THE PERCEPTIONS AND MECHANISMS OF VESTIBULAR EQUILIBRATION

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The last survey of experimental studies on the psychological functions related to the semicircular canals was limited, in large measure, to problems that were distinctively sensory and perceptual (41). It has seemed advisable to broaden the scope of the present survey so as to include a fair sampling of the physiological and anatomical studies that may have a bearing upon or contribute to the psychological functions. We shall also consider some of the findings of the clinical laboratories in so far as they seem to relate to psychological and behavior problems of balance. We shall report, in turn, upon (i) general surveys, (ii) apparatus and methods of stimulating vestibular reactions, (iii) perceptual functions related to the vestibule, (iv) modes of response, (v) anatomy and physiology, and (vi) clinical and pathological material.

(i) *General Surveys.*—The period under review has brought forth several general surveys of labyrinthine functions somewhat better in quality and less prejudiced than were one or two of those which appeared shortly after the war. Camis (16), for example, has written a most comprehensive survey of the entire field. He has made use of a bibliography of more than 800 titles and 65 figures serve admirably to clarify the discussion. The book begins with an account of vestibular work up to and including Flourens. A chapter on the anatomy and physiology of the labyrinth, together with a general survey of the development of the labyrinth through the animal series, appears to be well done. Camis is to be thanked for a faithful review of surgical methods of studying the labyrinth. He is fully aware of the tremendous difficulties which have attended this method of approach and his whole discussion can hardly help but lead to a refinement in technique. The method of surgical insult will continue to be of value only in so far as its attack on the labyrinth can be confined and localized. Camis' review includes an appraisal of the effects of partial and complete destruction of the labyrinth, an account of the effects of localized stimulation of various portions of the inner ear, some discussion of the relation between the labyrinth and sense perception, and of the general nervous connections between the labyrinth and other parts of the organism, especially the eye and the autonomic system. The survey is concluded with the argument that the vestibular apparatus is probably a collection of receptors which have a number of different reflex functions. Not all of these functions have to do with actual movement. On the contrary, they are concerned in the maintenance of normal posture and in the origin of such experiences as vertigo, nausea, and the like.

A short but highly adequate survey of the rotational method and of the so-called practice effect has been made by Holsopple (53). The bibliography is useful. In a study of the relation between the ear and the origin of language and writing, Tullio (124) argues for the dependence of certain types of perception upon utricular structures. It is assumed, for example, that the perception of pure tones and clangs is mediated by the cochlea, but that noises are perceived with the aid of other structures. It is intimated that the perception of tonal direction may be mediated by the semicircular canals. Baldenweck's (2) survey of the vestibular functions is written largely for medical students. On the whole, the study is competently done and useful for beginners. It gives a rather useful survey of the anatomy and physiology of the semicircular canals, a fairly penetrating description of various kinds of nystagmus, a somewhat studied classification of modes of stimulating the vestibular functions, and a brief excursion into the clinical field.

Of less general significance are Thornval's experimental studies, a series of five lectures by McNally, and a review of the clinical material by Demetriades (24). Thornval (119) reviews a good many different facts primarily for the sake of furnishing a proper perspective in which to place his own experimental work. This consists largely of a fresh determination of familiar principles. McNally (78, 79, 80) is lecturing primarily upon the anatomy and physiology of the inner ear. His papers, especially the second and third, afford a fairly good introduction to vestibular problems.

Of the many anonymous or secretarial reports of otological congresses in France, Germany, and Italy, we shall mention only one (1). Twenty of the twenty-nine papers read before a French society deal with nystagmus and its clinical application. The papers discuss, for the most part, methods of producing nystagmus, the distinction between centrally and peripherally aroused eye movements, the importance of a careful study of nystagmus as an aid to the diagnosis of disturbances in the labyrinth and in the central nervous system (after the fashion of Bárány) because of the light they may throw on the localization of cerebral abscesses and tumors.

(ii) *Apparatus and Methods.*—The period of research under review has seen a continued improvement in apparatus and much refinement in method. The interest in vestibular problems created by the war made it absolutely imperative that various forms of stimulating the vestibular receptors be refined to such an extent that a nearer approach to a one-to-one correspondence between stimulus and effect might be achieved. Definite progress in this direction is being made. On the side of apparatus, Dallenbach (**23**) describes a rotation table made out of parts of used automobiles. The apparatus is inexpensive but highly stable and suitable, therefore, for a variety of experiments. Zubizarreta (**132**) has constructed a bronze model of the semicircular canals as an aid to clinical observations. Cords (**18**) and Ohm (**95**) have fallen into an argument concerning methods of studying eye movement. At the end of a review and criticism of mechanical devices for measuring eye movement, Cords asserts that high precision in the study of eye movements is to be obtained only by optical methods. Ohm replies, partly, by way of a history of methods of measuring eye movements and, partly, by a defense of his own methods which are largely mechanical. In a general article on nystagmus Lebensohn (**70**) reviews briefly current research, mostly clinical, on eye movement and makes a small contribution to nomenclature. The method of anchoring a mirror over the eye has been adopted by Meyers (**82**) in order to obtain differential records of eye movements produced by winks, tremors of the eyelids, pulsation, head movements, and fatigue. Meyers reports that each of these eye movements can be distinguished from nystagmic movements. He reports further that objective records can be got indicative of pathologically induced nystagmus which differ significantly from normal nystagmus movements. No one, however, has as yet excelled Dodge and his students in these techniques (**25**). Fox and Dodge (**38**) describe an apparatus for measuring the contraction and relaxation of individual eye muscles. It was found that fixation of the fundus orbiti was absolutely essential if proper control of the eye muscles was to be achieved. Under these conditions reciprocal innervation of the inferior and superior recti appeared when the subjects were rotated around their longitudinal axis. Under rotation around the bi-temporal axis, analogous facts were gained save that more irregularities appeared. Somewhat similar studies had already been done by de Nó (88, 89) with negative results; but Fox and Dodge are inclined to suspect that these negative results were due to defective technique. The application of action current measurements has been attempted with considerable success by Meyers (82). The electrodes of the electrocardiograph were attached to the temples and graphic records of the action currents of the eye muscles in voluntary and nystagmic eye movements were obtained. Each type of nystagmus was found to give a characteristic record in which the slow and quick components were easily distinguished. Meyers concludes from his study that the quick component is due to active contractions of the antagonistics of the muscles producing the slow component. Steinhausen (113) appears to have found a new method for observing directly the physical events in the ampullae. It would seem that this method ought to be further examined partly because of the assertion that currents in the endolymph are said to cause actual movement of the cupula. This has been one of the long-standing problems of vestibular excitation.

All of the classical methods of stimulating the vestibular apparatus still continue in use but each has been surrounded by more adequate control. Most experimenters are more keenly aware than they were of the difficulties involved in localizing the effects, say, of surgical, galvanic, or caloric techniques and this very awareness has contributed in no small measure to a better type of experimentation. These observations are true, in particular, of the surgical method. Nylén (91), for example, reports that extirpation of various parts of the labyrinth is always accompanied by hemorrhage in nearby regions. He would argue, therefore, that nystagmus may be due to these pathological changes as well as to direct stimulation, especially when a change in the position of the head alters the pressure in the labyrinth. As we shall see, pressure phenomena have enjoyed a revival of interest. Benjamins and Huizinga (9, 10) continue their series of studies on the pigeon. Removal of the pars superior seemed to have the same effect as removing the entire labyrinth save that rotary eye movements were not disturbed. Removal of the pars inferior, however, was accompanied by disturbances of rotary movements of the eyes. These investigators concluded, therefore, that the pars inferior must be somewhat restricted in its functions. Groebbels (42, 43, 44, 45, 46), likewise, continues his long series of studies on pigeons. He has become, without doubt, one of the most competent users of this technique. A modification of the surgical method has been used by Rizzolo (103). The study was made on ten dogfish (Galeus Canus).

Bilateral sectioning of the olfactory tracts and the optic nerves was effected in conjunction with bilateral destruction of the labyrinths. The latter alone seemed to cause disturbances of equilibrium.

Galvanic methods of stimulating the canals have been used freely by Huizinga and Dohlman. In a series of experiments on the head and eye movements induced by galvanic stimulation of the ear, of pigeons, Huizinga (**56, 57, 58**) confirms results already obtained by Jensen. Although the reaction to galvanic stimulation was nearly normal after extirpation of the labyrinth, it gradually diminished until only a weak reaction resulted from the intense stimulation. This fact, together with the fact that the reaction vanished almost entirely after a period of time, was explained by the discovery that the eighth nerve and Scarpa's ganglion were found to have degenerated. Further studies on the extirpation of this ganglion and successive extirpations after long intervals of the one labyrinth and then the other led Huizinga to conclude that "the galvanic reaction is normally aroused by stimulating the vestibular nerve and especially its peripheral parts." The first half of Dohlman's study (**26**) is devoted to an historical review of the galvanic method. The review appears to be competent and furnishes a good introduction to this method. The review is summarized in such a way as to say that, under normal conditions, the passing of a galvanic current through the labyrinth results in nystagmus in the direction of the current and a tendency to fall to the opposite side. A period of stimulation is accompanied by a feeling of dizziness. In contrast to early investigators (Hitzig, Strehl, and Erb), who maintained that these results were due to a direct stimulation of the brain, and in contrast to Breuer, Jensen, and Bard, who concluded that they were due to stimulation of receptors in the labyrinth, Dohlman argues that the reaction is due to direct stimulation of the vestibular nerve. This argument is based on the proposition that reactions to a galvanic stimulation may occur after the destruction of the labyrinth. In support of his argument, Dohlman (**26**) turns to his own experiments. He concludes (1) that the galvanic reaction has no significance for judgments about the function of the peripheral labyrinth or of the sensory epithelium, (2) that the galvanic reaction is mediated in the vestibular ganglia, an interpretation which is taken to mean that ganglionic cells capable of such functions reside in this structure, (3) that the labyrinth must exert a genuine tonic effect since the falling reaction can be produced after the removal of the labyrinths by destroying the vestibular ganglia on one side, and (4) that modification of tonus in eye reflexes after injury to the vestibule implies a modification of the galvanic reaction by means of persistent vestibular reflexes. A similar result was obtained from rabbits by Dohlman and Engvall (27). Blohmke (14) followed faradic excitation of the brain stem with histological examinations which showed that the point of application of the stimulus was not truly superficial but penetrated much more deeply to the brain stem. That coördinating tissue rather than a motor nucleus was affected seemed probable in the light of the fact that there was a distinct latent nystagmus.

Caloric methods of stimulation have not seen as much improvement as have the other methods. There has been, however, an attempt to apply the method to new variations in the type of phenomena studied. In an earlier work Leise (72) had shown that a minimal effect of cold stimulation applied to the lower ear was produced when the head was inclined about 30 degrees toward the horizontal. In a newer study (73) the same investigator shows that rinsing the ear with cold water has no effect upon the nystagmus elicited from the other ear by warm water. He concludes, therefore, that the cause of the inhibition of nystagmus to be observed under strong stimulation in the caloric test is to be sought not in the effect of the cold upon the auditory nerve but in a sensory labyrinth effect in the form of vestibular over-stimulation. Schmaltz (107) maintains that the streaming movements in the endolymph after thermal stimulation have a negative acceleration until a zero point is reached, after which there is a compensatory streaming in the opposite direction. He finds a significant correlation between the rate of movement of the endolymph current and the observable responses described by Fischer and Veits (33). Errecart, also (29), finds a relation between the direction of the endolymph currents under caloric stimulation and the resulting nystagmus. In a review of a previous work an attempt was made to correlate the findings of such clinicians as Hofer and Meyer, Bárány, Brünings, and Kobrok. The paper is for the most part an attempt to validate the clinical value of the caloric and rotatory tests. A similar summary and appraisal of research on caloric stimulation is given by Veits (125). Confirmation of the observation that the position of the head is highly important for the nature of the equilibratory responses under caloric stimulation is furnished by Fischer and Veits (33). The character of the responses are determined by the plane of inclination of the head preceding irrigation. For cold irrigation the responses are opposite in direction to the antecedent head movement and for warm irrigation the head movement is in the same direction. In the median plane, the duration of the responses is found to be proportional to the sine of the angle of inclination with a maximum at 90°. In the sagittal plane, maxima are found at 45° but some variable factors obscure these latter facts. It is noted, for example, that the duration and direction of the equilibratory responses are related to the interval between inclination and caloric stimulation. Some of these interpretations appear to stand in contrast with interpretations made by Bárány (**3**). This is effected through a description of the conflicts that may obtain in the vestibular apparatus as a result of such factors as the inclination of the head during warm or cold water flushing in one or both ears. Any combination of these factors will have a determinable effect, but some of the effects may be prepotent over others. It is essential, therefore, in any caloric study, to describe not only the observable responses but to take account of the dominance which one set of circumstances may have over another set.

Rotational methods of exciting the vestibular mechanisms have long since passed into medical practice along with the caloric and galvanic methods but in spite of the critical work of Dodge and others not much improvement has been effected in them. Errecart (**28**) has reviewed the whole matter from the clinical point of view. Such clinical aids as the topolabyrinthograph, a device for determining the position of the horizontal canals, the Bartels glass for controlling convergence and fixation of vision, and the like, are critically examined. Support is given to the traditional belief that a reaction of less than fifteen seconds or of more than forty seconds is indicative of pathological conditions. From the clinical side the rotation method receives favorable criticism also from Ohm (**94**, **97**). Tiumjanzeff (**120**) has used a slight modification of the method with pigeons. He finds that rotation with the bill toward the periphery induces greater nystagmus than when it points toward the center. Terazawa (**116**) used the method of rotation in studying the deaf-mutes at the Tokyo Deaf-Mute School. Using a method of rotation perfected by Bartels, de Nó (**89**) studied the oculo-motor reflexes of dogs. The experiments were made with the animal's head in the normal position. Three types of reflexes were found, viz., (1) nystagmus, (2) a tonic reflex resulting from centrifugal force, and (3) a quick contraction occurring at the beginning and end of a rotation. It was possible to isolate each of these responses since (a) when the head was in the normal position and the rotation was about a vertical axis, nystagmus did not occur in the vertical and oblique muscles. The resultant reflexes in these muscles are, therefore, a combination of the second and third types. (b) If the animal is turned slowly with constant velocity the first and third reflexes finally die away, leaving only a second. (c) The second reflex, a response to centrifugal force, is eliminated by locating the axis of rotation between the ears. (d) The first and third reflexes occur at the cessation of rotation as well as at the beginning. The nystagmus, however, differs from the third reflex in that the former is reversed in direction at the end of a rotation, whereas the latter is not. Typical curves resulting from combinations of the three reflexes in the same and opposing directions and in varying strengths are shown and analyzed.

Recent experimentation has seen renewed emphasis upon the effects of pressure on the ear. Errecart (**30**) has discussed the problem in a rather general way from the clinical point of view. It is observed that the nystagmus produced by the pneumatic method may be both extensive and positive when caloric and rotary tests give no results. Dohlman and Engvall (**27**) draw contrasts between the pressure method and the galvanic method. The marked difference in the effect of the two methods is illustrated by the observation that the maximal rate of movement of a rabbit's eye under pressure stimulation was 70 per second, whereas galvanic stimulation gave a frequency of response as high as 150 per second. De Juan appears to have used this mechanical method most frequently. One of his studies (**59**) is given over to a description of the complicated ocular movements evoked both by compression and aspiration. In two other papers (**60, 61**) de Juan has gone at the problem more searchingly. A syringe was inserted through the bony wall of the utricle in such a way that the perilymph could be drawn out or put under pressure. In other words, currents were produced in the endolymph to and from the ampulla. Dohlman's method of placing a rubber cap on the cornea was used to record the eye movements. In general, compression was found to produce more violent response than aspiration, especially when the animal reclined with the operated side up. The nystagmus was toward the operated side after compression and toward the intact side after suction. The eye movements were found to have horizontal, vertical, and rotatory components. Of these, the vertical movements were most distinct, especially when the changes in pressure were rapid. Under certain circumstances aspiration following compression did not produce nystagmus if the compression had been very great. Meurman (**81**) has related these facts to increase in intracranial pressure. A spontaneous nystagmus on the side opposite to an artificial labyrinthine fistula was prevented by increased intracranial pressure. Under certain circumstances strong suction also produced nystagmus unless it had been preceded by compression. A suction applied to the inner ear was observed to diminish nystagmus due to compression. Portmann (**100**) applied pressure to the large blood vessels in the neck rather than to the ear itself. Four dogs were used as subjects. After a preliminary survey of the subjects which gave data regarding pulse rate, pupillary condition, mucous coloration, ocular-cardiac reflexes, and vestibular excitability, the animals were rotated twenty times in twenty seconds, first to the right and then to the left. The observations of the induced nystagmus were taken before and after compression and ligature of the blood vessels in the necks of the animals. No reliable difference was found between nystagmus values before and after the ligature, either of the carotid or the vertebral arteries.

The various modes of modifying stimulation of the inner ear through the use of drugs is most difficult to control. Only two experimenters seem to have chosen this method. Berggren (**11**) has studied the effect of bulbocapnin on both rabbits and men. Small doses (0.05–0.01 grain) have no effect on optical nystagmus. In certain types of spontaneous nystagmus, however, a decrease or even complete cessation of both nystagmus and vertigo was effected by doses of 0.1 gram injected subcutaneously. The greatest effect appeared about fifteen minutes after administration and remained effective approximately twenty-four hours. Ross and Fish (**106**) have also studied the effect of drugs. The average duration of nystagmus in ten normal dogs was from 18.2 to 22.4 secs. With 1 c.c. of 1 per cent epinephrine sol. per kgm., the average was 17.1 to 19.8 secs.; with .5 to 1 c.c. of 5 per cent $NaNO_2$ per kgm., 14.4 to 16.6 secs.; with 10 mgm. of cocaine hydrochloride per kgm., 16.0 to 18.3 secs.; with nicotine, .5 mgm. per kgm., 13.9 to 16.8 secs.; with 1 mgm. atropin sulphate per kgm., 17.7 to 18.8. In general, the drugs that decreased nystagmus after rotation had severe depressive results. Bearing some resemblance to these studies is the note of de Kleyn and Versteegh (**66**) on the effects of alcohol. Variable relations were found between degrees of rotation, labyrinth extirpation, removal of one or both maculae and alcoholic nystagmus. There is also a note by Leroux and Causse (**74**) on the vestibular effects of alcoholic intoxication. The effect is said to be the same as that exerted by atropin.

It is a little unfortunate perhaps that further work has not been done on the stimulus value of practical or industrial situations. Schubert's study (**108**) on the effects of spinning movements in airplanes appears to be the only contribution from the aviation service. Because of its clinical importance, miners' nystagmus has gained more attention. Haycraft (**48, 49**) describes the chief subjective symptoms of coal miners' nystagmus as consisting of poor vision, headache, photophobia, giddiness, insomnia, and apparent movement of stationary objects. There are also marked constrictions in the color sensitivity of the retina. A variety of physical symptoms are also described, the first of which is nystagmus. Haycraft believes that ocular movement is the result of defective illumination supplemented by general exhaustion of the nervous system; that is, a neurosis is said to contribute as much to the syndrome as does defective illumination. Similar data are given by Roche (**104**). The problem of miners' nystagmus has been much studied by Ohm. In an early study Ohm (**92**) sought to evaluate the amplitude and frequency of such movement. In contrast to values of only 8 or 8.5 grams for the power of the rectus muscles in maintaining voluntary fixation against resistance applied by means of Fischer's corneal cup, Ohm found that eye movements were substantially unaffected when opposed by a 30-gram weight and still persisted under a load of 50 grams and more. In a much more elaborate study Ohm (**99**) seeks both to distinguish and to correlate nystagmus of vestibular origin and nystagmus induced under industrial conditions. His argument, for the most part, centers on the proposition that nystagmus induced by rotation is essentially vestibular, whereas miners' nystagmus is initiated in some central nucleus. Lebensohn (**69**) has sought to draw a similar contrast between vestibular nystagmus and some of the phenomena characteristic of car-sickness. A rotating striped drum was used to induce optical nystagmus, while a stomach balloon was used to record gastric effects. Rotation and douching the ear both increased gastric tone, but since the same effect was gained by irrigating the skin in the neighborhood of the ear, Lebensohn concluded that the gastric response was the function of stimulation of the cutaneous nerves rather than of the labyrinth. In other words, the symptoms described as car-sickness do not seem to depend upon optic nystagmus.

(iii) *Perceptual Functions.*—The perceptual functions aroused by and mediated through vestibular stimulation still remain under dispute. In a discussion of the question as to whether the sense of rotation is mediated by the semicircular canals, Fischer and Sommer (**32**) stimulated by the caloric method subjects who were congenitally blind, subjects who had become blind in later life, and normal subjects who kept their eyes closed in a dark room. Since three-fourths of the subjects experienced a sense of rotation apart from visual stimulation, even though the intensity of the stimulation was increased to heroic proportions, the authors conclude that the experience of rotation may be elicited by caloric stimulation independent of visual experiences.

Intense argument still continues concerning the relation between auditory localization and the semicircular canals. Bard, for example (4), argues that the perception of sound depends upon reflex adjustment of the canals to the components of the sound complex. Holsopple (53), in a general study of the vestibular perceptions, argues that there is a form of spatial perception which cannot be explained in terms of sensory data without reference to the non-auditory parts of the ear. By implication, at least, the opposite point of view is taken by Young (131), who explains localization in terms of "muscle tonus" and general functions of the organism as a whole. Higginson (52), in a study of the performance of the white rat in a rotated maze, found "no experimental evidence for the claim that the white rat possesses a sense of direction located in the semicircular canals, or elsewhere, by virtue of which it is disturbed when the maze, previously learned at one position, is rotated to new cardinal positions." A similar conclusion might be inferred from the studies of Leuba and Fain (75). Leise (73), in an argument with Noltenius (90), also disputes the view that localization is mediated by the canals. He draws, first, a distinction between sensation and space feeling. Space feeling is described as the idea of an infinite space which can never be the object of perception. Since there is no sense by which we can perceive space, this function must rest upon a congeries of senses. Since the activity of the vestibular apparatus takes place without consciousness, the observed experiences of disorientation must be due to the "ramifying systems" which are connected with the canals. In other words, the vestibular apparatus is a receptor but not a sense organ. This same problem has been discussed from the clinical point of view by Fischer and Kornmüller (36).

One of the most puzzling circumstances in all work upon the vestibular functions lies in the fact that nystagmus and other types of equilibratory movement may appear without stimulation initiated within the vestibule itself. The facts just reviewed point in this direction. Keleman (62) has described a variety of other circumstances under which spontaneous nystagmus may appear. An illuminating table of spontaneous nystagmus compared with experimentally induced nystagmus is presented for the guidance of those who easily associate every disturbance of equilibration with the experimental technique itself. De Nó (87) has also studied this problem. Patterns of nystagmus following unilateral extirpation of *the labyrinth were found to show no consistency from animal to* animal or from time to time in the same animal. In other words, de Nó is arguing that the total condition of the nervous system as well as the insult to a particular receptor may have a bearing on the character of the responses. Any abnormal position of the head, even months after an operation, is likely to induce spontaneous nystagmus.

The effect of the position of the head on spontaneous nystagmus has been studied by Sommer and Yaskin (109). Changes in the position of the head would cause changes of pressure in the whole vestibular apparatus, especially in the horizontal canals. The relation between this work and recent studies on the effect of compression and aspiration has been discussed above. Spiegel (111) and Demetriades (24) find that the state of the vegetative nervous system has a pronounced bearing upon vestibular functions. This becomes true by way of the contractions of the arteries, the permeability of the vascular walls, and oscillations of blood pressure in the ear. Similar effects may be induced, according to Lunedi (76), by changes in the skin of the mastoid area, on the posterior surface of the neck and the mucous membrane of the nose. Lunedi argues that nerve impulses arising from sense organs in these areas act upon brain centers which are subject also to innervations from the labyrinth.

The most perplexing phase of this problem is to be found in direct stimulation of the visual receptors. Huddleston (54) remarks this fact by way of the observation that marked differences in nystagmus were found between pigeons which were rotated in the dark as compared with rotation in the light. Recent studies have brought about a marked increase in interest on autokinetic phenomena and their relation to nystagmus. Ohm (93) asked seven subjects, who were suffering from ocular disorders, to fixate a luminous point and to maintain fixation after all lights had been extinguished. All but one displayed eye movements having a characteristic nystagmic jerk. The direction of movement was fairly constant for each observer and the frequency varied from 30 to 72 per minute. In other words, the movements seemed to differ from normal dark-nystagmus in that they began immediately after the room was darkened and were jerky rather than pendular. Ohm attributed the movements to vestibular factors which might be overcome by attempts at fixation. This study has been supplemented by an account of similar phenomena in subjects suffering from diseases of the optic nerve (96). As we have seen, this conception lies at the basis of his study of miners' nystagmus. Cords and Nolzen (21) describe in detail the methods for inducing optokinetic nystagmus. They discover that this type of nystagmus is a function of the velocity of the stimulus and of the degree of concentration of attention. The nature of the phenomena in cases of hemianopsia, astereognosia, and motor aphasia is also described. In a further study (19), Cords attacks Lieri's theory to the effect that after-images of movement can be explained by after-nystagmus. He asserts that the theory is untenable because after-nystagmus is a purely local process, for it seems to depend upon the stimulus (in this case, a striped field) and on speed of movement.

Further studies have been made by Roelofs and Van der Bend (105), and Fischer and Kornmüller (37). The chief results gained by Roelofs and Van der Bend were (1) that nystagmus is more readily produced by left to right motion than right to left; (2) that its strength is, in general, inversely proportional to the speed of movement; (3) that the intensity of movement increases in proportion to an increase in the size of the perceptual field; and (4) that the optimal conditions for arousing nystagmus occur when the retina is stimulated by from three to twelve visual outlines per second on each retinal point. Kestenbaum (63) has introduced the genetic method in the study of these phenomena. At the second or third week a certain normal movement of the eye begins. At first the movements are saccadic, but by the third to fifth month they proceed more smoothly. Optokinetic nystagmus has been produced as early as the fifth week, but it does not appear regularly until after the third month. It would appear, then, that these phenomena are related to the development of fixation.

Travis (121) has continued the studies begun with Dodge on the nature of perception of movement during passive oscillation and rotation. Adequate perception of the direction of rotation is found to vary directly with vestibular excitation when the interval between rotations and duration is constant. When acceleration is constant, adequate perception varies inversely with interval and duration. When both acceleration and duration are constant, correct perception varies directly with the interval. Intense stimuli applied to the vestibular system inhibits less intense stimuli but less intense stimuli do not seem to modify a more intense stimulus. Both subjects were more sensitive to rotation to the right than to the left. The same technique was used in a further study of the problem (**122**). When ocular pursuit of a slowly oscillating object was superimposed upon vestibular reflexes induced by rotation of the body, the vestibular responses, both subjective and objective, were reinforced. When, however, the pursuit movements were in harmony with vestibular reflexes, the visual cues served to inhibit the vestibular events. Hallucinations of movements were reported frequently during control periods when the body was actually quiescent. Since obscure stimuli may play a part in problems of this kind, Travis implies that there may be some sort of central addition to peripheral excitations. These central events may now predominate over and then subserve the peripheral processes. In a study somewhat related to these, Malassez (**77**) describes the perceptual functions aroused by angular speed, especially on aviators and deaf mutes. Observed variations in perceptual events led him to suggest that the method might have clinical value.

(iv) *Modes of Response.*—The bodily outcomes of vestibular stimulation have been described frequently in connection with the methods of stimulation; but a few papers deserve special mention. We may begin with special studies of eye movement. De Nó (**86**) argues that ocular movements are always combinations of lateral, vertical, and rotational movements. This is, of course, by no means new. With characteristic thoroughness the slow phase of optic nystagmus undergoes description by Dodge, Travis and Fox (**25**). Hemmes (**51**), Esters (**31**), and Sorsby (**110**) describe some of the characteristics of latent nystagmus. Esters emphasizes the relation of latent nystagmus to visual localization and other eye movements. Sorsby reviews the literature in a helpful way.

On the clinical side, Fischer (**34**) has materially improved diagnostic technique by one of his most elaborate researches. With the aid of several refinements in apparatus, he studied eye movements by the after-image method. Within ranges of head or body inclination from 0° to 40°, rolling of the eyes increases the greatest amount, 5° to 6° being found at 40° inclination. This compensatory rolling has both a transitory and a persistent component, the former depending on the speed of inclination and corresponds to the "slow" component of rotational nystagmus. It vanishes after a few seconds in the inclined position. The other component remains so long as the inclination is maintained and is a persistent position-reflex. Fischer is mainly concerned with this second component. In a subsequent study, Fischer (**35**) finds that the maximal counter rolling of the eyes is from 4° to 6° when the body is inclined 60° from vertical.

Several papers are devoted to general problems of tonus. Langworthy (**68**) has studied by way of the literature the two components of the "walking reflex." This is a highly adequate review of the facts concerning the control of posture by the central nervous system. A "new" mode of response, attributable possibly to the labyrinth, has been described by Leidler (**71**). It appears that if a person in the erect position places his feet 30 cms. apart, raises the arms to the vertical parallel with the head, and then bends forward with eyes closed, a rotary motion of the head and upper trunk will initiate the feeling that feet are displaced in a diagonal direction. The chances are that these events are related to the phenomena of past-pointing.

Cleminson (**17**) verifies some work done by Tait and McNally (**115**) on the movements of particular muscles in response to surgical insult. The latter worked on frogs, whereas the former used a subject who had become deaf in the left ear and who showed no responses to caloric excitation. Fulton, Liddell and Rioch (**40**) find that one-sided destruction of the vestibular nuclei has a pronounced effect upon the knee jerk. The subject was a cat and the effect of surgical insult was to cause the knee jerk to become spinal in character. The authors conclude "that the vestibular nuclei are essential for the maintenance of decerebrate rigidity, and that they normally exert their influence through control of the inhibitibility of the lower spinal centers." Nishihata (**85**), following an example set by Magnus, studies the posture reflexes of birds. Head position, wing position, and leg and tail postures, in particular, were examined. On the whole, the researches verify the original studies by Magnus. In two papers, Benjamins and Huizinga (**9, 10**) study the general question of vestibular tonus. Pigeons were used and, with the aid of different methods, the tonus of the limbs and neck was studied before and after operation on the labyrinth. The greatest effect was found in the neck muscles. Evidence was found that the labyrinth may regulate wing tonus synergic with the proprioceptors. In the second paper (**10**) parts of the labyrinth were extirpated and an attempt made to discern the functional significance of these various parts. Destruction of the pars superior induced almost the same effects as total extirpation. The papers offer a good example of the way in which partial extirpation may disturb the function of remaining parts.

(v) *Anatomical and Physiological.*—We shall consider the anatomical and physiological features of equilibration in the most summary way possible, partly because so much has been implied in other parts of the review, partly because the literature is so large as to warrant a special review, and partly because not much of the work that has been done is particularly germane to the psychological aspects of equilibration. Controversy still prevails concerning the extent of movement in the otolith and the significance of such movement. Werner (129), in a study of the sacculi of fishes, rejects all grossly mechanical theories. He tends to favor the notion that the otoliths, as a result of their weight, betray differences of pressure in the fluid of the labyrinthine spaces without actually suffering displacement. Huddleston (55) has studied the relation between the saccular otoliths and labyrinthine reflexes in frogs. The reflexes were tested before and after removal of one and of both sets of otoliths. After an observation period of from ten to twenty days the brains of the animals were removed for microscopic examination. Parallel sections of the operated labyrinths showed the extent of labyrinthine injury. No appreciable changes in the labyrinthine reflexes in posture or in the tone of the muscles was found following the complete removal of one or both sets of otoliths. The author inclines, therefore, to the opinion that the saccular otoliths play an insignificant rôle in the mediation of the equilibratory reaction. De Kleyn, de Nó, and Groebbels remain the most persistent students of the anatomy and physiological function of the vestibular structures. De Barenne and de Kleyn (5) study the relation between the growth of eye muscles and equilibratory mechanisms. Cross transplantation, extirpation of all six external eye muscles, and other means were used in correlation with changes in nystagmus. De Nó (88) reports lengthy experimental work on the innervation of the eye muscles of rabbits when the head is rotated in various planes and at variable distances from the axis of rotation. A distinction is drawn between the otolith organs called sluggish receptors and the canals which are called quick receptors. An answer is sought to such questions as the relation between the intensity of the vestibular reflex and the cosine of the angle between the plane of rotation and the plane of the stimulated canal, the amount of current induced in a canal when rotation occurs in some other plane, how impulses from different canals are integrated in the central nervous system, and the like. This appears to be one of the best pieces of work de Nó has done. Groebbels (46) compares one set of results with a set that had already been reported and which could be used as a control. He argues that lesions in the labyrinthine structure show that both the labyrinth and cerebellum control and integrate the tonus of the neck and wings. Blohmke (14), in a well illustrated article, describes the inner ears of several species of amphibia, reptiles, birds, and mammals. He finds that vertebrate sense organs in the labyrinth may be divided into two groups, the one group (the three cristae ampullares, the macula utriculi, the macula lagenae, the macula sacculi, and the papilla neglecta) reacting to change of position of the organism and the other group (the papilla amphibiorum, the papilla basilaris, and the macula sacculi) reacting when the labyrinth is not in motion. The differences between various vertebrate balance mechanisms are described and the functions of the various parts tentatively assigned. De Burlet (12) has given a richly illustrated description of the labyrinth of petromyzon. Comparisons are drawn between his own and other descriptions and some additional observations are made such as the flow of liquid in the labyrinth, the slight right and left movements during swimming, and the like. Disorientation was induced by extirpating the labyrinths. An equally good description of the vestibular receptors of the lamprey is made by Versteegh (126). Like petromyzon, lamprey appears to have only two semicircular canals, the horizontal canal being missing. The inner side of the labyrinth is lined with ciliated epithelium. Furthermore, the endolymph is shown to be in constant motion. These are only a few of the papers on anatomy and physiology. Much work, some of which has been suggested above, on the central connections of the vestibular apparatus, falls properly to a special review.

(vi) *Clinical and Pathological.*—We shall make brief mention only of clinical and pathological material. French (39) has found material for psychoanalytic studies of ear infection of long standing. Evidence for hereditary factors behind the appearance of nystagmus has been gathered by Knighton (67), Cadwalader (15), Kitahara (64) and Steggerda (112). Steggerda suggests Mendelian inheritance. Menière's disease receives a general summary by Thornval (118). The bibliography is exceptionally useful. Mygind (83), and Mygind and Dederding (84), give clinical pictures of the Menière syndrome, including descriptions of the principal types of nystagmus. Helsmoortel (50) and Portmann, Despons and Retrouvey (101) describe the relation between encephalitis and residuary lesions of the vestibular tracts. Walter (128) finds that long continued rotation of rabbits causes a permanent compensatory twisting of the head. Cords (20) describes nystagmus movement incident upon skull injury. Examples of diagnostic technique and results are to be found in Thomas (117), de Kleyn and Schenk (65), Barr (7), Portmann and Mailho (102), and Vogel (127). Vogel's study appears to be most competent. Ohm (98) has made a special study of nystagmus in albinos, who comprise 7.8 per cent of all cases of non-occupational nystagmus. Horizontal movement is found most frequently. Voluntary nystagmus, related presumably to head congestion, has been studied by Bartels (8). Crowe (22) describes the anatomic changes which follow cerebellopontile and brain stem tumors.

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