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Original Articles

THE THIRTY-SECOND MAUDSLEY LECTURE: SENSORY EXPERIENCE AND BRAIN STRUCTURE*

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It was in my early youth that I first read Bergson's *Creative Evolution.* At that time, as I recollect, it particularly captured my interest and attention because it seemed to embody certain essential principles which I had not found to be expressed quite so forcibly elsewhere. It is true that the validity of many of Bergson's speculations and ideas have since been seriously controverted and so find little or no support today, but his philosophy also propounds certain conceptions which are perhaps worthy of renewed attention. I refer more especially to Bergson's contrast of those two aspects of conscious experience which he terms intellect and intuition. Intellect, he argues, is the product of a gradual evolutionary process which enables the individual with increasing efficiency to select and abstract just those several features of surrounding objects which are directly relevant to the problem of evolutionary survival. In so far as it selects and abstracts, the intellect by itself can provide only a partial view of external reality. "To conquer matter," Bergson says, "consciousness has had to exhaust the best part of its power"—it has had to "adapt itself to the habits of matter and concentrate all its attention on them, in fact, determine itself more especially as intellect." But there remains "around our conceptual and logical thought a vague nebulosity, made of the very substance out of which has been formed the luminous nucleus which we call the intellect". Therein reside certain powers that are complementary to the understanding—powers of intuitive recognition. Intellect is essentially based on a sort of derived symbolism gradually elaborated in the course of evolution, which serves its immediate purpose as a convenient, useful, and indeed essential device for gaining control over the material world; on the other hand intuition, according to Bergson, is capable of giving scintillating flashes of insight "into the very inwardness of life".

It would perhaps be presumptuous for an anatomist to express an opinion on the validity of Bergson's arguments, and I readily confess that I find some of them exceedingly difficult to follow. But it has always seemed to me a peculiarly interesting circumstance that Bergson's conception of a duality of

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conscious experience has some rather suggestive correlates in certain aspects of purely neurological phenomena. The fact is that the idea of a duality in modes of sensory perception is ever and again presenting itself in one form or another to the neurological investigator; indeed, the late Sir John Parsons, in his *Introduction to the Theory of Perception*, went so far as to suggest that "the whole nervous system, receptor and effector, is built upon a dual—dyscritic and epicritic—basis". Head's well-known hypothesis of a dual mechanism to explain his categories of protopathic and epicritic sensation commanded assent for many years, and even though the explanatory postulates which he himself put forward have now proved untenable (at any rate so far as the peripheral mechanism is concerned), the contrasting sensory phenomena which he described as characteristic of the earlier and later stages of nerve regeneration still require to be explained on a neurological basis of some sort. Dual mechanisms in the apparatus of the special senses have suggested interesting parallels; for example, the contrasting rod and cone mechanisms in the retina, or in the apparatus of smell the puzzling association (in most mammals) of a highly differentiated olfactory bulb with the cruder and more primitive organization of an accessory olfactory bulb. In the central nervous system, dual sensory pathways have long been known to exist, but they have gained increasing recognition in recent years as the result of the intensive studies of the so-called "reticular system" of the brain-stem and thalamus. And now, with the discovery and demarcation of secondary sensory areas in the cerebral cortex (somatic, visual and auditory), it seems that duality is a general principle even of cortical organization. I do not, of course, want to insist that this duality of the neural organization of sensory pathways is actually the structural basis of Bergson's contrast between intellect and intuition, or, indeed, that it has any direct relation to it. But there seem to me at least to be some rather interesting parallels which, even if they are no more than distantly analogical, are worth discussion.

About thirty years ago, the American anatomist G. E. Coghill carried out his classical experiments on the anatomy of behaviour in the larval amphibian *Amblystoma*, and showed that the first responses to external stimuli which appear in the course of the development of behavioural reactions are total responses—that is to say, the body and limbs act as a whole. Only later do separate limb movements become individuated as simple and isolated reactions independent of total movements of the body. The total responses are related to a stage in the development of the central nervous system when the latter is composed of a diffuse network of nerve cells and fibres, and the appearance of local, isolated, responses is presumed to be dependent on the "crystallizing out" from the initially diffuse network of circumscribed and segregated tracts of nerve fibres. These experiments were the first to indicate such a sequence of behavioural development, in contradistinction to the rather widely held view that it is the local reflex that is the primary unit of behaviour, and that these reflexes become only secondarily linked up by some integrating mechanism at a higher functional level of the nervous system. Coghill's general conclusions (which were later substantiated by the observations of Barcroft and Barron (1939) on the development of responses in sheep embryos) suggest a broad functional division of types of neural organization into (1) the fundamentally primitive foundation of diffuse networks of cells and fibres which mediate generalized motor and sensory activities, and (2) a more differentiated system of localized cell clusters and connecting fibre tracts which mediate activities of a more specific and circumscribed nature. One of the most interesting points which I want to stress here is that the primitive foundation still persists in large measure in the adult brain—even the human brain; in fact, it is this which comprises the basis of the whole reticular system.

In a sense, the reticular system of the brain is not a new discovery of recent years—it has simply been rediscovered. For, since the days of the early neurohistologists such as Cajal, Van Gehuchten, Kölliker and so forth, we have always known of its existence, and we have always known that, besides following the long and more direct ascending pathways to the higher levels of the brain, sensory impulses are also diverted by innumerable collateral branches of entering sensory fibres (as well as by many collaterals of the direct ascending tracts of fibres) into diffuse collections of cells which extend as a sort of continuous matrix all the way up to the thalamus in the forebrain. It has for a long time been apparent, therefore, that incoming sensory impulses may be conveyed to higher functional centres of the central nervous system by two routes—(1) by discrete and well-defined relay stations, and thence to the highest functional levels of the cerebral cortex, and (2) by the diffuse and ill-defined network of the reticular system through which they may be dispersed in almost every possible direction, and eventually conveyed to higher levels largely by a sequence of short internuncial neurons.

The idea presents itself that, just as anatomically the reticular system appears to provide a generalized sort of diffuse matrix or background against which the more specific tracts and nuclei stand out as circumscribed and discrete formations, so it provides the medium for a sort of background of generalized and diffuse sensory activity upon which, so to speak, the main (and immediately relevant) elements of sensory perception are high-lighted as discrete items of conscious experience. At any rate, there is the neural basis for such a functional collaboration, and it fits in rather well with some of the psychological interpretations of sensory experience. But I will return later to a brief consideration of some of the possible sensory roles of the reticular system, because I would like in this lecture mainly to give attention to the manner in which the specific sensory pathways become elaborated to serve their discriminatory functions. Probably it will be agreed that the extent to which we can gain an intellectual appreciation and understanding of the details of our material environment depends initially on (1) the capacity of the sensory mechanisms of the central nervous system for selecting, segregating and analysing the effects of the considerable variety of external stimuli which impinge on our sensory receptors, and (2) on the ability of the higher centres to re-synthesize impulses generated by diverse stimuli with such precision that the patterns which gave rise to them are accurately reproduced in their original configuration. In the language of more modern fashion, these two aspects of sensory perception are sometimes spoken of as "coding" and "decoding", a terminology which has the disadvantage (in common with the application of a number of other cybernetic terms to biological processes) of begging very vital questions. However, it seems clear that it is the capacity of the nervous system for selecting and segregating the effects of different stimuli which is primarily the most important factor in the development of powers of sensory discrimination, and what seems to be of outstanding interest (though it does not seem to be generally recognized) is that in the course of evolution the progressive improvement of discriminatory powers has to a large extent been determined not (as far as we have evidence) by any increasing elaboration and differentiation of the receptor organs themselves, but by the increasing elaboration and differentiation of the sensory centres which make possible a more complete analysis of gradations of stimuli to which the receptors themselves are *already* differentially susceptible. Let me illustrate this thesis in the first instance by reference to the visual system.

It is a somewhat remarkable fact that, in general, the intrinsic structure of the retinal epithelium shows no fundamental difference if the human eye is compared with that of some of the lowliest of placental mammals today. Yet the range of visual discrimination in man has reached a very high degree of perfection. This is no doubt partly due to the acquisition of full binocular vision, but the latter has been made possible by a differentiation of the main lower visual centre, the lateral geniculate nucleus, which has so re-arranged its pattern of cells that impulses from corresponding points in the two retinae are conveyed separately to adjacent zones and thence projected on to the same cortical locus. In sub-mammalian vertebrates the optic tracts are usually completely crossed, and in loer wmammals in which only a small proportion of fibres remain uncrossed there is considerable overlap in the geniculate nucleus of the termination of the crossed and uncrossed fibres. But in the human geniculate nucleus, as also in that of the higher Primates, there are separate layers of cells completely segregated from each other in relation to which homolateral and heterolateral retinal fibres terminate. So far as is known, there is no opportunity for functional interaction between these layers in the Primates, and thus no fusion of visual images from the two eyes can occur until the cortical level is reached. It seems evident that the segregation of crossed and uncrossed retinal fibres in each geniculate nucleus is the pre-requisite for full binocular and stereoscopic vision, and it is interesting to consider how this segregation has been achieved. After the decussation of the optic nerves at the optic chiasma, the two sets of fibres become more or less diffusely intermingled, and in each optic tract as far back as the geniculate nucleus those derived from corresponding sectors of the two retinae appear to remain almost entirely mixed up in a random disarrangement. But as soon as they actually enter the geniculate nucleus they become completely sorted out again so that each set is conveyed to sharply separate cell layers. Thus it is not that the laminar disposition of cells in the geniculate nucleus is secondarily imposed on the latter by a primary geometrical arrangement of crossed and uncrossed fibres as they arrive in the optic tracts—rather it is that the laminar differentiation of the geniculate nucleus, by some sort of positive selectivity, *secondarily* sorts out the incoming fibres from each of the two retinae. This phenomenon serves to bring into prominence a major feature of lower sensory centres in general—they are not merely relay stations, as so often seems to be supposed; their main function is that of sorting stations, a function which involves an unshuffling (rather than a reshuffling) of incoming impulses. It is at this level that sensory fibres become sorted out and classified in accordance with the category of impulse which they carry, and it is here that the analytical mechanisms are developed which provide the essential basis for sensory discrimination.

The developmental process whereby the different cell layers of the geniculate nucleus selectively determine the segregation of crossed and uncrossed optic fibres poses one of the most difficult questions of morphogenesis. But such a process of segregation has actually been studied experimentally in lower vertebrates. I refer to the work of R. W. Sperry in which he cut the optic tract in newts and studied the course of regeneration. In his experiments he found that at the site of the lesion the regenerating fibres became tangled in the scar in a quite irregular ravelling, so that they entered the central stump in random disarrangement. But on reaching the optic lobes they were in some manner sorted out again so that fibres from different sectors of the retina established their proper functional connections with their normal projection areas in the optic lobes. This "selective patterning of synaptic connections" (as Sperry has described it) has so far defied satisfactory explanation. But it has been abundantly demonstrated to occur in the developmental stages of lower vertebrates, and it may be supposed that some such process has perhaps also been involved in the evolutionary differentiation of the neural basis of sensory discrimination in general.

The sorting and sifting of retinal impulses by the geniculate nucleus in man goes much farther than the segregation of crossed and uncrossed impulses, for the fibres from the central area of each retina, and from every locus in the central area, are sorted out into three groups which terminate severally in three sharply-defined cell layers. In other words, the central area of the retina, in its projection on the geniculate body, is replicated three times.* What can be the significance of this triple map of the retina in the brain? When I first drew attention to this arrangement as the result of experiments carried out many years ago, I suggested that it might be related to the trichromatic theory of colour vision, for these experiments provided the first concrete evidence for the existence in the optic tract of a three-fibre unit such as had been postulated long ago on the basis of this theory. I drew attention to certain facts which seemed to support such a proposition, but at the same time emphasized its tentative nature. It is still no more than a provisional hypothesis, and is likely to remain so until it has been found technically feasible to compare by electro-physiological methods the relative spectral sensitivity of the three cell-layers related to each eye. But whatever may be the differential nature of the impulses (or the information conveyed by them) which are segregated at the geniculate level into three categories, clearly a segregation does occur, and it may be presumed to relate to a functional analysis of some sort. Obviously, also, colour discrimination must ultimately depend on a segregation of retinal impulses related to differentially sensitive receptors (though perhaps not in the simple form which I first envisaged in my own interpretation of the trilaminar organization of the geniculate nucleus).

Now, the interesting point has emerged from comparative and electrophysiological studies (particularly those of Granit) that a differential spectral sensitivity of the receptors may exist in lower mammals which appear from appropriate tests to be colour blind; in other words, the structural mechanism which could permit a *peripheral* analysis of the spectrum may be developed in the absence of a sorting mechanism in the brain whereby impulses related to different local parts of the spectrum can be sorted out. It might be difficult to understand such a situation if the spectral sensitivity of retinal elements is presumed to depend on a variety of pigments having different absorption curves, which have (so to speak) become specifically elaborated in direct response to the requirements of colour vision. But my colleague Dr. Barer has drawn attention to another possible explanation of the differential sensitivity—that it depends fundamentally on random slight variations in cone geometry, which determine corresponding differences in the refraction and dispersion of rays of different wave-length as they pass along cones of slightly different angles. "We have here", he says, "a possible filter mechanism which might result in differences in spectral sensitivity among the cone population", some cones trapping red, green, and blue light, others mainly green and blue, and still others blue only. If this attractive hypothesis should prove to be well

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* It should be noted that, so far as separate cell laminae are concerned, the more peripheral areas of the retina are only replicated twice, and the extreme periphery not at all.

founded, it is to the highest degree unlikely that there is anything but a continuous gradation in the geometry—and therefore in the "colour-trapping" ability—of the cones. In other words the selection, sorting out, and separation of the three main categories of retinal impulse which (on the trichromatic theory) are required as a fundamental basis for colour discrimination must be determined in the visual centres of the brain. Such an interpretation would conform with my general thesis that the progressive evolutionary development and refinement of powers of sensory discrimination are predominantly effected by a progressive elaboration of the central nervous apparatus which makes it possible to exploit more and more fully the potentialities of receptor mechanisms already in existence. Incidentally, this phenomenon seems to be an excellent example of what evolutionists have termed "pre-adaptation", that is to say, the incidental development of structural characteristics which are not *directly* adaptive in an ancestral type, but which do become adaptive in its evolutionary descendants.

A similar phenomenon appears to be exemplified in cutaneous sensation. It was for many years supposed that the enhancement of cutaneous sensory discrimination in higher types of organism depends on the progressive differentiation in the latter of various kinds of specialized receptor, e.g. Meissner's corpuscles for touch, Krause's end-bulbs for cold, Ruffini terminals for warmth, and so forth. However, it has now been demonstrated (particularly by Weddell and his collaborators) that these elaborations of nerve endings in the skin, whatever their real significance may be, are by no means an essential basis for the finer grades of sensory discrimination, for our discriminatory powers are quite well developed in areas of skin which are simply innervated by a diffuse network of free nerve-endings. But such an arrangement of interlaced free nerve-endings appears to be common to the whole range of vertebrates; in other words, it seems that, anatomically, the peripheral mechanism of cutaneous sensation remains more or less stationary throughout the course of vertebrate evolution. Like the visual system, however, the potentialities of this peripheral mechanism have been exploited by sorting devices which become primarily differentiated in the central nervous system. There is good evidence, both direct and indirect, of the existence of these devices. For example, when they reach the brain or spinal cord, cutaneous nerve fibres become to a considerable extent re-grouped both in respect of their topographical distribution in the skin, and in accordance with the functional category of impulse which they convey. Thus, fibres coming from diverse areas of the skin become thoroughly mixed up in random fashion as they travel back centrally in the main nerve trunks. But between the posterior root ganglion and the spinal cord, by some mysterious process they become once more resorted into fasciculi each of which is made up of fibres innervating a local area of the skin. Clearly this is a device which makes possible tactile localization by segregating from each other the actual terminations of impulses received from different local areas. It has likewise been demonstrated that there is a resorting of impulses related to different sensory modalities, for different rootlets of each spinal nerve may be composed of different categories of fibres—one rootlet may convey fibres subserving superficial tactile sensation, and an adjacent rootlet may convey only those subserving deep or proprioceptive sensibility (Kuhn). There is further evidence that fibres which are predominantly concerned with the transmission of "pain impulses" become segregated out in the posterior roots, and the well-established fact that impulses related to different modalities are to a large extent segregated in different ascending tracts in the spinal cord and brain stem is also difficult of explanation except on the basis of a selective sorting of sensory fibres when they reach the central nervous system.

As with the visual system it seems evident that the re-grouping of somatic sensory fibres (and of the impulses conveyed by them) as they enter the nervous system must be determined by some sort of positive selectivity exerted by the different groups of receiving cells in the lower sensory centres—that is to say, the analysis of the sensory inflow must depend primarily on their activity. We are entirely ignorant of the actual process underlying such a selection of cutaneous impulses, but, again, there is experimental evidence that it does occur. For example, it has been found that if in tadpoles a strip of the belly skin is transplanted to the back, it becomes innervated abnormally by the dorsal (instead of the ventral) rami of the spinal nerves. Yet when, in the mature frog, the transplanted skin on its back is touched, the animal wipes its belly with its fore-limb (as though the strip of belly skin were still in its normal position). Similarly, if an extra limb bud is grafted on the back, it becomes innervated by cutaneous fibres destined normally to innervate the trunk skin. But in the adult animal normal cutaneous reflexes were elicited from the limb "indicating that the sensory fibres had formed functional connections in atypical areas of skin and *central relations appropriate for those atypical terminals*" (Sperry). Further experiments of the same kind showed that if a posterior spinal root of one side is transplanted so as to enter the opposite side of the spinal cord, its fibres still make the appropriate connections with the sensory centres so that sensory impulses of different types each elicit the normal responses.

If time permitted, it would be possible to extend these observations by enlarging on the importance of the "sorting out" functions of the lower centres in the sensory pathways. Thus, the fibres from the cochlea of the inner ear terminate in most complicated nuclei in the hind-brain which anatomically can be subdivided into many groups. Indeed, it has been estimated that the length of the basilar membrane of the cochlea is replicated about a dozen times in as many cell groups. "In other words, the cochlea is 'unrolled' at the cochlea nucleus, not just once, but repeatedly" (Galambos). We do not know the precise functional significance of this multiple representation in the lower auditory centres, but it can hardly be doubted that (like the multiple maps of the retina in the geniculate nucleus) it is concerned with a sorting and unshuffling of information derived from the peripheral receptors so as to serve the requirements of a high degree of discrimination. There is also suggestive anatomical and physiological evidence that the several hundreds of discrete glomeruli in the olfactory bulb may provide the structural basis for the sorting and segregation of olfactory impulses.

Naturally, it must be supposed that, once the analysis has been effected by the selective activity of lower sensory centres, the segregation of these impulses is sustained up to the point where they reach the functional levels concerned with their final integration. There is no need here to recount in detail the evidence confirming this suggestion, for it is well known. The segregation of impulses from the retina to which I have already made reference is known to be continued (at least in the higher Primates) until the visual cortex is reached. Auditory impulses derived from different parts of the cochlea retain their spatial sequence through the medial geniculate nucleus up to the auditory cortex, so that in the latter there is rather a precise localization fore and aft in terms of vibration frequency. Recently published studies by Mountcastle, based on single unit analysis, have demonstrated that in the somatic sensory cortex the vertical cell columns (which are so clearly visible in ordinary microscopical sections) form a sort of mosaic, each vertical column being in most cases "modality-pure" in the sense that it responds only to one type of stimulus (i.e. movement of hairs, pressure on the skin, or mechanical deformation of the deep tissues). And there is also evidence that such a segregation is primarily effected at lower functional levels, e.g. in the posterior column nuclei of the medulla. Without expanding on the general theme of spatial localization in the cerebral cortex, and its well-established relationship to functional localization, it perhaps deserves some emphasis at this time because it seems to me that in recent years quite a deal of unnecessary verbiage has been expended in discursive articles relating to the concept of cortical localization—particularly in reference to cortical architectonics. Let it be fully recognized that the conception of cortical architectonics has a very real basis in the sense that a number of cortical areas are clearly to be distinguished by structural differences, and that the latter are correlated with differences in fibre connections and corresponding functional differences. The fact that some anatomists and physiologists have tended at times to push the conception too far does not invalidate the principle as a whole. Undoubtedly the integrating and synthesizing properties of the cerebral cortex comprise its outstanding functional significance, but integration is not possible unless there is something to integrate—analysis must precede synthesis. It follows that the cortex must first of all be presented with all the elementary components of sensory perception before it can weave them into a coherent whole, and it is clear that these elementary components are represented by a diversity of impulses initially sorted out by the lower sensory centres and projected to the cortex in more or less well-defined spatial and temporal patterns. Some of the anatomical correlates of the spatial patterns are to be seen in the diversities of cortical structure.

The proposition that the lower sensory centres of the central nervous system function as sorting stations involves a number of considerations. One of these is that, in the process of sorting incoming impulses, they appear to select and classify them in certain fundamental categories. It seems to me rather important to recognize this function. Some of the sensory physiologists of the past have been criticized for their attempts to codify cutaneous sensations in terms of sharply defined categories such as those of touch, warmth, cold and pain, and to relate them to different morphological types of sense-organ in the skin. Such criticisms have some justification so far as they apply to the supposed peripheral anatomical basis of cutaneous sensory discrimination, for (as already noted) diffuse, interlacing networks of free nerve endings with no obvious morphological differentiation seem to be adequate for quite a high degree of discrimination. Clearly, however, there must be *some* sort of a preferential sensitivity in different nerve endings, or in varying local patterns of nerve endings, in relation to different types of stimulus. If it is one of the main functions of lower sensory centres to sort, they must have a range of material from the periphery which is capable of being sorted. But it now seems more likely, on anatomical and physiological grounds, that it is not the sensory endings in the skin that are themselves divided into quite sharply defined categories of differential sensitivity—rather they may represent in their range of sensitivity a more or less smooth continuum with no very abrupt demarcations between those which are preferentially responsive to different stretches in the total range of stimulation. One functional type of cutaneous receptor may tend to grade almost insensibly into the next (at any rate to the extent that receptors of differential sensitivity are more closely graded than is commonly reckoned to be the case). In other words, the apparent sharpness of contrast in the cutaneous sensory modalities which we are accustomed to distinguish subjectively may depend not so much on an equivalent abruptness of contrast in the peripheral receptors themselves, as on the selection and classification, by the sorting action of the specific sensory centres in the nervous system, of impulses related to certain restricted foci in what is otherwise a more or less generalized field of sensory excitation. It is thus primarily in the lower centres that the sensory impulses are codified in the sharply-defined categories which we come to interpret in terms of sharply-defined modalities of sensation. It may also be surmised that impulses initiated by continuous gradations of stimuli affecting special sense receptors in general are likewise classified and sorted into compact groups on their arrival in the brain. By way of analogy, we may refer again to colour discrimination, which appears to operate as if on the basis of selective sensitivity to three local bands of wave-lengths in the red, green and blue parts of the spectrum respectively, and thus might be explained by the selection and segregation in the central nervous system of impulses initiated from these bands.

In addition to the selective action of lower sensory centres on the sensory input, the latter is always susceptible to modification by centrifugal systems of fibres derived from higher functional levels of the nervous system. Although examples of such centrifugal control have been known anatomically for more than half a century, it is only recently that their functional importance has been demonstrated by experimental observations. Centrifugal nerve fibres run forward in the optic tracts to the retina, and from the hind-brain to the sensory cells in the cochlea. The olfactory bulb is concerned with receiving and sorting impulses conveyed from the sensory cells in the olfactory epithelium, but the resultants of its activity are also controlled by centrifugal fibres running forward from the basal region of the cerebrum. The reactions of cutaneous receptors have been shown to be capable of modification by efferent impulses conveyed through the sympathetic nerve supply of the skin. Many other examples of such centrifugal systems could be enumerated; indeed, it now seems certain that at every level in every sensory pathway, as far up as the cerebral cortex itself, the pattern of input from peripheral receptors may be continually controlled and modified by the activity of central regulative mechanisms. This general principle of nervous organization is obviously of the greatest importance for the study of perceptual phenomena, for it determines that what we ultimately experience as a conscious sensation is not solely dependent on external stimuli alone; the effects of the latter may be variably conditioned by intrinsic activities emanating from the brain itself. In other words, altogether apart from the initial selection and fractionation of sensory impulses in the afferent pathways, there is opportunity for still further selective control of these impulses by efferent pathways. Obviously, therefore the sensory material which ultimately reaches consciousness may be limited and fractionated to a degree which is hardly realized.

If it is the function of the lower centres of the specific sensory pathways to select and sort into categories impulses which have been initiated at the periphery by a continuously graded range of stimuli, if, that is to say, the effect of their selective activity is the abstracting of isolates from a continuum, clearly the higher centres (including the cerebral cortex) are likely to be presented with only an incomplete and patchy replica of external reality by these particular pathways. It is as though we were presented with a series of arbitrary points on a continuous curve, with the result that we interpret the abrupt contrasts between such discontinuous points as if an even curve did not exist. Such a conclusion makes an interesting comparison with one of the main themes of Bergson's philosophy to which I have already drawn attention—that purely intellectual processes inevitably involve selection and abstraction to the extent that they can only provide a partial view of external reality. I do not wish to push this comparison very far, for I have already emphasized that it may be no more than a very distant analogy. But it is too tempting to refrain altogether from enquiring further whether in the organization of the nervous system there is in fact any counterpart to what he termed "a vague nebulosity around our conceptual and logical thought", which he supposed to represent intuitive processes.

Now, I have already called attention to the fact that there are two main routes in the central nervous system which are traversed by sensory impulses from the periphery when they reach the spinal cord and brain—(1) the specific pathways which I have so far been discussing and which convey impulses by well-defined fibre tracts to circumscribed sensory nuclei, and thence more or less directly to clearly localized regions of the highest functional levels of the nervous system, and (2) the non-specific or diffuse system, that is to say, the so-called reticular system. The reticular system is exceedingly difficult to define simply because it does not clearly define itself in terms of anatomical topography. It can be visualized as a sort of central core composed of scatterings of nerve cells entangled in an irregular and closely meshed network of nerve fibres, and extending up from the spinal cord through the brain stem to run into continuity with the intralaminar nuclei of the thalamus. As is now well known, the whole system is eventually linked up indirectly with the cerebral cortex and by circuitous routes is capable of influencing and profoundly modifying cortical activity as a whole. Into the reticular formation stretching through the spinal cord and brain stem there stream numerous collaterals from the incoming sensory fibres of peripheral nerves, as well as a continuous succession of collaterals from many (perhaps all) of the ascending tracts of the specific sensory pathways. Thus, on the sensory side of brain function, there is abundant opportunity for impulses initiated by every variety of sensory receptor to activate the reticular system and through the latter to modify fundamental processes of cortical activity. In recent years considerable progress has been made in the anatomical analysis of the reticular system, and one of the important points which has emerged is that it is not quite so diffuse or non-specific as some had supposed. For example, Brodal in the Anatomy Department of Oslo University has demonstrated that in the brain stem many of the cells of the reticular system are disposed in more or less well-defined groups, and some of the latter have rather well-defined fibre connections. Similarly, the intralaminar nuclei of the thalamus have been shown by Powell and Cowan, working in my own department, to have localized and rather precise projections to different regions of the corpus striatum. (Incidentally, this work, taken in conjunction with other studies in recent years, has led to a virtual "rediscovery" of the corpus striatum, in the sense that it is now obvious that this mass of grey matter is far more than the relic of a primitive motor system of the forebrain as commonly supposed; it is in fact a highly important "sensory ganglion" which receives, by way of the intralaminar nuclei, patterns of afferent impulses mediated by the reticular system as a whole.) But although the reticular system certainly shows some intrinsic differentiation of cyto-architecture and fibre connections, it does not appear, on either anatomical or physiological evidence, to provide for the sharp segregation of sensory impulses into different categories such as evidently takes place in the lower centres of the main or specific sensory pathways. It might be supposed therefore, that the information conveyed through the system to the higher functional levels would be less completely analysed and thus less clear-cut so far as sensory perception is concerned. To this extent, indeed, the information which it transmits to the higher functional levels may actually be a more accurate reproduction of the real nature of things, for the very reason that the natural interrelationships of the initial sensory stimuli are more freely retained, and therefore the information which they provide is presented more as a unitary whole than as a variegated mosaic of discrete sensations. We might say, perhaps, that the specific sensory pathways dissect out essential and immediately relevant items of information from a common matrix of sensory stimuli, while the non-specific pathways convey the impression of the matrix as a whole. These are speculations which naturally arise from the circumstance that for this lecture I have deliberately used certain Bergsonian conceptions as a sort of text to introduce my subject. Pursuing the same theme, I may further recall that Bergson equated "intuition" very closely with "instinct", for he remarks that "by intuition I mean instinct that has become disinterested, self-conscious, capable of reflecting upon its object and of enlarging it indefinitely". It is therefore rather interesting to note, in connection with my speculative correlations, that in birds where activities may be said to be almost all basically instinctive, the higher functional levels of the sensory pathways appear to be represented entirely in the homologies of the intralaminar nuclei of the thalamus (i.e. the thalamic extension of the reticular system) and the elaborate corpus striatum. So far as is known, the cerebral cortex of the avian brain (which in any case is of very trivial extent) receives no ascending pathways directly from the thalamus. If then, as appears certain, instinctive behaviour in lower vertebrates is mediated at the higher functional levels of the brain by the intralaminar nuclei and the corpus striatum, it is to be supposed that the equivalent system in mammals (and Man himself) may be concerned with equivalent functions. At any rate, it seems to me to be a point worth consideration in the light of Bergson's suggestion that intuition is really the ultimate development of instinct.

It must not be supposed that in the mammalian brain the specific and non-specific sensory pathways are quite independent systems. On the contrary, they are closely linked at all functional levels by interconnections. At all levels, therefore, the activities of the reticular system are susceptible to modification by sensory impulses ascending by way of the well-defined tracts of the specific pathways, and these sensory impulses in their turn can be modified by impulses transmitted from the reticular system. The functional interaction between the two systems at the cortical level is still uncertain, and one of the problems now awaiting investigation is the significance of the secondary sensory areas of the cerebral cortex. It is known, on physiological evidence, that the secondary areas receive impulses directly or indirectly from the thalamus, but (unlike the primary areas) it has not so far been possible to trace the source and course of the fibres conveying these impulses. For while the excision of (say) the primary somatic area is followed rapidly by a focal degeneration of cells in the main sensory nucleus of the thalamus, excision of the secondary somatic area alone gives rise to no perceptible change. It is interesting to conjecture the possibility that the secondary sensory areas of the cortex (which, in terms of functional localization, are more diffuse and overlapping than the primary areas) may represent the cortical level of the diffuse sensory pathways of the reticular system of the brain, thus providing a background of more general information against which the individual items, segregated and classified by the sorting activities of the lower sensory centres, are high-lighted as the "luminous nuclei" of Bergson's analogy. Perhaps, with an effort of mind, one can occasionally get a glimpse of this general background and thus, by a flash of intuitive insight, suddenly recognize relationships and conjunctions between the highlights which had previously been obscure and unobserved. At any rate, it is an intriguing conception, and perhaps quite an apposite one, that sensory impulses poured into the reticular system of the brain may, through its plurality of multisynaptic connections, set going inter-weaving and variegated patterns of activity as it were at random, or at any rate uncontrolled by predetermined selective influences, and that the resultants of this activity may every now and again be fed back into the higher functional levels of the specific sensory pathways, there to be abstracted and construed in terms of intellectual concepts revealing new coherencies and new congruities hitherto unperceived and unexpected. Perhaps, indeed, a mechanism of this sort is the elementary structural basis of what has been termed inventive thinking, that is, imagination. If the criticism should be made that, with our present ignorance of brain-mind relationships, the basis for such a suggestion is too tenuous for it to be considered even as a purely hypothetical idea, it may be answered that of course it is tenuous—but it is at least permissible to suppose (1) that ultimately there must be a neurological correlate of inventive thinking, and (2) that this correlate, however complex it may be, must subsume somewhere within its organization just such interacting systems as I have envisaged.*

Some of my digressions in this lecture are of course frankly speculative. This has been my deliberate intention, partly because I think a lecture of this sort invites the ventilation of ideas rather than the reiteration of facts, and partly because it seems to me that in the present state of neurological enquiry (and more particularly the central problem of brain-mind relationships) there is a very real need for the formulation of new ideas to supplement the routine investigations of the microscope and calculating machine. But let me now briefly refer once more to my main theme (for which a considerable body of evidence has accrued in recent years)—that sensory discrimination is primarily determined by the selective agency of the lower sensory centres of the brain and spinal cord, as the result of which sensory impulses related to different functional categories are unshuffled and sorted, canalized into specific and stereotyped channels, and thence projected in set patterns to the higher centres at a cortical level. In other words, so far as the specific pathways are concerned the sensory input of the central nervous system is very far from being a random input. I said earlier that the fundamental processes underlying this selectivity constitute one of the most difficult problems of the morphogenesis of the central nervous system. It would perhaps be more in accordance with the facts to say that at the moment it has all the appearance of being an insoluble problem. It may be that the interesting analogy of computing machines will help toward an understanding of some of the more elementary manifestations of cerebral activity, but there is one obvious contrast which presents itself. The connections which are required in a machine to permit the sorting and analysis of relevant data are planned and constructed for the machine. The living and developing brain plans and constructs its own connections, and even

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* As an extension of this hypothesis, it may be presumed that such interacting systems also underly one of the most remarkable features of dreaming—that however unwonted or grotesque the juxtaposition of the individual items of a dream may be, they do commonly form a coherent and sequential whole. The oddments of random recollections are, so to speak, strung together by the integrating effects of cortical activity into a consistent story—a story which (as well recognized) can often be shown by analytical methods to be full of meaning.

if after they have been established in the early stages of development these are smashed and pulped to an unrecognizable tangle, it can reconstruct them. Perhaps no contrast is more expressive of the fact that the brain contrives—the machine is only contrived.

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