SOME EXPERIMENTS WHICH INDICATE THAT THE FROG'S LAGENA HAS AN EQUILIBRIAL FUNCTION

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THE following experiments resulted from an inspiration received after reading the report of the electrical studies on the frog's labyrinth by D. A. Ross (1936). He recorded and studied action potentials set up in the frog's VIIIth nerve in response to vestibular and vibrational stimuli. He concluded: "Gravity receptors fall into two classes: type (*i*) responding best when the head is tilted out of the level position, and type (*ii*) signalling only the return of the previously tilted head to level. Type (*ii*) receptors have not been encountered often, but so far they have always been found on the posterior ramus. It is tentatively suggested that of the three organs of unknown function found on the course of distribution of the posterior ramus (*i.e.* the lagena, the pars basilaris, and the pars neglecta) one is a vibration receptor, one a gravity organ type (*i*), and the remaining one a gravity organ type (*ii*). No experimental evidence is yet available on the subject of which is which".

The labyrinthine (VIIIth) nerve divides into an anterior and posterior ramus. In all vertebrates the anterior ramus supplies the anterior vertical and horizontal semicircular canals, the utricle and most of the saccule. The posterior branch supplies the posterior vertical ampulla, the macula lagena, the pars basilaris or the cochlea and when present the pars amphibiorum (also called pars or papilla neglecta).

Early writers such as Hasse (1873), Kuhn (1880-1882), Retzius (1881-1884), Villy (1890) and Ayers (1892) were all concerned with the close association embryologically and anatomically of all the endorgans on the posterior branch of the VIIIth nerve (with the exception of the posterior vertical ampulla). They assumed a similar physiology for all three endorgans and as a result of their writings the lagena, the pars basilaris and the pars amphibiorum were regarded as forerunners of the cochlea and were considered to be part of the hearing mechanism.

Harrison (1903) stated that "the lagena is an endorgan which first appears in the internal ear in fishes and persists in amphibians, reptiles, birds and mammals though in the latter group it is without a sensory area".

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The Frog's Lagena has an Equilibrial Function

Alexander (1901) and Harrison (1903) engaged in a controversy as to the development of the lagena and its relationship to the pars amphibiorum and the other cochlear sense organs in the transition stage from amphibia to reptiles. Alexander cast some doubt as to whether the lagena is the same structure throughout the series from fishes to mammals. Harrison believed that the lagena and pars basilaris by partial fusion give rise to the single cochlear sac of the reptiles.

Breuer (1891) was the first to suggest that the lagena might be connected with the equilibrial mechanism of the ear. Based upon his observations of the topography of the labyrinth he argued that in the pike the lagena is in the best position to be stimulated by any up or down movement in the vertical direction, that is, movements in the frontal plane. The utricle is best suited to respond to movements in the horizontal plane and the saccule to movements in the sagittal plane. He concluded that the semicircular canals appreciate turning movements or angular acceleration and that the otoliths detect change of position and progressive movements. He further pointed out that the lagena is generally lacking in mammals who for the most part live on the ground and are not so much in need of a mechanism to detect vertical movements. They, therefore, have no lagena.

Breuer attempted direct experiments upon the lagena in pigeons. He was able to remove the lagena and part of the cochlea without disturbing the remainder of the labyrinth. A bird subjected to this operation did not show any specific abnormality in flying around the room. He attempted galvanic and direct mechanical stimulation of the lagena of the pigeon. He was not satisfied with these experiments upon the lagena. He was unable to advance any direct experimental proof for his idea that the lagena is concerned with detecting vertical movements in the frontal plane. It should be pointed out that arguments based upon the topography of an endorgan are sometimes misleading. This proved to be the case with the conclusions which Magnus drew about the equilibrial function of the saccule based upon the topography of the endorgan. When it became possible to carry out direct ablation experiments upon the saccule it was found not to have any equilibrial function. It is noteworthy, however, that Breuer was the first to suggest an equilibrial rather than a cochlear or hearing function for the lagena.

Matte (1894) described an operation in which he removed the cochlea on both sides in a pigeon. He did not mention what happened to the lagena but presumably it was damaged during the operation. He reported that when the pigeon had recovered from the operation its movements could not be distinguished from those of a normal bird.

Lee (1894) attempted direct stimulation of the lagena in the dogfish and he reported that the lagena is less responsive to stimulation than is the saccule or the utricle. He did not exclude the possibility of

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simultaneous irritation or damage of the other labyrinthine endorgans during his experiments.

Manning (1924) experimented with the common goldfish (Carassius auratus). In this fish the otoliths of the utricle, saccule and lagena are definite stones. He studied the conditioned reflex reactions of this fish to a range of sounds from 43 to 2,752 cycles. He was able to detect very definite and characteristic fin and other movements which indicated that the normal fish could hear this range of tones. When he removed the utricle and semi-circular canals the fish no longer reacted to the middle range of these tones. He devised an operation for breaking up the otoliths of the lagena and the saccule but the otolith of one could not be destroyed without some injury to the otolith of the other. After destroying the otoliths the fish no longer responded to notes above 1,300 cycles. There was no loss of equilibrium after destruction of the otoliths of the lagena and saccule. Manning concluded that for notes above 688 cycles the lagena and saccule are the receptors and of these two parts he believed the lagena to be much the more important. As further proof of his idea, he stated that in certain deep sea fish such as the cod the lagena is rudimentary or absent whereas the saccule is enormous. He suggested that sounds, particularly high pitched sounds, probably do not play much part in the lives of these fish in the depths.

Thornval (1926) operated upon the pigeon's labyrinth and he used caloric stimulation as a test. He concluded that removal of the cochlea and lagena from one or both ears did not cause any change in the vestibular reactions.

Benjamins and Huizinga (1928) removed the lagena on one and on both sides in the pigeon and they were unable to detect any abnormality in the vestibular reactions. The birds flew and landed normally; the turning reactions were normal; there was no change in the tone of the neck or wing muscles; compensatory eye reactions were normal. They concluded that the lagena is not concerned with any of the known vestibular reflexes.

de Burlet (1929) mentioned the lagena in connection with a discussion of hearing of the catfish (Siluridae) as though he considered it part of the hearing mechanism but he did not discuss the function of the lagena in particular.

Werner (1929) reported the results of operation upon a bony fish, the gudgeon (Gobius niger). The lagena was destroyed and rendered functionless at the same time that he removed the saccule but in spite of injury to both these otoliths there was no disturbance of the fish's vestibular reactions. After one experiment the lagena was the only part of the labyrinth remaining intact and yet the fish behaved as though a complete labyrinthectomy had been done. After he removed the lagena and saccule from only one side he was unable to detect any asymmetry in the fish's movements.

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The Frog's Lagena has an Equilibrial Function

Ross (see Tait 1932, p. 701) studied the electrical reactions from the saccular and lagenar nerves in the sucker (Catastomus) and he found that the oscillations which occurred when the head preparation was subjected to sound vibrations completely disappeared after he destroyed the lagena.

Von Frisch and Stetter (1932) removed the saccule and lagena from a group of fifty-five common minnows (Elritze) which had been previously blinded and some of the fish lived for more than a year after operation. None of the fish showed any signs of disturbance of equilibrium. Von Frisch (1936) reviewed the subject of hearing in fish and he stated that the lagena has no vestibular function but that it is concerned with hearing.

Löwenstein (1932) found that in the common minnow (Elritze) none of the known equilibrium reactions are in any way affected by a bilateral extirpation of the pars inferior of the labyrinth which includes the saccule and the lagena.

Beatty (1932) in the course of a discussion of hearing in reptiles stated that the lagena is reserved for hearing and may be considered as an uncoiled cochlea. He further stated that in insects there is nothing similar to the cochlea of mammals or the lagena of reptiles.

Forkas (1936) considered the lagena as part of the hearing organ in the guppie fish (Lebistes reticulatus Peters). He also stated, however, that the external semicircular canal is concerned with sound perception in the fish.

Tait and McNally found during their early investigations of the equilibrial reactions of the frog's labyrinth (McNally 1931) that severing the nerve to the lagena on one or both sides did not cause any change in the frog's vestibular reactions except that the operated frogs did have a slight wobble on coming to rest which was not present in normal blinded frogs. It was erroneously concluded that the wobble or oscillation was due to post operative weakness. Since elimination of one or both lagenae did not cause any gross change in the known vestibular reactions, it was concluded that the lagena is not concerned with the equilibrial reactions of the labyrinth.

Technique of Operation

To reach the lagena the posterior approach to the frog's labyrinth described by McNally and Tait (1933) was used. The nerve to the lagena is most easily severed by exposing the posterior ramus of the VIIIth nerve just as it leaves the brain cavity. The lagena nerve can be completely severed by inserting a small hook around the nerve. With practice a quick jerk severs the lagena nerve without damage to any other labyrinthine endorgan. All operations were carried out under ether anæsthesia. The frogs (Rana sylvatica and Rana palustris) were first blinded by bilateral section of the optic nerves. After recovery each frog was examined to be sure that it reacted normally to the usual

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vestibular tests ; slow and quick tilting about a horizontal axis, rotation about a vertical axis ; and the chin drop and chin lift tests described by McNally and Tait in 1933. Spontaneous behaviour on land and in water was also noted. The righting reactions from supine to prone were noted. Frogs showing any abnormality to these tests after recovering from the operation of severing the optic nerves were discarded.

Ablation of the Lagena from One Labyrinth

Section of the nerve to one lagena caused a slight upward tilt of the head on the homolateral side. This was in the opposite sense to the effect of a unilateral ablation of the utricle—a homolateral down tilt of the head as reported by Tait and McNally (1934). During spontaneous behaviour the frog had a slight tendency to circle to the operated side. The reactions to tilting and to rotation were indistinguishable from the normal frog. The righting reaction from supine to prone was prompt and could take place to either side.

Ablation of the Lagenae from both Labyrinths

It was difficult to differentiate the bi-de-lagenate frog from the normal. Elimination of the remaining lagena by nerve section had the effect of correcting the slight upward tilt of the head on the homolateral side which occurred after elimination of only one lagena. Bi-de-lagenate frogs were a trifle sluggish and did not right from the supine position as promptly as did the normal frog. There was a slight oscillation or wobble of the head noted when coming to rest after spontaneous movements. As previously noted the significance of this wobble was overlooked by Tait and McNally.

Section of the Anterior Ramus of both VIIIth Nerves

The anterior ramus of the frog's VIIIth nerve was called the " conjoint " nerve by Tait and McNally (1934) and a frog with both anterior rami severed was called a " biconjoint " frog. Such a frog had the nerves to the utricular maculae, to the saccular maculae and to the ampullae of the horizontal and vertical semicircular canals severed. Remaining intact on each side were the endorgans supplied by the posterior ramus, namely, the posterior vertical semicircular canal, the lagena, the pars basilaris and the pars amphibiorum.

Tait and McNally (1934) have given a full description of the reactions of this biconjoint frog together with an illustration to show its prevailing posture which was one of axial ventriflexion. These details will not be repeated herein—suffice it to say the frog was ever driven forwards and downwards. Since the utricles and the anterior vertical and horizontal semicircular canals were missing there was no reaction to slow tilting, to a quick forward tilt or to rotation around a vertical axis unless the rate of

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rotation was high enough to stimulate the remaining posterior vertical semicircular canals.

To any forward tilt the biconjoint frog was unresponsive. A quick backward tilt on the table or a chin lift test elicited a response—the spectacular " irrelate reaction " described by McNally (1931, p. 13), by McNally and Tait (1933, p. 175) and by Tait and McNally (1934, p. 258). They noted that this reaction followed a backward tip in the " biconjoint " frog or a forward tip in the " bisoliutricular " frog. They concluded that the irrelate reaction is the result of a spinal neural relationship between the utricules and the ampullae of the posterior semicircular canals. According to the degree of angular acceleration employed any grade of the so-called irrelate reaction could be evoked in the biconjoint frog from a forward body thrust with ventriflexion to the final stage in which the frog with scrambling arms and wildly beating hind limbs kept its body oscillating in tempo with the alternate movement of its limbs.

Two Intact Posterior Vertical Semicircular Canals, Partes Basilares and Partes Amphibiorum

If the nerves to both lagenae were severed in the biconjoint frog, the resulting " biconjoint de-lagenate " frog did not show any marked difference in its reactions from the biconjoint frog.

Two Remaining Lagenae, Partes Basilares and Partes Amphibiorum

If the nerves to the ampullae of the posterior vertical semicircular canals were severed in the biconjoint frog the resulting " biconjoint decanaliculate " frog had the lagena, the pars basilaris and the pars amphibiorum intact on both sides. The frog was able to right itself from the supine position readily. The posture of fixed axial ventriflexion in the biconjoint frog was released and the head was held low but clear of the ground. At times the arms extended laterally and the knees pointed outwards. At other times all limbs would be tucked in normally. A surprising finding and one which was repeatedly checked was that the irrelate reaction was present in response to the chin drop test and the tetanic reaction in response to the chin lift test. Tait and McNally had concluded that the irrelate reaction could be elicited from stimulation of the utricles and from stimulation of the posterior semicircular canals. The above experiments showed that stimulation of the lagena could also give rise to the irrelate reaction.

The " tetanic reaction " was described by McNally (1931, p. 11) and by McNally and Tait (1933, p. 175). The reaction was first noted in a frog in which the nerves to both posterior vertical ampullae had been severed. When such a frog is tipped backwards or subjected to the chin lift test under ordinary circumstances the head is raised and the arms are

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extended forward and the body slews back slightly between the thighs. Sometimes, however, just at the top of the movement the frog develops what might be termed tetany. The arms become more rigidly extended, the body is curved backward, the legs are extended outwards and laterally and the whole body trembles with spasm as if by avalanche action the frog is made actively to rear upwards when it is suddenly chucked under the chin. Sometimes the animal will actually go off the tilt table as though doing a backwardly directed swan dive. At other times the spasm passes after a few seconds and the animal recovers and stays on the table. This reaction was first noticed usually after sectioning the nerve to both posterior vertical canals but occasionally after sectioning the nerve to one canal. The occurrence of the tetanic reaction in the " biconjoint decanaliculate " frog shows that stimulation of the lagena could also give rise to the tetanic reaction.

One Intact Lagena, Pars Basilaris and Pars Amphibiorum

If in the biconjoint de-canaliculate frog one labyrinth was completely destroyed, the frog after recovery still showed a prompt righting reflex. It usually turned from the supine to the prone position with the operated side under. The irrelate and tetanic reactions were not elicited in these frogs which had only one lagena intact.

The Pars Basilaris and the Pars Amphibiorum Intact in one or both Labyrinths

It did not prove possible to carry out uncomplicated severance of the nerves to the pars basilaris or to the pars amphibiorum. In order to get some idea of their relation to the equilibrial reactions of the frog the nerves to the two lagenae were severed in the biconjoint de-canaliculate frog leaving only the nerves to the partes basilares and partes amphibiorum intact. One could not distinguish these frogs from the de-labyrinthized frog. In other experiments the pars basilaris and the pars amphibiorum were kept intact in only one labyrinth. Again these frogs could not be distinguished from the de-labyrinthized frog. They showed the righting reaction only occasionally and they did not show any tetanic or irrelate reactions. There was no reaction to quick or slow tilt back into level position (Ross' gravity receptor type (ii)).

Interaction between the Lagena and the Utricle

McNally and Tait (1933) and Tait and McNally (1934) reported that a pendular oscillation occurred in frogs which had had an ablation of any two diagonal vertical semicircular canals or an ablation of the four vertical semicircular canals. The pendular oscillation was also reported in frogs with only the two utricles intact. The pendulation was particularly noticeable at the beginning and end of any movement. The

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amount of pendulation varied somewhat from frog to frog but the significance of any variation in pendulation was not recognized until the present series of experiments had shown that the lagena has some equilibrial function. It occurred to one of us (I. P. J. McN.) that there is a significant difference between the pendulation of a frog with only two utricles remaining intact and the pendulation of a frog from which all six semicircular canals have been removed. It was decided to compare a series of frogs subjected to each method of operation.

" Bisoliutricular " Frog

The posterior vertical semicircular canal can be ablated by sectioning the whole posterior ramus of the VIIIth nerve. The nerve to the saccule can be severed at the same time as are the nerves to the ampullae of the horizontal and vertical semicircular canals. Such a frog has only its two utricular maculae remaining intact—it is what the name signifies, a " bisoliutricular " frog.

On attempting any movement this frog invariably showed a marked pendular oscillation of the head and body. This pendulation was first described by McNally and Tait (1933) in the case of the frog in which all four vertical semicircular canals had been removed and by Tait and McNally (1934) in the case of the frog with only the two utricles remaining intact. It was concluded that the utricles are responsible for this pendulation.

The reaction in the " bisoliutricular " frog under discussion was so severe as frequently to upset the frog during its attempt to compensate for a slow tilt on the tilt table. The number of pendulations on coming to rest after being disturbed averaged six to eight times. The righting reaction was prompt. To a quick tilt, the bisoliutricular frog showed a prompt anti-compensatory slew of the body in the direction of a tilt—a reaction which Tait and McNally (1934) termed the second mode of utricular response.

" Decanaliculate " Frog

When the terminal branch of the posterior ramus of the VIIIth nerve was severed just before it reached the ampulla of the posterior vertical semicircular canal, this canal was functionally ablated. When the nerve to the saccule was left intact when severing the nerves to the ampullae of the horizontal and vertical semicircular canals such a frog had intact in addition to the utricles : the saccules, the lagenae, the partes basilares and the partes amphibiorum. When the operation was bilateral the frog was " decanaliculate ".

On attempting spontaneous movements the decanaliculate frog showed pendulation but it was less marked than the pendulation of the bisoliutricular frog. The number of pendulations on coming to rest after

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being disturbed averaged two to four times. The head swayed in the arc of a circle and sometimes if the head was brought up suddenly a spontaneous " irrelate " reaction was precipitated. Its righting reactions were more obvious because the pendulations were less. In response to a quick tilt this frog also gave the anti-compensatory reaction, the result of the second mode of utricular stimulation mentioned in discussing the reactions of the " bisoliutricular " frog.

In order to prove that it was the lagena which lessened the pendular oscillation in the " decanaliculate " frog the nerves to the lagenae were severed in this frog. After recovery from operation such a frog showed a definite increase in pendulation. It could not be distinguished from any " bisoliutricular " frog.

The following table is reproduced to emphasize the difference which the presence or absence of the lagena made in a frog from which all six semicircular canals had been removed.

	" Bisoliutricular " frog	" Decanaliculate" frog
Pendulations at the beginning and end of movements	Averaging 6 to 8 times	Averaging 2 to 4 times
Righting reaction	Present	Present
Irrelate reaction	Present	Present
Reaction to slow tilt	Accurate (Pendulation troublesome)	Accurate (Occasional pendulation)

Ablation of Four Vertical Semicircular Canals

Severing the nerves to the four vertical semicircular canals leaves the frog with the following endorgans still intact on each side, the horizontal semicircular canal, the utricle, the saccule, the lagena, the pars basilaris and the pars amphibiorum. The detailed reactions of this frog have been described by McNally and Tait (1933). The frog pendulates when disturbed, the number of pendulations averaging about two to four on coming to rest. Severing the nerves to both lagenae in such a frog definitely increases the number of pendulations to an average of six to eight after each movement.

Ablation of any diagonal pair of Vertical Canals

The reactions of this frog have also been described in detail by McNally and Tait (1933). During or after spontaneous movements such a frog pendulates in the plane of the absent vertical canals. Removing the lagenae in such a frog definitely increases the number of pendulations.

It should be noted that some frogs tend to pendulate more than others with apparently the same labyrinthine lesions. Naturally the better the

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general condition of the frog the better are all the reactions. Removing the lagenae in the great majority of cases does increase the tendency to pendulation but not in every case.

Résumé

1. The lagena is an endorgan which is present in the labyrinths of fishes, amphibians, reptiles and birds.
2. The majority of writers were of the opinion that the lagena is part of the hearing mechanism.
3. Breuer (1891) was the first to suggest that the lagena is connected with the equilibrial part of the labyrinth.
4. Ross (1936) suggested the presence in the frog of at least one and probably two gravity receptors on the posterior ramus of the frog's VIIIth nerve in addition to the posterior vertical semicircular canal. Our experiments show that the lagena is one of these gravity receptors.
5. Removal of one lagena causes a residual pose consisting of a slight upward tilt on the homolateral side. Removal of both lagenae causes very little disturbance in the frog's vestibular reactions. There is a slight oscillation of the head on coming to rest after spontaneous movement.
6. A frog with both lagenae intact in the absence of all the known equilibrial endorgans, still retains a prompt righting reflex. It gives the irrelate and tetanic reactions in response to certain head movements showing that the lagena is an equilibrial endorgan.
7. The lagenae together with the vertical semicircular canals control and check utricular pendulation. Normally during movement the vertical semicircular canals and also the lagenae have a controlling or regulating influence upon the utricles.
8. These experiments do not throw any light upon the identity of Ross's probable third gravity receptor on the posterior ramus of the frog's VIIIth nerve. As far as these experiments do go they indicate that the pars basilaris and the pars amphibiorum have no equilibrial function.

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