THE JOURNAL OF NEUROLOGY AND PSYCHOPATHOLOGY.

Vol. VI.

FEBRUARY, 1926.

No. 24.

Original Papers.

A THEORY OF DECUSSATION.

NOTE ON A POSSIBLE ADAPTIVE SIGNIFICANCE OF THE TRANSLATERATION OF THE UPPER MOTOR AND SENSORY NEURONES.

By IAN D. SUTTIE, PERTH.

ON the supposition that the decussation of the main nerve tracts in the central nervous system lengthens these and complicates the course of ontogeny, and is thus to some extent biologically disadvantageous, it is permissible to ask whether this transposition of centres confers on the organism any countervailing advantage. Although a 'crossed' central nervous system seems to be 'the rule,' the student is offered no functional evolutionary interpretation of this striking fact. Perhaps the very regularity of this arrangement causes it to be accepted as a matter of course calling for no explanation. But it must either have some functional utility or else must date back to the origin of the central nervous system itself, upon the phylogeny of which, therefore, it must throw some light. In either case it is a matter of great interest and equal obscurity, justifying tentative inferences on unusually scanty evidential bases.

For convenience we shall term 'homolateral' all those synapse centres which are mainly concerned with stimuli-originating receptors, or with impulses proceeding towards effectors, on the same side of the body as themselves. A centre, however, which deals mainly with neural processes initiated and terminated in the opposite side of the body, will be called 'heterolateral.' Of course, many tracts and centres have peripheral connections on both sides of the mesial plane, or control functions which have no particular spatial reference. With such centres and tracts we are not concerned, our task being merely to investigate

the reason for the almost uniform location of sensory and motor centres in that side of the central nervous system opposite to their main peripheral connections.

The main homolateral systems are :—

1. The sympathetic system.
2. The lower motor and sensory neurones of the central nervous system, except the trochlearis.
3. The secondary and higher centres of smell, and perhaps to some extent of taste.
4. The vestibular centre.
5. The cerebellum.

The main heterolateral systems are :—

1. The upper sensory neurones of the cord and their receptor centres in the tectum and thalamus.
2. The upper neurones of the cochlear nerve and of other cranial sensory nerves, except those previously mentioned.
3. The tertiary continuation of all these paths to the cerebral cortex.
4. The motor cortex and tract and their associated nuclei in the pons, medulla, etc.
5. The red nucleus.

The decussating tracts are those which lead from homolateral to heterolateral centres or *vice versa*. By a 'commissure' I understand a direct connection between two paired centres. The elaborate crossing of the cerebellar connections shows how 'clear cut' the functional distinction of the two systems (homo- and heterolateral) must be.

The ophthalmic system is anomalous and will be considered later, as it suggests a solution of our problem.

To deal, in passing, with the possible objection that decussation and the heterolateral arrangement of centres serve in some way to integrate the two halves of the body, it should be noted that :

1. The upper connections of the vestibular portion of the eighth nerve are *not* crossed, although it is particularly concerned with the function of balancing, and hence with the co-ordination of the two halves of the body. If decussation promoted co-ordination, the cerebellar centres more than any others should be crossed, but as a fact they are not. The central auditory paths, on the other hand, are crossed, though their bilateral integrative significance cannot be anything like so great.
2. If the crossed arrangement has been evolved by variation and selection within the vertebrate phylum, we would expect to find it more definite and complete in higher than in lower forms, improving *pari passu* with general integration ; this, however, is not the case.
3. Leaving out of account commissural connections, the highest degree of bilateral integration would *theoretically* be achieved where the

centre on each side is *equally* connected with both sides of the body. This is the only way in which decussation can subserve bilateral integration. If half the fibres of any tract decussated, it would be reasonable to suppose that the function of this arrangement was bilateral integration, but where a vast majority of fibres—as in the instances mentioned—decussate, this end is defeated. For the functional isolation of the two halves of the body is not affected by the mere shifting of the nerve centres belonging to each half to the opposite side of the middle line. Crossed sticks are just as separate as parallel ones.

Let us consider the respective components of these two systems (homo- and heterolateral) with a view to discovering some character common to one group which in turn might suggest a functional or evolutionary interpretation of the arrangement. Reflexes involving only one side of the body are subserved by synapses on the same side of the central nervous system. Co-ordination of the different levels of the same side of the body is also maintained by homolateral mechanisms. These primitive levels, as well as the sympathetic system, being uncrossed, we would infer that this arrangement is the primary one. The mechanism of smell and perhaps of taste, also of great antiquity, is likewise homolateral, as are the vestibular centres (lateral line organs). We may interpret this as evidence of the phylogenetic antiquity of the homolateral arrangement, but it should also be noticed that these organs are practically incapable of being differentially stimulated (e.g., on one side only). Differential stimulation, on the other hand, is important in general sensation and in the special sense of hearing (we find elaborate adaptations of the external ear for the further discrimination of the *source* of sound). We have, then, the suggestion that the central nervous system was originally uncrossed and that the crossing is connected with the spatial appreciation of environment, the *location* of stimuli.

Morphologically, we find the transliteration of centres most complete in the mesencephalon, where the optic tracts come into relation with other sensory paths. But the optic apparatus itself is not easy to classify as homo- or heterolateral. In all animals it is functionally heterolateral; in those animals, however, which possess eyes whose field of vision crosses the middle line, we find elements of this system which are *structurally* homolateral. "In mammals a complete decussation of the optic tracts is rare. . . . The beginnings of partial decussation are seen in fishes. . . . The number of uncrossed fibres seems to depend on the position of the eye. When the eyes are laterally placed, as in most mammalian orders, the uncrossed fibres are at a minimum. Among mammals those whose eyes are lateral so that the fields of vision do not overlap have few uncrossed fibres." (Johnston, *Nervous System of Vertebrates*, pp. 146-7.)

If this is correct, we have here a series of structural adjustments

which seem uniformly to achieve a functional correlation of each half of the brain with the opposite half of the organism's environment. The structural adaptation is remarkable in so far as it affects an arrangement so general and constant as that of the decussation of nerve fibres. Functionally, also, this arrangement would appear to have great significance, as we know that each half of the brain is already related to the opposite half of the body. That is to say, there are received in each half of the brain all stimuli affecting the opposite side of the body and all light stimuli whose source is the opposite hemi-environment. It would appear to be of some importance, as we can easily understand, that the data of sight should be readily brought into relation with other data spatially related, perhaps with a view to economy of commissural fibres. The structural adaptation is a most striking one, for in animals with frontal eyes we find the two right hemi-retinæ jointly performing the same function as the left lateral eye in an animal whose eyes are laterally placed. That is to say, they deal with the left hemi-environment and are connected with the right tectum and thalamus. The evolution from one optical system to the other, involving as it does either the establishment of new homolateral central connections or the suppression of these, is so complex an adjustment that we cannot believe it has no functional significance.

So far as these considerations carry us, the inference would appear to be that the proportion of decussating optical elements is nicely adjusted so as to maintain the functional heterolaterality of the sensorimotor centres. Perhaps we might generalize from this and suggest that *all* decussation has this function of grouping and co-ordinating sensory and motor centres according to their *spatial reference*, and that this adaptive function is their evolutionary *raison d'être*, each cerebral hemisphere dealing with one hemi-environment. But if lateral eyes and a complete decussation at the chiasma, as in fishes, represent the primitive arrangement, this hypothesis would not explain why there is *any crossing at all*; it merely explains *why there is a partial crossing where fields of vision overlap the middle line*. It is not, however, inconceivable that the optical arrangement present at the evolutionary inception of the crossed nervous system might have been that of parallel axes, or even possibly of mesial eyes. Treating the two eyes as functionally one, as equivalent to one mesial eye—as they are—it is apparent that such an optical system is structurally homolateral, like all the other primordial nervous mechanisms. But the optical eye is unique as a sense-organ, inasmuch as the lens necessarily reverses the image of the environment and thus *transposes the stimuli before they affect the nervous mechanism at all*. The outgrowths of the brain, which are the retinæ, are in fact *affected by a reversed environment*. In this unique circumstance we find a possible reason why a structurally homolateral optical system, as e.g., the 'pineal'

eye, should be *functionally* heterolateral. Connections must then be evolved with the motor centres on the *other* side of the body, and centres must be built up for the correlation of optical data with those from the different sense-organs, also mainly on the other side. The question we have to answer is, why these correlation centres and the higher motor centres are built up beside the optical centres—that is to say, crossed—rather than in immediate relation to some other sense-organ, that is to say, homolateral.

There is no question but that the evolution of crossed centres must have taken place at an exceedingly early phase of vertebrate phylogeny, i.e., prior to the evolution of any very elaborate brain. The process of cephalization itself must have been largely determined by the influence of optical stimuli, and the same influences which account for the building up of the higher sensorimotor centres at the *head end* of the cord would also account for their location in the *opposite side* of the central nervous system from their peripheral connections. That is to say, if the process of cephalization has been determined by a tendency for the higher co-ordination centres to be built up near or round the receptor centres for the special senses, then if the optical centres (which are crossed) play the chief part in this process—if they are the centres of attraction, the nuclei round which the brain develops—these secondary correlation centres will also be crossed. So far as cephalization is dependent upon smell, we would expect to find the resulting brain homolateral ; so far as it is dependent upon the lateral line (vestibular) organs, the same holds good. If the hypothesis here suggested is valid, we should expect, as indeed we find, that all the sensory and motor centres closely associated with the tectum opticum would be heterolateral. At this early phase of evolution it is obvious that the sense of hearing could not play a dominant part in determining the location of the correlative centres ; in any case it does not belong to the extreme cephalic end of the central nervous system.

A considerable number of facts could be adduced which could plausibly be interpreted as supporting this hypothesis, notably the structure and distribution of the pineal organ. As, however, I am not a biologist and cannot pretend to offer a systematic presentation of evidence, I could hardly avoid selecting my facts, and I prefer therefore to present the hypothesis as a purely theoretical possibility, that the decussation of the central nervous system is a response, to a considerable extent adaptive, to the reversal of images produced by a lens-containing eye whose field of vision crosses the middle line.

If the hypothesis here put forward is correct, it supplies us with a functional or 'adaptational' interpretation of a very remarkable and general structural arrangement. It might even explain why the leg centres are situated at the superior end of the post- and præcentral

gyri. At any rate, it subsumes under one biological interpretation all those centres, etc., which are heterolateral, and, even if erroneous, leaves us with a defined problem—why are these centres crossed, while others, as, e.g., the cerebellar, are homolateral? It also explains the remarkable adjustment of the central innervation of the two halves of the field of vision, whereby each cerebral hemisphere deals with optical stimuli from the opposite side of the body, whether these are received *viâ* the whole opposite retina (monocular and heterolateral) or *viâ* both hemi-retinæ of the same side (binocular and homolateral). This correlation appears to be maintained very closely, no matter what the divergence of the optic axes may be, though this involves a most remarkable and radical step-by-step reorganisation of the retino-cerebral connections. Macular connections are bilateral, thus subserving bilateral integration. The chiasma, however, affords a sorting junction, whereby optical impulses are classified according to their environmental origin (with eyes at rest), and not on any apparent physiological or developmental principle. This strongly supports a functional or adaptive interpretation.

If my theory should be verified, it would, moreover, throw some light on the early evolutionary phases of the vertebrate nervous system and perhaps upon the origin of this phylum.

If it should be wrong, the very wealth of inference deducible from it will speedily demonstrate its fallacy. It is therefore, I think, worth while considering it particularly closely in connection with the problem of that other anomalous decussation, that of the fourth nerve and of some of the fibres of the third.

If this theory is valid it would lead us to imagine the early evolution of vertebrates as follows:—

First, a worm-like creature, swimming or crawling at the bottom of relatively shallow water. Dorsal cephalic eyes develop, either median or paired. In the latter case the optical axes are still roughly vertical and therefore their field of vision overlaps the middle line.

At first these eyes might be without muscles. The nicety of 'fixation' would be valueless in the absence of (a) an area (macula) of exceptional visual discrimination, (b) a mental development at least to the perceptual level, and (c) a locomotor and manipulative apparatus capable of taking advantage of accurate spatial localization of light stimuli. Since (b) and (c) at least do not belong to this level of organization, we may therefore suppose that at most a primitive eye musculature would be able to direct the eye, or eyes, to one side or the other and perhaps forward and back.

Supposing—as is generally held—the retina of this vertical eye is a diverticulum of the brain roof, then its right side will be most closely connected with the right tectum, and *mutatis mutandis*; this is the case,

too, with human eyes whose axes are also in a sagittal plane and as appears to be the case with all primitive sensory centres.

Thus stimulation will proceed from object A_1 *viâ* the lens to retina at A_2 and hence to the tectum at A_3 (see *Fig. 1*).

Now to turn the eye to this source of stimulation requires a muscle inserted in the same side of the eye. Its 'origin' *might* of course be

Fig. 1.—Diagram of hypothetical mesial eye and its neuromuscular connections.

A , median plane; A_1 , object and source of light; A_2 , retinal sense organ stimulated by A_1 ; A_3 , visuosensory centre; B_1 , ocular muscle on the side opposite to the stimulus and on the same side as the light source (A_1); B_2 , oculomotor centre; B_3 , kinæsthetic centre for the ocular muscle at B_1 ; C , cornea; L , lens; $O.N.$, optic nerve; S , association centres; T , tectum; X_1 , decussation of fibres from the primary light sensory centres to the oculomotor nuclei on the opposite side, which serve to turn the eye towards the source of stimulus; X_2 , site of decussation (omitted from the diagram for the sake of simplicity) of fibres from the kinæsthetic centres to the sensory association centres.

The tailed arrows give the course of the reflex resulting in movement of the eye. The plain arrows give the path of kinæsthetic impulses which result in appreciation of position.

from the opposite side of the body, but we cannot assume this without very good grounds, which—as far as I know—are lacking. To obtain a reflex movement of the eye towards the source of stimulation A_1 , it is necessary that the excitation at A_3 should be communicated to the muscle at B . Again we need not and will not assume that there is any peripheral nerve that carries this impulse direct from the sensory centre A_3 , or a neighbouring and associated motor centre, to the muscle B . A decussating peripheral nerve is the exception which we wish to reduce to terms of the rule. We will therefore suppose that the course of the reflex arc is from A_3 (or its associated motor nuclei) to B_1 , a motor centre on the same side as and supplying the muscle B .

This crossing, by my theory, is the archetype of all true decussation, i.e., of all crossings except commissural or bilateral innervations. It is here plainly an adaptation to the optical fact that a *lens forms an image inverted in all its radii* (i.e., transposed laterally as well as inverted). It is not biologically feasible to secure an 'upright' image by the use of a second (field) lens as in a telescope, and therefore every retina is stimulated by an inverted image of environment. Stimuli are transposed—brought across the functional middle line, *before ever they reach the nervous receptors*, and my thesis is that the decussation of nerve paths is a response to this optically inescapable condition. At the level of organization here portrayed, I imagine this will be admitted.

In passing, and since it seems 'up to' this theory to explain the unique decussation of the trochlearis, I would suggest—entirely on logical and mechanical grounds and without biological evidence—that originally the eyes developed mesially, in series, on the neural crest, and that subsequently they deviated to become paired organs. (This is of course the reverse of the usual interpretation of the existence—as in lampreys—of a *second* mesial ophthalmic rudiment.) Bilateral symmetry is *so nearly attained* that the serial origin of the two eyes is obscured. (Is the relation of the two optic nerves, where there is no chiasma, constant? I.e., does one always pass ventrally to the other?) In deviating to one side the eye naturally carries with it—in an evolutionary sense—its orbit and musculature, and thus it will come about that the muscle B, which ancestrally deviated the eye towards its own side, is now itself on the opposite side of the body; *but its nerve has its central attachment as formerly*, and thus this unique pair of motor nerves comes to be crossed.

Whether or not anything of this sort happened, there is no doubt that centres for reflex eye movements must have evolved in close relation to the visual receptor centres, and not only the oculomotors but also the motor centres for the direction of the cephalic end of the body (which ultimately determines the direction of locomotion). These centres must be linked up to some part of that segment of the arc marked in the diagram A3—B2, and thus the decussating tracts will tend to become larger and more complex. But while the motor neurones proper do remain in their own side of the central nervous system, associated centres will show the general tendency to migrate towards the source of stimuli. In this case a large proportion of stimuli are received from the visual centres.

But visual impressions by themselves are not of much value to the organism. Their biological utility depends on the accurate spatial meaning they convey—the recognition of objects by shape and the precise direction of the organism's own movements that they render

possible. Visual impressions *by themselves* do not, however, possess this accurate spatial reference so essential to their utility; they only acquire it by reason of their correlation with the data of muscle and joint sense and their primitive equivalents. Centres for the correlation of these data with visual sensation must then be evolved in close connection with the visuo-sensory centres proper, and these correlation-centres must also be in most intimate connection with the oculomotor paths. Conceivably at first they are mere adjuncts to the visuo-sensory centres and not very large or complex. By degrees, however, a nexus of centres will be built up round the visuo-sensory, such as visuo-motor, visuo-tactile, etc., which subserve appreciation of position, direction, shape, size, etc. These centres, then, are connected with both the visual sensory centres and for other modes of sensation. Being, however, more dependent upon and more closely related to the visual sense than to any *one* of the others, they are built up round the former. That is to say, they are evolved round a crossed centre and are therefore themselves crossed.

At the evolutionary level at which we can imagine this happening, cephalization is not far advanced. Indeed the visual centres are one of the three important groups of centres of attraction which determine cephalization. The smell-taste functions, indeed, have not nearly so elaborate and intimate a motor correlation as has sight, and such crossed structures as belong to this group (smell-taste) are not conspicuous or fundamental and may be regarded as secondary, conforming to the transliteration of the visuo-kinæsthetic-motor group of centres. The third group of motor correlation of the whole body for locomotion, etc., is crystallized round the lateral line or labyrinthine centre. It is homolateral and has less direct need to be situated at the forward end of the body. The primary and main determinants of 'cephalization,' then, are smell and vision, and this process consists essentially in the building up of 'higher' correlation and association centres round the centres for smell and vision, paths being laid down to relate these association centres with the lower afferent and efferent centres. The visual and olfactory-gustatory sense centres act as it were as centres of attraction for the new and 'higher' centres. This is accepted, but I would suggest that if the visuo-sensory centre is able to determine the location of other centres at the cephalic end of the central nervous system, away from their primary centres, then for the same reason it will be able to locate them on the other side of the central nervous system from these primary centres. So far as cephalization is determined by the attraction of the olfactory-gustatory sense, it merely requires the lower sensory centres to send forward nerve tracts to these cephalic nuclei. So far, however, as cephalization is determined by the attraction of the *visual* sense, so far the other sensory centres must send their communi-

eating paths not only forward *but also to the other side* of the central nervous system. Translateration, therefore, is merely an extension of the principle of cephalization and quite homologous with it. It depends on the fact (if it is a fact) that the primordial visual centres are functionally heterolateral though structurally homolateral, like all the rest of the then existing nervous system. The translateration of visual stimuli (formation of a reversed image on the retina) in the primitive median eye laid down a functionally heterolateral centre, to which the evolving nervous system responded by building up association centres which were *both functionally and structurally heterolateral*; and the subsequent acquisition of lateral eyes was too late to affect this ground plan, though early enough and widespread enough to conceal from us (*now*) how it came about. This arrangement of the central nervous system represents thus an adaptation and economical response of the central nervous system to the sense organ which is unique in that it transposes its stimuli across the middle line.

Following out the conjectures here put forward with a view to testing their reliability and suggestiveness, we have arrived at the tentative conclusion that the 'crossed' systems of the central nervous system are built up in relation to a functionally crossed visual sensorium, which, however, like all primordial centres, sympathetic or central, is *structurally* homolateral. The pineal eye and the paraphysis represent rudiments of, or regressions to, the primitive condition we postulate. The crossed nervous systems are an adaptation to the optical reversal of images.

We have further suggested that one orbit deviated to the right and the other to the left, so that a serial pair of eyes became a bilaterally symmetrical pair. And as the mesial eyes must have had—as the simplest possible arrangement—one muscle at least on each side, then one muscle of each eye, with its bony origin (orbit), would be carried over to the opposite side as the eyes become bilateral instead of mesial organs. The *whole* oculomotor apparatus, however, is not yet entirely concentrated in the half of the body to which it now belongs; the motor nerve of the transposed muscle still arises from the central nervous system in the side to which this muscle originally belonged. It might be conjectured that the rest of the neuromuscular mechanism is evolved in the side to which the eye now wholly belongs, and largely from the *original* oculomotor apparatus of that side and eye. The trochlearis nerve of the right eye thus represents the innervation of the *left* muscle of that eye when it was median. We might even regard the two oblique muscles, which form a separate group in the fishes, as representing the simple archaic muscular system of the median eye which has come secondarily to belong wholly to one side.

(The function of the original oculomotor nerve would be to deviate

both eyes towards its own side. One branch of each nerve would be carried across the middle line and function would not be greatly disturbed.

The hypothesis here advanced would thus account for :—

1. Certain nervous systems being crossed and others uncrossed.
2. The optical system in certain animals being functionally crossed and structurally uncrossed.

3. The remarkably close correlation between the overlap of visual fields (across the mesial cephalic plane) and the proportion of homolateral connection between hemi-retinæ and cerebral hemispheres. By this adjustment of the chiasma the functional heterolaterality of the optic centres is maintained at the expense of retaining homolateral and heterolateral retinal connections in their just proportion.

4. The unique and remarkable dorsal decussation of the fourth nerve.

But while offering an evolutionary and adaptational interpretation of these highly remarkable arrangements of the central nervous system, it is obvious that, before it is accepted, my theory will require a very great deal of evidential corroboration. A great number of facts from embryology, palæontology and comparative anatomy could be adduced in its support : but for me to do so would be to select the evidence, since I have not thoroughly and systematically studied these topics. In the interests of sound methods, therefore, I must leave the verification or otherwise of this theory to the judgment of others. I should like, however, to deal with two obvious difficulties as much logical as biological in the way of admitting the theory even as a working hypothesis. These are :—

1. If the eyes originated, as here assumed, as mesial diverticula in the roof of the tectum which gradually diverged from the middle line to form bilaterally paired organs, then it is easy enough to understand how their stalks, fusing in the middle line, formed a chiasma similar in plan to the chiasma of man. *But such a chiasma would be dorsal to the neuraxis.* It is difficult even to conceive what course of evolution could bring this chiasma to the ventral aspect of the central canal. Three or four explanations have suggested themselves to me—all artificial and far-fetched. I would prefer to evade the difficulty by suggesting that the present chiasma *is* dorsal in an evolutionary sense, and that the infundibulum develops at the site of the neuropore and thus represents the anterior pole of the neuraxis. The cerebrum with the optic lobes would then be a *dorsal* upgrowth between the forward-stretching optic tracts.

This speculation is probably at variance with ascertained fact, and I include it merely for the sake of presenting a comprehensive theory. For the same reason I will permit myself to indulge in another

free conjecture although, like the above, it is not a corollary of my main thesis.

2. The rudimentary eyes, pineal and paraphyseal, which we find with mesial attachments, are of the invertebrate type. The lateral and frontal eyes which my theory suggests originated in the same way (unless these lateral outgrowths merely usurped the orbital mechanisms originally belonging to the mesial eyes) are of the vertebrate type. It is not perhaps incumbent upon this theory of decussation to explain the substitution of vertebrate for invertebrate eyes, but it is methodologically desirable that it should do so.

The vertebrate eye is inferior to its invertebrate precursor in three respects. First, it must always have a blind spot; second, its nerve fibres and cells must be adapted to permit the passage of light without refracting this or themselves suffering injury; third, the course of development—sealing of choroid fissure, etc.—is one which allows of frequent imperfections and aberrations. It is natural to look for countervailing advantages in this (retinal) type of eye, since the organ has such intrinsic importance and has supplanted the other, and since its possessors have become dominant. No such advantages are obvious. Alternatively we would expect this to represent the overcoming of some evolutionary difficulty from the standpoint of the conception here advanced of the evolution of the visual apparatus. I would suggest the following interpretation of the transition from the invertebrate to the vertebrate type of eye.

The *anlage* of the retina is the extreme dorsal surface of the tectal diverticula. When the latter are thrust out sideways to become lateral paired, instead of median serial, eyes, the retina still develops from the extreme dorsal aspect of the optic vesicle. Probably—in a ventro-dorsally flattened head as in *Limulus*—the optic axes do not at first diverge acutely even when the eyes are quite widely separated. A time will come, however, when the bottom-swimming proto-vertebrate becomes free-swimming and requires lateral and ventral vision more than dorsal vision. *Pari passu* the chiasma shifts cephalad, and the development of the dorsal cephalic nuclei compels a ventral flexion of the anterior end of the central nervous system. The transition from dorsal to ventral eyes may then well be a mutation, the extreme lateral position in a flattened head never being taken by the eyes. The lens rudiment, instead of being an invagination of the dorsolateral ectoderm, is thus an invagination of the ventrolateral ectoderm. But the retinal *anlage* is still the dorsal aspect of the optic vesicle, so that the lens rudiment being applied to the ventral aspect of the vesicle is now in contact with the non-retinal portion of the optic vesicle. The optic cup thus formed with the retinal *anlage* outermost (on the dorsal internal and convex surface), and facing away from the lens instead of towards the lens as

we actually find it, is the vertebrate eye. The choroidal fissure is then a necessary adaptation to secure the central attachment of the optic nerve to the retina. The accompanying diagrams will illustrate the conception (*Fig. 2*).

The collective improbability of all the hypotheses here advanced is very great. Yet, as they are to some extent independent of each other, it is possible enough that some of them may be valid. Even should they be of the thousands of hypotheses Faraday refers to, which have to be raised merely to be rejected, I feel these speculations are worth passing consideration. They correlate and supply a more or

FIG. 2.—Diagrams to illustrate how a decussating oculomotor nerve might arise.

A, diagrammatic cross-section of a median eye.

B, diagrammatic cross-section where the median serial eyes (as in diagram A) have become lateral paired organs by each eye deviating to one side, carrying with it the muscle and distal end of its oculomotor nerve, thus occasioning the decussation of the trochlearis.

A, median plane; B, oculomotor muscles; C, skull; E, eye; N, oculomotor nerve; N₁, decussating trochlearis nerve; N₂, oculomotor nerve that remains uncrossed; O.N., optic nerve; T, tectum.

less unified evolutionary and adaptational interpretation of a number of very important and puzzling morphological features of the optical apparatus and its central nervous connections.

They purport to explain :—

1. Why certain neurone systems are homolateral and others heterolateral, with the consequence that all connections between a system in one group and a system in the other must decussate.
2. The unique decussation of the fourth nerve.
3. The close and remarkable functional adjustment of the chiasma to the optical axes.
4. The relation of mesial serial ocular rudiments to paired lateral eyes.
5. The evolution of the vertebrate eye.

All these remarkable facts are here brought into relation with each other and presented as an adaptation to the unique character of the optical sense organs—namely, that they reverse their stimulus pattern.

Notwithstanding the gravity and unsupported character of the hypotheses involved, and the gaps which nevertheless persist in the theoretical ‘explanation,’ I feel it is justifiable to put these speculations forward. It serves at least to state a problem and to suggest lines of reflection, and brings into one conspectus a group of facts whose relationship is not inherently improbable.