

COMPENSATORY MOTIONS AND THE SEMI-CIRCULAR CANALS

BY

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WITH TWO FIGURES

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I REACTIONS OF THE FROG TO MOVEMENTS OF ROTATION

When a frog is slowly turned in a horizontal plane by moving or rotating the vessel in which the frog is at rest the animal turns its head in a direction opposite to that of the rotation. When the rotation has proceeded beyond a certain point, the frog will jerk the head back into alinement with the body, and then again turn it in the opposite direction, and so on, as long as the rotation is continued. The existence of this back-jerk or "nystagmus" is specifically denied by von Cyon ('97, pp. 45, 73) and by Lyon (1899, p. 86), and has been overlooked by other observers. When the frog is restless or active, it will frequently jump or walk in a direction opposite to that of the rotation, bringing the head and body into alinement; then turn the head again and follow this movement with a jump, and so on, while the rotation is continued. But when the frog is fairly quiet, there is always a back-jerk.

When the vessel containing the frog is tilted on a transverse horizontal axis, the animal nods its head up or down, according as the rotation is upward or downward anteriorly. When the base upon which the frog rests is tilted on the longitudinal (horizontal) axis—too slowly to dislodge the animal—the movements

of the head are such as tend to keep the plane of the mouth horizontal; that is, the animal raises the head on the side that is lowered, and vice versa. (At the same time there is a contraction in the limbs on the ascending side and a corresponding flexion on the descending side.) There can, of course, be no question of a nystagmus in these two cases, since the rotation cannot be continued beyond a small arc of a circle without dislodging the animal or causing it to make definite efforts to hold its own, and in neither case are there compensatory responses to rotation. Nor are the responses normal if the animal is fastened to the support.

When a frog is moved about in a circle having a diameter of two to three meters (by walking about with a jar containing the animal), the animal turns its head away from the center if the frog faces the direction of motion, and toward the center if the animal is carried facing in the direction opposite to that of the movement, that is, backward. This movement and the response are virtually the same as in the case of rotation about a vertical axis, in a large circle and at a slow rate.

The movement of the head in the cases referred to is in general in a direction opposite to that of the displacement of the body. Such responses have long been known in the frog¹ as well as in other animals, and are frequently spoken of as "compensatory movements." The implication of this designation, as well as the expressed belief of many physiologists, is that the movements in question are in some way related to the orientation of the animal with regard to gravity, or, what is mechanically equivalent, to acceleration of motion in some direction. The movements have been regarded as reflexes set up by the sensation of the semicircular canals.

2 THEORIES OF THE FUNCTION OF THE SEMICIRCULAR CANALS

The oldest theory as to the function of the semicircular canals was that they were concerned in the perception of the direction of sound, and was deduced from their intimate anatomical asso-

¹ Some of these responses seem first to have been described by Goltz ('69, p. 71), and many of them have been shown by Steiner ('85, p. 126) to take place in frogs whose fore- and mid-brain have been removed.

ciation with the other auditory organs and the fact that the three canals of each side lie in planes almost exactly at right angles to one another; that is, in planes corresponding to the three dimensions of space. It can be readily shown that the perception of the direction of sounds is actually accomplished otherwise; and this theory as to the function of these organs has been long abandoned.

In 1828 Flourens (1 and 2) made the observation that, as a result of cutting one of the membranous canals in a pigeon, the bird moved about an axis at a right angle to the plane of the injured canal; that is to say, the movement was in the plane of the divided canal; the sense of hearing, however, was in nowise affected. The disturbed movements were so much like those resulting from injuries to the cerebellum that Flourens concluded that the canals were concerned in the coördination of movements; but he made no attempt to explain the method of their operation.

In 1870 Goltz offered an explanation of the method of the working of the semicircular canals. According to this theory it is the downward pressure of the endolymph on the various parts of the sensitive lining of the membranous canal, according to the position of the head, that gives rise to the corresponding sensations. This theory has been called the "hydrostatic theory."

A few years later, Breuer ('74, '75) and Mach ('75) proposed hydrodynamic theories of the action of the canals. According to Mach the sensations in the canals are aroused by variations in the pressure of the endolymph in the ampullæ, and the variations in pressure result from the streaming of the endolymph, which is caused by movements of the head. According to Breuer it is the movements of the endolymph, resulting from the movements of the head, that arouse the corresponding sensations, through their pressure on or movement of the lining hairs of the canals.

About the same time Crum-Brown ('74, 1, 2 and 3) urged the view that the movement or pressure of the perilymph was as much concerned in the production of the sensation as the disturbance of the endolymph; and he also pointed out that the canals operate in pairs.

In 1878 von Cyon rejected both the static and the dynamic theories of the workings of the semicircular canals. After drawing off the endolymph and replacing it with gelatin, and after the introduction of pieces of laminaria into the canals, thus producing great changes in pressure, there were none of the disturbances of equilibrium that had been observed by Flourens as resulting from divisions of the canals. Without advancing any other explanation of how these peripheral organs *are* excited, von Cyon maintained that the canals assist but indirectly in giving the organism a knowledge of space relations; the sensations in the canals set up reflexes in the eye muscles, and it is from the sensations of the eye muscles and the retinal images that the notion of spatial relations of the head and of the body are obtained.

In 1883 Sewall ('83) from experiments on skates and sharks concluded that the results were not sufficient to warrant the opinion that the semicircular canals are the organs of equilibration

3 THEORETICAL OBJECTIONS TO THE SEMICIRCULAR CANAL HYPOTHESIS

Whatever the real manner of operation of the semicircular canals may be, there have appeared certain theoretical objections to Goltz's static theory as well as to the various dynamic theories; these explanations seem to be out of harmony with the observed fact that the responses of the frog's head to rotation are not coördinated with the position of the animal in relation to the axis of rotation. Thus, in Fig. 1, a frog in any one of the four positions on the turntable, will always turn his head to the left if the table is turned to the right (clockwise), and vice versa, as indicated by the dotted outlines and the peripheral arrows. The action of gravity, or acceleration, in relation to the frog, or whatever dynamic principle it may be that does act, seems to work in a different direction in each of the four cases. The special sense of the action in each case is indicated in Fig. 1 by a small arrow. In other words, the animal responds uniformly to what is apparently a variety of stimuli; the stimuli in these cases are the same in kind and in degree, but differ in sense or direction, or incidence in the animal's body;

but the response to every stimulus is the same in degree and in direction.

Lyon ('99, p. 89) has already called attention to this anomalous appearance, and the facts had been observed much earlier (Cyon '97, p. 42; Ewald '90, Fig. 51; Schäfer '87), and had caused great confusion largely because the earlier writers described the responses with reference to the periphery and the axis instead of

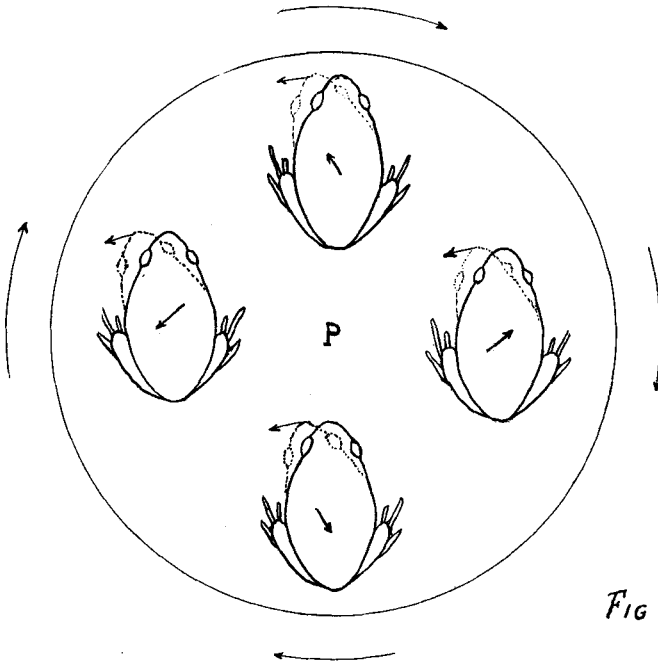


FIG 1.

with relation to the body of the animal. The anomalies and confusions did not lead directly to a rejection of the hypothesis that the semicircular canals were the peripheral organs for perceiving acceleration or spatial relations. Yet these theoretical considerations would seem to make the semicircular canal hypothesis of equilibration untenable without radical modification. The experimental evidence is conflicting and inconclusive.

4 EXPERIMENTAL OBJECTIONS TO THE HYPOTHESIS

On removing the semicircular canals entirely, or on cutting the acoustic nerve, Girard ('92) and Schrader ('87, p. 87) report complete loss of compensatory motions; while Tomaszewitz ('77), Breuer ('75, p. 99), Baginsky ('81), Cyon ('88), Kreidl ('92, 2), Ewald ('92), Strehl ('95, p. 216), Bechterew ('96), and others, found all the phenomena in response to rotation continued as in the normal animal; and Steiner ('85, '89) concludes that there is not complete loss of compensatory movements. Breuer ('91), Ewald and Delage-Aubert ('88) observe, however, that the compensatory movements disappear after the operation if care is taken to exclude the use of the eyes also, and therefore they do not abandon the theory; but Cyon ('97) speaks sarcastically of the logic of this argument.

When single canals only were operated upon, Hensen ('79) found the movements disturbed in the plane of the canal in question; whereas Ewald ('90, Experiment 66) cauterized the membranous canals in pigeons without in any way affecting the movements of the animals.

According to Girard and Ewald, the destruction or removal of the labyrinth on one side of the head caused the frog to take on an unsymmetrical attitude, the head and body being inclined toward the operated side; Ewald found that this new attitude was maintained in one case for a year after the operation. According to Loeb ('91, 2) cutting the acoustic nerve brings about a permanent tendency in the shark to turn toward the injured side. On the other hand, Cyon, Steiner ('89), Baginsky ('85) and Bechterew ('96) found on cutting the acoustic nerve that "all the phenomena that served to support the assumption of the sensory function [of the semicircular canals] continued to appear" (Cyon, '97), while Mach found that under these conditions the eye- and head-nystagmus appeared as in normal animals.

Breuer ('89) found that mechanical, thermal and electrical (galvanic) stimulations of separate canals set up head-turnings in the corresponding planes; the movements are in response to the streaming of the lymph, and are in the same direction as the stream-

ing. "Galvanic dizziness * * * is caused by irritation of the vestibular nerve endings, as galvanic phosphorescence is produced by irritation of the retina." Lee ('93, '94, '98) found the responses to stimulation of the canals and ampullæ such as to lead to the conclusion that the canals are directly concerned in equilibration. Mach's theory that compensating movements are set up by variations in the pressure of the endolymph seems to be disproved by the experiments of Cyon ('88, pp. 294-297), Spamer ('80) and Ewald ('90, Experiment 42), who secured normal reactions after producing permanent changes in the pressure of the endolymph by removing the liquid entirely, by replacing it with gelatine or with amalgam, and by inserting into the canals dry bits of laminaria, which swelled up on absorbing moisture, and so increased the pressure.

On the one hand Ayers ('92) draws from his morphological studies the conclusion that the canals are specially modified lateral-canal organs, that have no relation whatever to equilibration. On the other hand Schaeffer ('94) tells us that whirling produces no effect upon tadpoles until after the semicircular canals become developed. But Streeter ('06) has succeeded in separating the action of the canals from that of the rest of the ear vesicle and concludes that while the ear vesicles are essential to the development of the power of equilibrium in tadpoles, the canals are not.

Schäfer ('87) succeeded in demonstrating to his own satisfaction that the responses to rotation are due solely to the inertia of the loosely jointed head; he made a wooden model that behaved on the turntable just like a frog or a pigeon, with a few exceptions to be noticed later.

Other minor experiments have been reported by various investigators, with equally definite but conflicting and inconclusive results.

5 ANALYSIS AND NEW EXPERIMENTS

This then appears to be the situation:

1 From the structure of the semicircular canals it was inferred that they were somehow related to the perception of *space* or *direction*.

2 The manner in which the semicircular canals operate to bring about perception of space has been variously explained as resulting from (a) static inertia of the endolymph; (b) variation in pressure of the endolymph; and (c) movements or acceleration of the endolymph, or of the perilymph, or of both; brought about by movements of the head.

3 Theoretical considerations seem to show that this function cannot be ascribed to the canals for the reason that identical reactions are produced under conditions in which the sense of the acceleration may be opposite. (As explained in connection with Fig. 1.)

4 But operations to remove or destroy the semicircular canals, or to sever the connections of the VIII nerve, show (a) in some cases that the movements of the animals are seriously affected, and (b) in other cases that the animals continue to respond to rotation as do the normal animals.

5 Mechanical, thermal and electrical stimulations of the single canals show (a) in some cases decided disturbances of movement related to the planes of the respective canals, and (b) in other cases the absence of related responses.

On examining again the movements represented in Fig. 1, it will be seen that a given rotation will produce for the frog a displacement of the retinal image or "view," and always in the same direction without regard to the position of the animal on the turntable. Whereas the actions of centrifugal force and of acceleration depend upon the position of the animal with relation to the axis of rotation, the sense of displacement of the field of vision does not so depend, and it may therefore be supposed that the uniform turnings of the head are in response to the changing view; the frog seems to be trying to keep the same view before him.

To test the responsiveness of the frog to the apparent displacement of his surroundings, a "revolving environment" was arranged, consisting of a cylinder of stout paper about 60 cm. in diameter and about 35 cm. high, attached to a wooden hoop which was suspended so that it could be readily rotated in either direction. A portion of the cylinder consisted of light colored material bearing black vertical stripes about 5 mm. wide and from 2 to 5

cm. apart. Another portion of the cylinder was of black paper in which had been cut numerous holes of various shapes and sizes. When in use the cylinder was always part striped and part fenestrated, or part open and part one or the other of the described surfaces. (The proportions were varied, but the character of the surface did not seem to make a constant difference.)

Frogs placed in the middle of this "circus" arrangement could be made to turn their heads and to give the nystagmus or back-jerk by revolving the cylinder, the same as when the animals themselves were rotated on the turntable. The response was not, however, equally marked in all cases, nor was it in any case as quick as in the actual rotation of the animal. When the revolving of the cylinder was very rapid or very slow, there was no response at all; but when the optimum rate was found, the responses were well marked and continuous. These experiments with the moving environment would indicate that the visual impressions do, or may, play an important rôle in setting up compensatory movements; and in the case of the animal rotated on the turntable one might conclude that it is the displacement of the retinal image that is the constant, and therefore the determinant factor. But such a conclusion would be false, and for the following reasons:

If a frog is placed on the turntable, in every possible position with relation to the pivot, and the table is turned to the right, (that is, clockwise) the frog's head will always turn to the (animal's) left, and the animal will seek, humanly speaking, to keep the same view before his eyes. But if now the vessel containing the animal is completely surrounded by some opaque material, the frog will respond in precisely the same way. If the frog is taken into a room almost dark—one barely light enough to permit the observer to discern the outlines of the animal against a white background—the animal will respond in the same way. If the animal is placed upon the turntable together with the source of illumination, and completely cut off from the sight of external objects, rotation will result in the same reactions. If, finally, the animal's eyes are covered with a mixture of vaseline and lamp-black (which will entirely exclude vision without in the least irritating the frog) the responses to rotation are still the same.

It may accordingly be safe to conclude that while the turnings of the head on rotation may be responses to visual impressions, they may also be quite independent of visual impressions. One is therefore driven back to a reëxamination of the semicircular canal theory, or to search for some other means of perceiving movement or acceleration.

It had already been found that there is not complete loss of the compensatory movements on cutting the acoustic nerves,² or on destroying the semicircular canals. This is comprehensible, since the eyes are *also* capable of leading to similar results. If a frog that has been operated upon is rotated with the eyes covered, or surrounded by some opaque medium that rotates with him, there is no response. This excluding of visual impressions is not, as Cyon supposed, eliminating *the* determining factor, since the normal frog under the same conditions will continue to react, though Cyon failed to observe this. The results referred to in this paragraph I have verified experimentally.

The following is the record of one frog whose semicircular canals had been destroyed by piercing into the capsule from the dorsal side. The animal was etherized; there was no bleeding.

1 Immediately after the operation (the animal recovered consciousness and began to move about sluggishly within two or three minutes after the operation):

a Animal lies on back quietly over one-half minute at a time without making efforts to right itself.

b Rights itself only with great difficulty and after making many awkward movements.

c Limbs not correlated in crawling about; does not hop.

d On turntable, no response.

e In swimming, rolls from side to side.

2 After thirty minutes:

a Lies on back for short intervals, but not quietly.

b Rights itself with difficulty, but more quickly than at first.

c Moves about awkwardly, but better than at first; can hop, but in jumping frequently lands on back.

²Vide *supra*.

d On turntable responds as normal, but more slowly.

e Responds as normal to "revolving environment."

3 After one week:

a Lies on back indefinitely, quietly.

b Rights itself more easily than before, but still awkwardly.

c Walks about unsteadily; leaps awkwardly, falling on side.

d On turntable, responds normally.

Another frog, with both sets of semicircular canals destroyed by boring into capsule from the dorsal side, showed after three weeks a marked lack of coördination of movements, though not as great as at first; this was evident in swimming as well as in walking, and in both swimming and in jumping the animal frequently turned over on its back; it righted itself rather quickly, but movements still showed awkwardness. On turntable, responses were as in the normal animal.

As has been pointed out above, the summation of mechanical disturbances or accelerations on the rotation of an animal upon the turntable in a given direction seems to depend upon the position of the animal with reference to the axis of rotation, whereas the sense of the response in relation to the animal's own axis is constant. Thus, the rotation being to the right (clockwise), the factor of wind, or resistance of the air, acts upon the *right* side of the animal if the animal faces the periphery, but on the *left* side of body if the animal faces the pivot; but in any case the response is to the *left*. The same apparent contradiction is observed if we consider the direction of the centrifugal force of the rotation; the direction of the centrifugal pressure of the viscera or other loose parts, of the strains on the skeletal articulations, and of the friction of the body on the supporting surface, is toward the periphery, however the animal may be placed; but the response to a given rotation is constant with reference to the axis of the animal. The same apparent contradiction is found when the attention is directed to the inertia of the viscera or of the contents of the semicircular canals. In addition to these contradictions is the further fact pointed out by Schäfer in 1887 and by others, and referred to above (§4), that the inertia of the head, because of its loose articulation to the trunk, is sufficient to account for the

“responses” to rotation even in a wooden frog; and these responses agree in sense with those described for the live frog. That is to say, with a given rotation of the turntable the “turning” of the head is constant, without regard to the position of the body in relation to the axis of rotation. These considerations in detail have led many physiologists to abandon the theory that the canals are the organs for the perception of movement or acceleration, since they so obviously arouse the same response to opposite sets of stimuli, and since the responses can be obtained from wooden animals as well as from Nature’s own. *But there is one element in the mechanical theory that seems to have been overlooked as a constant source of rotation stimuli.*

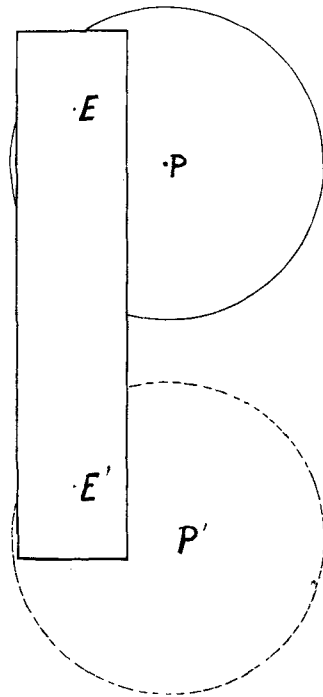
The inertia of a loosely jointed head as an explanation of the phenomena may be left entirely out of account because in the first place it cannot account for the back-jerk, in the second place the inertia is overbalanced by the centrifugal force when a certain rate of rotation is reached, whereas the responses do not disappear at this point, and in the third place the responses can be inhibited by stimuli that do not seem to affect the freedom of the head articulation.

Steiner ('85) has described the reactions of the frog in response to rotation essentially as given here, and analyzed the movements in terms of tangential force; but he concludes from the persistence of the reactions after the division of the eighth nerve, that the canals are not concerned in the matter at all. It is to be noticed that when the animal is rotated on a turntable, the posterior end of the body is constantly changing its position with reference to the anterior end, as is the right side with reference to the left, etc. This movement is constant in direction, and parallel (in direction) to the rotation. That this is a real motion and quite distinct from the motion of translation or rotation, is known to every physicist and to some laymen; but the physicist has a name for it.

Prof. Albert P. Wills, of the Department of Physics of Columbia University, has kindly helped me to get the matter clear by assuring me that this kind of motion is well recognized in mechanics, and by giving me the technical name for it. It is known as the “spin.” This *spin* it is that remains constant in direction on

a given rotation, unaffected by the position of the animal on the turntable; when the rotation is clockwise, the spin is clockwise, and vice versa; when the spin is to the right, the head of the frog turns to the left, and vice versa. It is the "spin," therefore, that determines the compensatory movement.

To test the validity of this interpretation, it is necessary to eliminate this factor from the rotation of the animal. For this purpose an eccentric was arranged on the turntable in such a

*FIG 2*

manner that the animal could be moved in a circle with its long axis always parallel to its first position (Fig. 2).

When the frog is rotated on this eccentric turntable, the response takes the form of a pendulous movement of the head; during one portion of the revolution the head is turned to the right, and then the head is turned in the opposite direction. This back and forth swinging of the head continues as long as the rotation

is continued, and there is no nystagmus whatever. The head turns to the left in that part of the rotation which carries the animal's body to its right, and vice versa, whether the rotation be clockwise or the reverse, and without regard to the size of the circle described; that is, without regard to the proximity of the animal to one of the pivots. If the animal is placed in an opaque vessel and the rotation on the eccentric set up, there is no response whatever.

To show the effects of the various factors that have been considered as having a possible relation to the "compensatory movements," the following comparative table may be helpful. In the experiments whose results are given under I the animal was

| | I | | II | |
|-------------------------------------|-----------------------|-------------------|-----------------------|-------------------|
| | A Facing Periphery | B Facing Pivot | C Facing Periphery | D Facing Pivot |
| 1 Air pressure | ← | → | ← | → |
| 2 Inertia (of viscera, lymph, etc.) | ← | → | ← | → |
| 3 Centrifugal action | ↑ | ↓ | ↑ | ↓ |
| 4 Friction of support | → | ← | → | ← |
| 5 Displacement of retinal image | ← | ← | ← | → |
| 6 "Spin" | ↻ | ↻ | ○ | ○ |
| Response | ← | ← | ← | → |

rotated to the right (clockwise) on the ordinary turntable; in those represented under II the eccentric arrangement was used and the results given are for a portion of the revolution only, since a continuation of the rotation beyond 180° is virtually equivalent to a reversal of the motion. (It is of course understood that the rotations in the reverse direction gave corresponding results but in the opposite sense.) The arrows indicate the directions in which the respective factors are supposed to act.

On comparing the arrows in the four columns it will be seen that whereas all in II seem to be related to the direction of the head turning, none in I are so except 5 and 6 (retinal and spin impressions).

In experiments on the turntable (I) the factor 5 could be eliminated in a variety of ways: By surrounding the vessel containing the frog with some opaque material, or placing it in a tall opaque cylinder; by covering the eyes with the opaque non-irritant mixture already referred to, or with a pad of absorbent cotton mixed with vaseline and lampblack; by placing the source of light on the turntable with the animal. In all cases the turning of the head in response to rotation was the same as in the usual rotation as to direction; but frequently it was less in degree. In other words, while the displacement of the retinal image can and does set up the compensatory response, the eye is not the sole sense organ through which such movements can be initiated.

This leaves the spin as the only other factor to be further considered. According to the results indicated in columns A and B of the table, the spin is the only factor (of those considered) in addition to vision that can constantly set up the head turning. In the experiments on the eccentric (columns C and D) where the spin is already eliminated, the further elimination of sight results in a total loss of the response.

The slightest amount of spin is sufficient to set up a perceptible amount of head turning; considerable displacement of the retinal image is required to bring about the same amount of response. It is possible to move the frog in a right line without the animal giving any response whatever; but if the movement is not smooth, that is, if there is vibration, or very slight turning in a horizontal plane, the head responds at once. That the response to the spin is quicker and greater in amount is also certain; the two factors may be caused to operate in opposite directions in the following manner:

A dish holding the frog on a horizontal plane and facing the observer, is swung about slowly by the observer at arm's length. The head will be seen to turn in the *same* direction as the movement of translation; that is, in a direction opposite to what we

should expect on the anthropomorphic view of the animal "seeking to keep the same vision in sight." But the turning of the head is opposite to the direction of the spin that the observer unconsciously imparts to the dish in moving his arm outstretched, which is thus in the radius of a horizontal rotation.

That the perception of spin or rotation is located in the organs of the inner ear seems likely from the fact that the response is eliminated when the semicircular canals are destroyed or removed, or when the acoustic nerve is cut. That the sensation concerned involves a factor of rotation or turning is indicated by the fact that rectilinear acceleration does not yield the same constant response.

It may, therefore, be concluded that the compensatory movements of the frog's head set up by rotation arise in response to two distinct sets of stimuli, visual and dynamic; that the response to the visual stimulus is relatively feebler and slower than that to the dynamic stimulus; that the organ for the perception of the dynamic factor is probably located in the internal ear; and that the dynamic perception involves a rotation or turning element in the stimulus, as distinguished from an acceleration or movement in a single direction.

6 SUMMARY

1 There is apparent contradiction between the various responses of the frog to rotation on the turntable and any theory of mechanical stimulation of peripheral organ as the origin of the responses.

2 There is considerable contradiction among various experiments that have been made in connection with the relation of the semicircular canals and compensatory movements.

3 A reëxamination of the compensatory movements and of the conditions under which they arise shows the presence of a mechanical factor, the "spin," the significance of which in this connection seems not to have been considered before.

4 From an examination of the results obtained by earlier observers, a repetition of some of their experiments, and new experiments made in the course of the study, the following conclusions are drawn:

a The compensatory movements of the frog's head set up by rotation arise in response to two distinct sets of stimuli, visual and dynamic.

b The response to the visual stimulus is relatively feeblér and slower than that to the dynamic stimulus.

c The organ for the perception of the dynamic factor is probably located in the internal ear.

d The dynamic perception involves a rotation or turning element in the stimulus, as distinguished from an acceleration or movement in a simple direction.

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