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THE EVOLUTIONARY HISTORY OF EYE MOVEMENTS[1]

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Abstract—The nature of eye movements is discussed from the evolutionary point of view. Their origin lies in the need to keep an object fixed on the retina, not in the need to scan the surroundings. Distinctions are made between egocentric and oculocentric directions in their dependence upon voluntary and involuntary eye movements. The possibility, in Man, of retinal correspondency between two regions of the same eye is discussed.

Résumé—La nature des mouvements des yeux est discutée d'un point de vue évolutionniste. Leur origine provient de la nécessité de conserver la fixité d'un objet sur la rétine, et non du besoin de balayer les environs. On fait la distinction entre les directions égocentrique et oculocentrique, en liaison avec les mouvements volontaires et involontaires des yeux. On discute la possibilité, chez l'homme, d'une correspondance rétinienne entre deux régions du même oeil.

Zusammenfassung—Es wird die Natur der Augenbewegungen vom entwicklungsgeschichtlichen Gesichtspunkt betrachtet. Sie entspringen der Notwendigkeit, Bilder von Sehobjekten auf der Retina zu fixieren, nicht der Notwendigkeit, das Umfeld abzutasten. Es wird unterschieden zwischen egozentrischen und okulozentrischen Richtungen in Abhängigkeit von willkürlichen und unwillkürlichen Augenbewegungen. Ferner wird die Möglichkeit einer retinalen Korrespondenz zwischen zwei Bereichen des nämlichen Auges beim Menschen diskutiert.

OF ALL the questions that may arise about eye movements, probably the least likely one is the simple question: "Why?" Optometrists, ophthalmologists and neuroanatomists seem never to wonder why our eyes should move at all. I am none of these, but a backslid zoologist, with my attention still—from force of habit—upon the evolutionary backgrounds of things. Looking at any biological system, I may wonder about it in several ways; but one of my wonders will always be, how did it come to be as it is—how did it get this way?

Man seems to have to have eye movements. I have a fovea in each retina. With it, I see fine detail in a patch of space as big as three or four full moons. To see this well here and there, I must aim the fovea here and there—and it is more economical to turn an eyeball than a whole head. Again, unless my convergence could be altered I would see most objects double. Here, head movements could serve in place of eye movements only if the head were carried toward or away from the object until the latter was imaged upon both foveas.

Lacking eye movements, then, Man would require to have far more elaborate head-movements, and he would really be better off with one eye than he is with two. But, there are other animals, such as the owls, which have both foveas and binocular vision and yet have no eye movements. On the other hand there are many animals, including most fishes, which have

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[1] Essentially as read before the American Academy of Optometry in its annual meeting; San Francisco, 10–13 December 1960.

neither foveas nor binocular fields of any consequence, and yet have conspicuous ocular motilities. What is the rhyme and reason of all these differences?

If I keep my head and body still and slowly swing my eyes from extreme left to extreme right, I survey a large field which may contain scores or hundreds of objects. If not one of those objects is moving, I do not see anything as moving. The field with its contents is stationary with respect to myself. The image of the field has swept over my retina, but something has kept me from supposing that this connotes a group of objects moving in external space.

Now let me again sweep my eyes from left to right, but this time let me be following the flight of my pet parakeet which has been let out of his cage to play. As the bird moves and my eyes "pursue" it, its images are motionless upon my retinas and yet I perceive the bird to be in motion, with everything else at rest in spite of moving retinal images. Something here has kept me from supposing that a stationary retinal image of a bird connotes a stationary bird.

Lastly, let me observe my playful parakeet while keeping my head and eyes still, fixating something else. The bird's image is not now stationary on the retina, but again I see the bird as a moving object among stationary objects.

Stationary objects, then, may appear stationary both when their retinal images are stationary and when they are moving; and moving objects may appear moving both when their retinal images are moving and when they are stationary. What makes the difference is the matter of whether the eyes themselves are moving or not. The visual movement of an object is really a continuous changing of its direction from the self as a center, its egocentric direction. If I tell my eyes to turn to the right, the potential apparent movement of all stationary objects in the opposite direction at the same angular velocity and through the same angle is interpreted as no movement at all. Egocentric directions stay put. Something about the eye movement keeps equal-and-opposite retinal-image movement from connoting object movement. But whether I tell my eyes to turn or not, any movement of a part of the whole retinal image that is not being caused by what the eyeballs are doing makes me perceive an object changing its egocentric direction, i.e. moving in external space.

For eye movements to be employed in egocentric directionalization, so that I am not deceived as regards what is really moving and what is really stationary, it is not necessary that the eye movement be voluntary. I can fixate an object and slowly shake my head in the gesture of "no", and the object will keep a constant egocentric direction and appear motionless. Yet each swing of my head is accompanied by an opposite swing of the eyeballs in the orbits, which I have not ordered and of which I am unaware. These involuntary "compensatory" eye movements, then, are kept from making me think that the object is oscillating when the eyes are oscillating and the image is fixed upon each retina.

It is quite easy to show that it is the pattern of motor innervations flowing to the oculorotatory muscles, to give the eyeballs particular final postures in the orbits,[2] that gets employed in the process of egocentric directionalization along with the oculocentric direction of the object (which is determined by where on the retina, with respect to the fovea, the object is imaged). Apparently, whenever the eyes are moving because they have been "told to" by

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[2] During the eye movement, until it is completed, its effect upon egocentric direction breaks down or rather is suspended. This is nicely shown by the rhombic distortion undergone by a television image when the gaze is swung across the picture-tube face. As the eye swings, images of successive line-elements build up a rhombus on the retina. If each line were being directionalized correctly during the movement, the whole frame-image would be perceived as a rectangle despite the rhombic shape of the retinal image.

any of their control centers, the resulting movements of retinal images are unconsciously interpreted correctly to mean that the objects are not moving. If, however, we search through the armamentarium of human eye-movement types for a kind which does not in itself correct for retinal-image movement so as to stabilize egocentric directions, we can find one, and only one.

This kind of eye movement, in which a record of the innervations to the muscles is not offered to the mechanism of perceptual egocentric directionalization, is that which arises from stimulation of the semicircular canals. We are provided with a whole family of involuntary, vestibular-reflex eye movements, the value of which is to compensate for head movements whether we are fixating anything or not, or whether indeed our eyes are open or closed.

If I make myself dizzy by spinning on my heel, and then stand still and will my eyes to be still, my whole visual field appears to be swimming around me. My eyes are not still. They are in an unsensed "vestibular nystagmus", with slow strokes initiated from the labyrinths and with fast recovery strokes operated, apparently, from the reticular formation of the midbrain (GERNANDT, 1961). During each slow stroke the movement of my retinal images connotes movement of my whole visual world just because the innervations for these eye movements are unrecorded, unemployable. No provision was ever made, in the evolution of the vertebrate visual system, for their employment to stabilize directions; for it was never to be expected that vestibular eye movements would ever take place in the absence of the head movements for which they regularly compensate.

This very imperfection of the vestibular eye movements, in that they alone fail to provide the essential motor factor in egocentric directionalization (when the head is still), is the key to the whole question of why vertebrates have any eye movements at all in the first place.

Consider this: if human vestibular eye-movement innervations cannot help to keep the stationary environment visually stationary, then subhuman ones never had such a function. Why should it have been lost, if it were ever possessed? And now consider also this: if we go from Man and his relatives downward through the vertebrate subkingdom, to its roots in the lowest fishes and the cyclostomes, we can note the loss of one class of eye movements after another, until the only eye movements left are those initiated from the semi-circular canals.

This is really putting things in the wrong order. What we should say is that the vestibularly-controlled reflex eye movements are historically the oldest of all, with all other kinds of eye-muscle controls and operations accreted to them above the primitive fish level of evolution. Even in Man, the afferent fibers concerned are still of a coarse sort, "indicative of a powerful and anatomically determined rigid connection" (SZENTAGOTHAI, 1961)—quite in keeping with archaicness.

If the original control of the eye muscles was from the labyrinths, then one may say that the resulting movements of the globes must have been the very *raison d'être* of the muscles themselves—in evolution, the oculorotatory muscles came to be required, to impart appropriate movements to the eyes, dictated by the labyrinths. This means, compensatory movements of the eyes as dictated by head movements. Now why should a fish's eyes always have to turn one way whenever his head turns the other? So that the image of the outside world can stand still on the retina for as much of the time as possible. Otherwise—pretending that a fish can think—he would think things to be in motion which were not, and really-moving objects, enemies and foods, would be difficult or impossible to notice and deal with. For neither the fishes nor any other vertebrates have ever found a way, or even needed a way, of letting vestibular eye movements compensate for retinal-image movement to keep egocentric directions constant.

This one big idea, namely that the ancient and original function of the eye muscles was not really to move the eye but rather to hold it still with respect to the environment, can also explain the large mystery of the oblique muscles. A human, born without oblique muscles, would grow up with no need for them at all. There are no essential human eye movements which the recti, with a little practice, could not then carry out perfectly well. But, in the first fishes the obliques were indispensable. It is safe to assume that with the eyeballs originally back-to-back in the head, the obliques originally operated in the plane of the eyeball's equator, and were not co-operative but antagonistic. Let the fish tilt to swim upward or downward to a new level in the water, and the obliques would impart wheel movements to the eyeballs around the optic axes, keeping the retinal images from rotating while the compensatory actions of the recti were keeping the images from sliding on the retinas in any meridian.

These archaic vestibular eye-muscle reflexes, having the function of holding the image of the visual field still upon the retina while the head was moved actively or passively through the water, may be called for short field-holding reflexes. Their continuing operation, even in modern Man, is seen in the slow component of vestibular nystagmus, which will appear in a person with his eyes closed, who is rotated in a swivel chair with changing angular velocity.

Early in fish evolution, it seems, the vestibular reflexes were supplemented by another system of field-holding eye movements instigated by stimulation of the retina itself. The reflex arc for these, beginning at the retina, necessarily traveled through the optic lobes, the "highest" visual centers of the ichthyopsidan brain, which have dwindled to become the relatively inconspicuous superior colliculi in the brains of the mammals and Man. I could speak of "optic-lobe field-holding reflexes" in fishes and amphibians, but they may as well be called "collicular field-holding reflexes"—which is only to anticipate the fate of the optic lobes, and keep us reminded that even the highest vertebrates have these same reflexes.

It may be wondered why both vestibular and retino-collicular field-holding systems should co-exist. The vestibular system is necessarily crude, and entirely too crude for an animal which has visual consciousness and a fovea or area centralis. But, it is valuable as a coarse approximator. Fine adjustments of intraorbital eye posture are better made by the collicular system, operated as it is by the visual stimuli themselves. In the view of COGAN (1961), a "retinal contribution to ocular motor control . . . probably plays a role served elsewhere by proprioceptive end organs". Specifically here, the collicular field-holding reflex precisionizes the work of the older, cruder, vestibular field-holding reflex.[3]

In the shaking of the head in the gesture of "no", the steadiness of egocentric object-directions would not be what it is if the only compensatory eye movements were the vestibular. On the other hand the reflexes operated over the retino-collicular path help to hold the field steady without necessity of fixation of anything. Even in a "blank stare" the "no" gesture, at any reasonable velocity, causes no subjective oscillation of objects.

The operation of the collicular field-holding eye-movement system is well seen in the laboratory phenomenon of "optokinetic nystagmus". This is elicited by confining an animal to a small platform surrounded by a large cylinder bearing vertical stripes, alternately black

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[3] Further precisionization is probably applied to *all* eye-movement circuits through the colliculus, by feedback from the eye-muscle proprioceptors. At least, their messages travel no higher than to the colliculus, for they do not reach the cortex to participate in the determination of egocentric directions.

and white, with this cylinder set into slow rotation. The animal's eyes turn, following the moving stripes (sometimes as far as they mechanically can) and then snap back to their primary positions (sometimes overshooting), to repeat indefinitely these slow stripe-holding movements and quick returns. This is a nystagmus by definition, but there is nothing pathological about it.

The fast return-movements of the optokinetic nystagmus imply that when in a moving animal the eye or head has turned as far as it can and the image does then begin to move (undesirably) on the retina, the saccadic snap of the eye back to the primary position will momentarily blur vision completely. The movement of the image over the retina, as the eye "centers itself", is so very fast that no illusion of object-movement can develop. Here, then, even in the lowest fishes, we see a good reason for saccadic eye movements to be as quick as they notoriously are.

Optokinetic nystagmus has been found in every mobile-eyed vertebrate in which it has been looked for. It can be made to supplement the vestibular field-holding reflex if the animal's support is rotated one way and the striped cylinder the other; or, with the same apparatus and animal, vestibular nystagmic eye movements can be isolated by turning the taboret alone with the illumination of the cylinder shut off. The relative "strengths" of the two nystagmi can be measured by playing one off against the other (REINECKE, 1961).

The first investigator to perceive the field-holding function of the slow phase of optokinetic nystagmus was perhaps BRECHER (1936). With a particularly large cylinder, he was able to elicit the response in the rabbit. Others had failed, since this animal perceives an ordinary-sized striped cylinder not as a moving environment but as an object-in-motion—to which its response is to "freeze", with all eye movement inhibited. At the same time TER BRAAK (1936) was using the term "fixation without attention" for the field-holding following of a striped cylinder where the eyes turn in a blank stare. Such "stare nystagmus" is the only kind possible for animals with homogeneous retinas; but a "look nystagmus" is also possible when there is a fovea with which a single object can be pursued across a fixed background.

Not surprisingly, optokinetic stare nystagmus persists in the absence of the visual cortex in rabbits, cats, dogs and monkeys (TER BRAAK, 1936; PASIK, PASIK and KRIEGER, 1959; REINECKE, 1961). Stare nystagmus is thus indicated to be merely a repeated execution of the retino-collicular field-holding reflex. Look nystagmus, which requires the integrity of the visual cortex in monkeys (PASIK *et al.*, 1959) and apparently in Man, where it may be the only form of optokinetic nystagmus (REINECKE, 1961), appears on the other hand to be a repeated execution of the pursuit reflex (*v.i.*).

In the higher vertebrates where there is a well-developed visual cortex, there are eye-movement reflexes whose arcs go via the cortex, traveling the course: retina → lateral geniculate → Area 17 cortex → colliculus → nn. NN. III–IV–VI. On the assumption that since these reflexes are accompanied by visual awareness of the stimuli, some or all of them may really be set off at the cortex by aspects of the conscious or preconscious image, the cortically mediated reflexes have long been called "psycho-optic" reflexes. Included, certainly, are "fixation" and "pursuit" reflexes; and there is no good reason not to call the reflex component of convergence "psycho-optic" (and the accommodation reflex as well, if its arc does include Area 17). The obvious motor elements in Area 17 for some or all of these arcs are the cells of Meynert, whose axons have been traced downward alongside the optic radiations, into the midbrain and to the superior colliculus and the oculomotor complex (METTLER, 1961).

The fixation reflex, which operates to slide the fovea underneath the retinal image of a new, initially peripheral, attention-taking stimulus, is prehensive. Once fixation is attained, it is maintained by a different reflex mechanism. This, we may call the "pursuit reflex" if the fixated object and/or the organism is in motion; but the fixation-maintaining mechanism is the same if the object is stationary. The drifting and saccadic eye movements associated with the physiological nystagmus represent the nutation of the pursuit-reflex system in its aspect as a servo mechanism. As mentioned above, the slow phase of the "look" type of optokinetic nystagmus seems only to be a laboratory version of the pursuit reflex, operating for whichever stripe happens to be in the fovea at the end of a quick "return" phase.

These mammalian psycho-optic reflexes are of course of relatively recent origin. Dealing with them, for best understanding, in proximity to the field-holding reflexes has taken us away from the true chronology. We must return to the fishes, where, if we can judge by the situations in existing forms, then following the evolution of vestibular and collicular field-holding movements, the next kind of eye movement to appear historically was the voluntary kind. This is not to say that once voluntary eye movements came along in a few (not many) fishes, they came to stay. They have assuredly appeared and disappeared again and again, and each time they have been re-invented they may have employed new or different parts of the central nervous system. We know a good deal about the control of voluntary movements in Man—but some essential parts of the human control system are not even present in the brain of any fish.

If we wonder why some vertebrates should move their eyes at will and others not, a logical first guess is that the amount of space visible at one time may have a lot to do with it. An animal with a broad visual field might not need to turn the eyes to shift attention from one object to another, whereas a creature with anything approaching "tube vision" would seem to have to do so. This, in fact, is found to be not so. Frogs and prairie-dogs exhibit no voluntary eye movements, whereas lizards and some fishes do, and yet all of these have eyes back to back, and extensive corneas and retinas, and can "see everything at once".

One has to look inside various eyeballs for the answer to voluntary eye movements. They occur only in vertebrates which have a fovea, or at least a relatively small retinal area of superior resolving power whether there is a foveal pit in it or not. Any such vertebrate has an incentive to aim the eye, in order to aim the fovea at an object of attention, and will be found to have developed such aiming as a "voluntary" act.

The fovea, and voluntary eye movement, are not monopolies of the highest animals. The combination occurs in forms as low as the bony fishes, where the presence of an egg-shaped pupil always suggests that a temporal fovea is present, and the eyes may be seen to move even when the fish is motionless among motionless objects.

In Man, voluntary eye movements are instigated variously, but the one part of the cortex from which the "commands" start downward to the nuclear muscle-control stations is Area 8 $\alpha\,\beta\,\delta$ in the second frontal gyrus. At each point, in this area, one may conceive a sort of push-button which will operate all of the eye muscles so as to put the eyeball in a specific secondary posture in the orbit. Whenever one of these buttons is pressed, a signal must also travel back to the occipital cortex to inhibit temporarily those psycho-optic reflexes which would interfere with the execution of the voluntary eye movement. We have no inkling as to how this intricate system evolved, for the pathways for voluntary eye movements have not been experimentally searched out in any non-primates.

In Man and other primates, several phenomena are clustered which can all be seen to be entangled with the evolutionary history of eye movements. Voluntary eye movements, tied to a fovea, have been mentioned. It remains to be mentioned and emphasized that in Man these movements are binocularly co-ordinated, or conjugate (whereas below the mammals only reflex eye movements are conjugate). Man and his close cousins also exhibit disjunctive eye movements—i.e. convergence and changes thereof—and have a correspondency phenomenon, and have a maximal percentage of non-decussating optic-nerve fibers.

The big question about the higher evolution of eye movements is, in what historical sequence may these characteristics have appeared—semi-decussation of the optic nerves, binocular correspondency, conjugation of all eye movements, and convergence interlocked with the conjugation? We may or may not be able to develop a satisfying answer, according to whether we can see, or not, which of these characteristics were necessary antecedents of others, which so to say are causes or results of others, and which if any may really be meaningless in relation to the others. The big question is really a bundle of questions.

To begin to get answers, we must turn away from Man and look at the group just below the mammals: the reptiles. The lizards will do nicely; and among the lizards, the African chameleon is most popular of all for the purpose of a discussion anything like this one.

The chameleon's very extensive eye movements, and their usual voluntariness, and their total lack of binocular conjugation, are all made conveniently conspicuous by the fact that the creature's huge eye bulges prominently and has the lids permanently fused with its surface, leaving only a small round aperture opposite the pupil. As the chameleon's eyes swivel about, "turret-like" is the term that occurs to any observer.

The chameleon has a central fovea, of a quality almost without equal, even among raptorial birds. That he should have voluntary eye movements is no surprise. That he can be looking upward or forward with one eye, while looking sideward or backward with the other, is a surprise—to any human-vision-minded person. How can the chameleon avoid diplopia?

Clearly, the chameleon escapes diplopia because with each eye he sees any object in the direction in which it is. This statement is deceptively simple. Contrast the situation in Man: If in a normal human, all extraocular muscles should be disconnected and the eyeballs passively turned so as to aim at different objects in different directions, whatever two objects were imaged upon the respective foveas would have to be seen in a single egocentric direction. This might (but need not) be the true direction of one of the foveal objects; but it could not simultaneously be the true direction of the other. The single perceived direction of both objects would be determined by what the brain supposed to be the common, conjugated aim of both visual axes—i.e. by the innervations going out to the disconnected muscles.

The big difference, here, is caused by the fact that Man has a binocular correspondency phenomenon whereas the chameleon does not. Man inevitably "projects" two foveal images to one place in space, whether they are images of the same object, of two identical objects, or of two very different objects.[4]

Consider, now, one chameleon eye. If it is aimed leftward and a fly is imaged on its fovea, the fly is seen to the left. If the eye is aimed upward and there again happens to be a fly imaged on its fovea, that fly is seen overhead. Clearly, the innervation-pattern of the extraocular muscles must solely determine the egocentric direction in which a foveal object will be perceived to lie. The directions of extrafoveal objects will then be to the left, to the right, above, or below the fixated object according to where their retinal images lie with

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[4] It may seem very remarkable that the lowly chameleon should be able to attend to two separate foveal objects at once. By bringing the palm of one hand up to the end of the nose, a human can see for himself what this problem may be like.

respect to the fovea. The chameleon must gain the same knowledge that we do, as to whether an object is moving or not (when its retinal image may be moving or not), from the interplay of eye-muscle innervations and retinal-image locations. Indeed, this must be true also even for some of the fishes—those few which have a fovea and have voluntary monocular movements.

If the chameleon's two eyes are so aimed that nothing imaged on one retina is also imaged on the other, he sees two regions of external space which do not even overlap, let alone superimpose. For a normal man, the two monocular fields are seen inextricably superimposed not because they contain about the same set of objects, but because of the correspondency phenomenon, which the chameleon does not have. Let the chameleon now swing both eyes forward, and as he does so object after object becomes imaged on both retinas. But any such object is seen "where it really is" with each eye, and continuously so, even while the eyes are still converging to bring some particular object on to both foveas. If an object is seen in one place with both eyes no matter where it is imaged on either retina, then for the chameleon "binocular single vision" is not only possible but inevitable, and this is because there is no correspondency. It begins to look as though the possibility of diplopia is a price the human has to pay for having binocular correspondency.[5]

When the chameleon is seeing an object ahead of him binocularly, bifoveally, how does it look to him? This is something we cannot know; we can only guess. But if the chameleon has no corresponding points such that similar images lying on them are binocularly "fused", then it is hard to see how he can have any fusions. Binocular singleness of direction, alone, is not tantamount to fusion. If the chameleon's foveal images of a single object are not fused, then I cannot believe that he perceives the object with stereoscopic three-dimensionality, "solidness". Fortunately for the chameleon, his interpupillary distance is so small that his left- and right-eyed images are not so different from each other that their superposition creates a mess, as it would for a human who could neither fuse both images nor suppress one of them.

The chameleon, then, can secure binocular single vision, but can have neither genuine fusion (with or without stereoscopy) nor diplopia. We can have fusion, and we can therefore have diplopia, and we can have both because we have correspondency. It is also safe to say that without correspondency we would not have a stereoscopic appearance of a fused binocular object.

Now it cannot be asserted that stereoscopic perception has been the goal of all vertebrates which ever "frontalized" the lateral eyes and secured a large binocular field. From the fishes to the mammals inclusive, there are scattered small groups and single species which are strongly binocular, either by reason of permanent anatomical arrangements or (as with the chameleon) extensive ocular motility. But a deep-sea fish with parallel optic axes and a pure-rod retina assuredly does not see stereoscopically. There is nothing for him to see but the dots of bioluminescence on the bodies of other deep-sea organisms. His receptor-to-conductor ratio is so huge that his imagery is, rather, shadowry. In the first place, if a fish has no consciousness, how could he benefit from genuine fusion underlying stereoscopic perception, as compared with mere superposition of images with singleness of direction?

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[5] There has been at least one "human chameleon", a patient of Dr. Meredith Morgan's named Ted Chapman. Chapman, for a period, had no correspondency phenomenon and did not see his monocular fields superimposed. Being an exotrope, he never had diplopia. He could drive a milk truck down the street, and could be watching where he was going with one eye while reading the house numbers with the other, without the least confusion.

In any group of vertebrates, swinging the eyes physiologically or anatomically forward in the head entails a sacrifice of ability to see possible enemies to the rear. What is gained, that warrants this sacrifice? For the primates, we may say that it is stereoscopic perception that is gained, conferring fine depth-discrimination and the ability to apprehend instantly the three-dimensional shape of an object never seen before. This is important to any animal with curious hands—and the monkeys are compulsive "manipulators". But if binocularity does not always mean that there is correspondency, and if without correspondency there can be no fusion and no stereoscopy, then the binocular sub-mammals have gained other things in exchange for "periscopy". In forms which are active in feeble illuminations, binocular brightness summation may be the reward. In such a form as the chameleon, range-finding by triangulation with two eyes may be much more accurate than distance-estimation in monocular vision, at least for unfamiliar objects whose true sizes are not well known to the chameleon.

By evolving binocular correspondency the primates, at least, gained stereoscopic perception along with other aspects of binocular sensory fusion which do not demand correspondency as a prerequisite (e.g. singleness of the object, *per se*). But in order to maintain stereoscopic vision continuously, Man and the other primates are required to have a class of eye movements not needed, and not exhibited, by other groups of vertebrates. These are the disjunctive movements, i.e. convergence and changes of convergence (with continuous conjugation).

When we say that the monkeys, apes and Man possess fully co-ordinated binocular eye movements and that lower vertebrates do not, what we really mean is that the primates uniquely possess co-ordinated disjunctive movements. In other vertebrates all reflex, involuntary, movements are binocularly conjugated as thoroughly as they are in primates. But if a sub-mammal has foveas and performs voluntary movements, these are not co-ordinated and the fact is conspicuous. In primates, even voluntary movements are binocularly co-ordinated, but it is the continuous maintenance of appropriate convergence upon the object of attention that characterizes—nay, constitutes—this final perfection of binocular co-ordination.

It is probably not worth while to speculate as regards which of the four classical components of convergence (accommodative, reflex, proximal, tonic) evolved last or next-to-last. Certainly tonic convergence must have evolved early if not initially. But the convergence reflex must also be ancient in primate history. I submit that reflex convergence was necessary as soon as binocular correspondence was invented, for unless the monocular images were automatically kept upon corresponding spots (within the leeway provided by Panum's areas), the stereoscopic image would break up into a horrid, uninterpretable, diplopic mess and all advantage of binocularity would be lost.

The occurrence of diplopia is most conspicuous, to us as practitioners, as a clinical complaint—which comes loudest from a non-comitant squinter. I suggested above that diplopia may appear to be a threat held over the human binocular system, a potential price paid for correspondency and stereoscopy, to be exacted whenever the oculomotor system slips into sloppy operation. A second, deeper, thought reveals that diplopia is actually essential and indispensable—if it triggers the convergence reflex that maintains fusion. A chameleon cannot have diplopia, and for him this is a good thing since diplopia could do his vision nothing but harm. A man can have diplopia (since he has correspondency), and for him this is a good thing, for diplopia sets off a mechanism to eliminate itself, and this insures correspondent imagery, fusion with stereoscopy, and the most rewarding kind of visual perception.

At this point we can summarize the inter-relationships of most of the advanced features of human binocularity, thus: With a correspondency system at work, there can be both sensory fusion and diplopia. With sensory fusion occurring, there can be—and is—stereoscopic perception. With stereoscopic perception attainable, there needs to be—and there is—disjunctive eye movement with binocularly co-ordinated control. This co-ordination of convergence is handed over to a reflex system, for the operation of which the slightest diplopia is a loud signal.

The one thing whose place in this situation is not at all clear is the semi-decussation of the optic nerves. Corresponding points in the left halves or the right halves of the two human retinas project to a single point in the left visual cortex or the right visual cortex. This situation looks like an underlying basis for binocular fusion, with stereoscopy and so on. It looks like a prerequisite for the correspondency phenomenon itself. Why are points in two retinas correspondent, if it is not because those points are brought together (courtesy of semi-decussation) at one point in the cortex? How could monocular images be seen not just superposed but fused, integrated, if it were not for semi-decussation?

The idea that there must be semi-decussation of the optic nerves at the chiasma occurred to more than one early scientist, or natural philosopher, long before the actual existence of semi-decussation was ever demonstrated anatomically. Correspondency, stereoscopy, binocular singleness of direction and so on, seemed to demand such a basis.

Two considerations spoil this picture. Firstly, there are great numbers of animals with semi-decussated optic nerves which have such low visual acuity that they assuredly do not have stereoscopically "solid" percepts and hence have no clear incentive for semi-decussation, if this serves to create correspondency and to enable fusion. Secondly, there is a rare situation in human vision in which a correspondency phenomenon and sensory fusion of two retinal images into one percept exist with respect to monocular vision, where it cannot possibly be said that these phenomena have semi-decussation of the optic nerves as a prerequisite (*v.i.*).

With the exception of a couple of reptiles, all vertebrates other than the mammals have each optic nerve completely crossing over to become the contralateral optic tract. Among the mammals, on the other hand, a proportion of the fibers in each optic nerve pass into the ipsilateral optic tract. Up to one-third of all fibers behave thus, in carnivores and primates. A few fibers are non-decussating even in rabbits. Only in completely monocular forms, such as whales and guinea-pigs, is the decussation total. The percentage of non-decussating fibers goes roughly with the extent to which the eyes aim frontally rather than laterally ("Law of Newton, Müller and Gudden").

It would appear that the habit of semi-decussation was adopted at the beginning of mammalian evolution. But it could have done nothing, in any sensory way, for the nocturnal pure-rod low-acuity early mammals or for the bats and rats that came along later. Not for a long time were there any mammals with visual acuity good enough for them to have, at the cortical level, right- and left-eyed images with those slight but firm and sharply recorded differences that make for stereoscopic perception. Semi-decussation may have conferred correspondency upon the first mammals but, if so, they certainly did not know what to do with it. Initially it was as meaningless as is decussation *per se*, which is scattered all over the central nervous system, but makes no real sense anywhere.

If correspondency can be found to exist without regard to whether the optic nerves are semi-decussated or not, it cannot be argued that the nerves had to become partially decussated before correspondency could evolve. The correspondency phenomenon exists when simultaneous activation of separate retinal areas by compatible stimuli leads to a unitary percept which may be different from either percept evoked from one of the areas by one of the stimuli. This definition covers the binocular correspondency so familiar to us in our own vision. It also embraces the correspondency that can exist between pairs of areas within a single retina.

This monocular correspondency phenomenon can be demonstrated in cases of monocular diplopia which do not have an objective optical cause—perhaps in every such case, although it has been looked for, and studied thoroughly, only in three. The first of these was described by BIELSCHOWSKY (1898). The patient, a former squinter, had had one eye removed. For the remaining eye, any object was seen in two directions separated by a fixed angle. Two objects could be laid before this eye, separated by that angle, and the patient would see one image of one object fused with one image of the other object, although the only optical images involved were now falling on separate retinal areas.

In the other two cases, that of PURDY (1934) and that of MORGAN (1955), the patients were also squinters, but each had two systems of harmonious anomalous correspondence so that there was monocular diplopia with either eye and diplopia in binocular vision, with the two images always separated by the angle of squint. The kind of study pioneered by Bielschowsky was repeated and extended by Purdy and by Morgan. The subjects, with one eye covered, would see three images when viewing a pair of objects separated by the angle of squint. When for example the objects were different in color the middle, "fused" image was seen with fusion of the colors, or rivalry, or with Henning effect.

One may say that in these cases, appropriate stimulation of separate areas in one retina imparts a single direction, a single identity, and a new perceptual character to the one "thing" seen. In short, those retinal areas are just as correspondent as if they were in separate eyeballs. The correspondency phenomenon can thus exist for one eye only, and correspondency *per se* could have been evolved by the best-seeing mammals whether their ancestors had given them partially decussated optic nerves or not.

What, then, is partial decussation basically good for? It is older than is stereoscopic perception by diurnal, high-acuity mammals. It is not essential for correspondency *per se* nor for fusion *per se*. The only value I can see for it is in relation to the smooth and prompt co-ordination of binocular eye movements, disjunctive ones in particular. Even if partial decussation is historically older than diplopia, and even if binocular correspondency and diplopia might have evolved without it, partial decussation does at least put the entire substrate of the diplopia of almost every object in one cerebral hemisphere. The sensitivity of the convergence reflex system to small extents of diplopia must then be greater, with the diplopia the more promptly and more nearly continuously eliminated, than it could be if the physiological left- and right-eyed cortical images had always to communicate between hemispheres in order to agree as to what "fusion movements" were needed at the moment.

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