evidently not Tactile.)
   - *b.* Thin-walled and with multiple nerve-cells. (Chemo-receptive.)

5. Ampullaceous.
   A development of the Coeloconic in which the cuticular cavity is much deeper and more flask-like, or may even be a long tube. (Chemo-receptive.)

II. Campaniform.
   Variable in shape, but having, externally, the form of a thin-walled dome or bell, or derived from such forms and having one sense-cell. (Function doubtful, probably Tactile.)

III. Placoid.
   This has chitinous plates overlying large pores or cavities in the cuticle. (Often called " pore-plates.") Innervated by a group of sense-cells. (Chemo-receptive.)

The chordotonal organs have already been dealt with and are not included in the above classification. The fact that there are so many different types of sense-organs for which we can suggest only two functions shows how very little we really know about insect senses and how much remains to be done by intelligent experiment. The Campaniform organs are the " Olfactory Pores " of McIndoo, who has described their distribution in all the principal orders of insects. Their olfactory function has not, however, been completely demonstrated, and, as Snodgrass has pointed out, organs presumed to be chemo-receptive are usually innervated by multiple nerve-cells. The Placoid type of sensilla seems more definitely associated with the sense of smell. In *Dytiscus* extremely small Placoid organs are found on the antennae to the number of nearly 5000. In the honey bee these organs are very numerous on the antennae and vary in a significant way according to the sex, there being some 30,000 in the male, 6000 in the worker, and 2000 to 3000 in the female. They are the principal form of organ in the terminal segments of the antennae and, as Frisch has shown, the removal of these segments inhibits its response to odours. I am not aware of any notable experiments on the olfactory sense of the cockchafer, but in this insect the antennal organs are mainly of the Coeloconic type and there are said to be some 39,000 in the male and 35,000 in the female.

We have no time to consider organs for which a function cannot even be suggested, such as Johnston's organ, found in the antennae of most insects, Jordan's organ, or the Chaetosema, on the head of Lepidoptera, Graber's organ in the larvae of Tabanid flies, and other interesting structures.

From what I have already said we see that insects possess faculties which may in a limited fashion be compared with those of the higher animals. They are sensitive to waves of light, sound, and heat, and to chemical stimuli of the nature of tastes and odours. In some instances their power of detecting volatile substances seems far to transcend anything of the kind found in other orders, though they probably respond to a very limited range of such stimuli. The least developed sense would seem to be that of hearing, since organs of sufficient complexity are found in but a few species, and, as might be expected, principally in those insects which are themselves capable of sound production.

The tactile sense is so highly developed and widely distributed that there is some difficulty in distinguishing between true hearing and a mere tactile sense of aerial vibrations. Taste, limited in ourselves to about four principal sensations, may be equally limited in insects, though other parts of the body than those associated with nutrition may be directly involved. Sight may be very efficient at close quarters, and an eye constructed on the same plan as that of a vertebrate would probably serve no better, even if it were not, on account of its small size, actually less efficient.

Insects seem but little less well equipped than other animals within the limitations of their always specialised requirements. Ants can recognise each other and distinguish members of a rival colony. They can even communicate in some way, and induce others to join them in some apparently purposeful action. But of the psychology of creatures so remote from ourselves we can hope to learn little. We have discussed their senses, we cannot estimate their sense. It has been widely held that every action which is now instinctive must once have had its origin in intelligent departure from previous behaviour. It seems, however, equally possible that what has now become a useful instinct may have originally been a departure from previous conduct, due to a favourable variation in nervous reflexes, inherited and then, if we may use the term, encouraged, by natural selection.

At the present time it seems the fashion to deny to every animal except ourselves any power of independent action. One lecturer at the last meeting of the British Association seemed to maintain that even dogs and cats are totally devoid of the least glimmer of what we term intelligence, and that all their actions may be ascribed to unconscious reflexes. We might discuss the matter at very great length without coming to any definite conclusion, the more so since we lack clear definitions of the very words and thoughts we must perforce employ. We can only define the word " consciousness " by " awareness," and, as Snodgrass observes in his essay " On the Mind of an Insect," " to define a thing by its synonyms is only to shift from one foot to the other, but it is the best that can be done, since no one knows anything at all about the true nature of consciousness, and if one shoe fits and the other pinches, it is better to stand in the easy one."

I commend that very interesting essay to those who wish to pursue the matter further, though it contains one paragraph that seems open to argument. The author denies the possibility of the existence in insects of any sense unknown to ourselves, on the ground that in spite of the discoveries of the physicists there is no known force in nature except radio-activity that we have not long known by means of our sense-organs. This may hold good for the nature of the force, but does not apply to its range. Already we know that insects are sensitive to light rays that we cannot see, to chemical stimuli that we can neither taste nor smell, and probably to sounds that we cannot hear. At the risk of treading on the forbidden ground of anthropomorphic comparison I feel justified in quoting Lord Avebury's words, which, though written nearly a quarter of a century ago, seem still to be worthy of our attention.

"Sound is the sensation produced on us when the vibrations of the air strike on the drum of our ear. When they are few the sound is deep; as they increase in number, it becomes shriller and shriller; but when they reach 40,000 in a second, they cease to be audible. Light is the effect produced on us when waves of light strike on the eye. When 400 billions of vibrations of ether strike the retina in a second, they produce red, and as the number increases the colour passes into orange, then yellow, green, blue and violet. But between 40,000 vibrations in a second and 400 billions we have no organ of sense capable of receiving the impression. Yet between these limits any number of sensations may exist. We have five senses, and sometimes fancy that no others are possible. But it is obvious that we cannot measure the infinite by our own narrow limitations.

"Moreover, looking at the question from the other side, we find in animals complex organs of sense, richly supplied with nerves, but the function of which we are as yet powerless to explain. There may be fifty other senses as different from ours as sound is from sight; and even within the boundaries of our own senses there may be endless sounds which we cannot hear, and colours as different as red from green, of which we have no conception. These and a thousand other questions remain for solution. The familiar world which surrounds us may be a totally different place for other animals. To them it may be full of music which we cannot hear, of colour which we cannot see, of sensations which we cannot conceive. To place stuffed birds and beasts in glass cases, to arrange insects in cabinets, and dried plants in drawers is merely the drudgery of preliminary study; to watch their habits, to understand their relations to one another, to study their instincts and intelligence, to ascertain their adaptations and their relations to the forces of nature, to realise what the world appears to them; these constitute, as it seems to me at least, the true interest of natural history, and may even give us the clue to senses and perceptions of which at present we have no conception."

To-night marks the close of my tenure of the office with which, two years ago, you honoured me. I regret that in recent months my attendance has not been so regular as I could have wished. Many of you know the cause, and I would express my heartfelt thanks for the sympathy that has been so freely expressed. We are approaching the completion of our hundredth year. I am sure you feel with me that it is a fitting climax to a century of continual progress, that our meetings and celebrations during the coming year are to be presided over by the most distinguished Entomologist of our time, of whom it may justly be said that in thus honouring him we do but honour ourselves.

I would take this opportunity to record my deep appreciation of the continual help and kindness I have received from all the Officers, and for the unfailing support and good-fellowship of the members of the Council. We are indeed a happy family, and there can be no misgivings as to the future of a Society in which all co-operate so well for the furtherance of our aims and the high standard of our work.

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