Some Features of the Action of the Utricular Maculae (and of the Associated Action of the Semicircular Canals) of the Frog

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INTRODUCTION

As is well known, the operation of unilateral labyrinthectomy produces a persistent leaning of the head accompanied by spinal torque. BREUER (1875) once ventured to suggest that damage to the utriculus might be responsible for this effect. Subsequent work by many observers, *e.g.*, LAUDENBACH (1899), G. H. PARKER (1908, 1909), BENJAMINS (1920), MAXWELL (1920), MANNING (1924), McNALLY and TAIT (1925), VERSTEEGH (1927), VON FRISCH and STETTER (1932), has tended to support this original conjecture. One of the main obstacles to certainty on the subject is the operative difficulty of reaching the utricular macula and of carrying out its uncomplicated ablation. Hitherto the clearest evidence on the matter is that of Versteegh (1927). In the rabbit he succeeded, without damaging other structures, in making a partial severance of the utricular nerve on one side. As a consequence the animal exhibited persistent "Kopfdrehung" towards the side of the operation. If damage to one utriculus causes spinal torque and head twist, the inference is that the utricular maculæ, in keeping the head horizontal, are adapted to respond to the field of gravity. Nor is it difficult, considering their anatomy in the light of Kreidl's (1893) work on the statocysts of the prawn, to imagine how these otolith-bearing receptors might operate. The true mechanism of utricular action must, however, remain mere conjecture until experimental work on their mode of stimulation is more advanced. One of the objects of the present investigation was to provide a basis for more profitable discussion of this question. Another was to establish more clearly the reflex effector result of utricular stimulation.

Types of Operation

As in our previous work on labyrinthine receptors—*cf.* Tait and McNally (1925), McNally and Tait (1925), Tait and McNally (1929), McNally and Tait (1933)—we again made use of the frog. (The operations were all carried out by W. J. McNally. The general technique is described in the last-named communication by McNally and Tait.) Two main categories of ablatory procedure have been employed, each involving nerve severance wholly outside the membranous labyrinth. In the one procedure all the labyrinthine receptors except the pair of utricular maculæ (or one single macula) were put out of commission. In the other more difficult type of operation the nerves to the utricular maculæ (or that to one solitary macula) were divided without damage to any of the other nervous branches. By subsequent histological examination we have sufficiently controlled our interventions to know that the operations precisely achieved their purpose.

The eighth cranial nerve of the frog has two main anatomical divisions, an anterior and a posterior. The posterior division supplies the lagena, the papilla basilaris, the papilla amphibiorum and the ampulla of the posterior vertical canal—*cf.* de Burlet (1928). The anterior division likewise supplies four receptors, viz., the saccular macula, the utricular macula and the cristæ of the horizontal and anterior vertical canals—*cf.* de Burlet (1929). Because of the trouble initially encountered in dividing the nerve branch to the utricular macula alone, and as a first step in developing the requisite technique for the ultimate clean operation, a third, impure type of utricular ablation was for the time being frequently employed. This consisted in cutting, on one or both sides, the anterior division of the eighth nerve after it has given off its branch to the saccular macula. The trunk so divided contains not only all the fibres coming from the utricular macula but also those derived from the cristæ of the horizontal and of the anterior vertical canal. This equally novel type of lesion gave results possessing their own peculiar interest.

Another point here deserves mention. A frog deprived of utricles by section of these composite nerve trunks still retains two important equilibrial receptors, viz., its posterior vertical canals. As problems occur concerning the possible influence of these canals, it was necessary to exclude one or both of them. Thus, to the primary operation certain secondary operations were occasionally added. Even after uncomplicated severance of the nerves to the utricular maculæ, the animal being then in possession of six canals, it was also necessary, as an elucidatory measure, to perform various secondary ablations of canals. Without an account of the effect of these accessory canal ablations a description of the effect of the original utricular ablation would have been incomplete. It is for this reason that the bracketed insertion appears in the title of our communication.

Because vision was found to exercise a certain definite, if subordinate, role in relation to gravity adjustments, we always divided the two optic nerves as a first step in the study of any gravity-orientation reactions. Unless a contrary indication is given, it should be understood that all frogs reported on in this communication had thus been rendered sightless.

Physico-physiological Considerations

We may here introduce two preliminary considerations with a bearing the one on the action of the utricular maculæ, the other on the action of the canals.

By " gravity " reactions in a wide sense we must understand the compensatory alterations of static posture that reflexly occur in response to simple change of direction between two things. These are the plane of the substratum available for support and the ultimate acceleration momentarily acting on the animal. It happens that three means are available for the study of these reactions. First, there is the tilt-table method. By this simple device the inclination of the substratum is changed, while the acceleration (that, namely, of terrestrial gravity) remains constant in direction. This method gives the easiest means of measuring the change of angle between the two essential elements concerned, while the corresponding adjustments of the frog are also under ready observation throughout. Secondly, there is the method of centrifugal force, in which the horizontal substratum is rotated about a vertical axis, *i.e.*, without change of direction of its plane. Here the change of angle results from alteration in the direction of the acting acceleration. Lastly, one may, again without changing the direction of the animal-supporting substratum, subject it to simple linear acceleration, preferably in a direction at right angles to that of terrestrial gravity. By this means the direction of the resultant acceleration is again changed. In essence all three methods are identical, and further, under equivalent quantitative circumstances, the animal's reaction to each is the same.

In accordance with hydrodynamical theory, any rigid, ring-shaped, hollow tube, filled with liquid, moves as one solid piece when subjected to direct linear acceleration. In these circumstances no displacement or disturbance of the fluid occurs with respect to the inclosing walls. In order that internal commotion of the liquid should occur, the ring must be subjected to a rotation of some sort. For direct flowing movement of the liquid along the hollow shell, the best conditions arise when the rotation occurs about a centrally placed axis that is normal to the plane of the ring. Rotation about any axis that lies obliquely to this plane may also cause flowing movements along the course of the ring, but in proportion as the axis departs from normality and makes a smaller and smaller angle with the plane of the ring, circular flowing movements are less readily excited. When the rotation occurs about an axis that forms a chord or a diameter of the ring, the internal commotion takes the form, not of circumferential flow, but of vortices. Thus, about whatever axis the ring is made to rotate, the angular acceleration tends to disturb the internal liquid.

Provided we consider that the membranous canals are rigid, we should expect from these principles to find (1) that each semicircular canal is best adapted to signal a rotation that occurs in its own plane ; (2) that a canal might conceivably, by vortex movement of its contained liquid, signal rotation about an axis that lies actually in its own plane ; but (3) that the canals are irresponsive to any simple linear acceleration. McNally and Tait (1933) have already stated that there is experimental support for consideration (2) for both the posterior vertical and the horizontal canals. We shall shortly provide evidence for the validity of consideration (3) as well.

Preliminary Physiological and Experimental Matters

Before we proceed to consider the particular ablatory experiments that mainly justify the publication of the present communication, it will be well to clear the ground by stating certain results that are operatively more simple of establishment.

Types of Body-Taxis

In observing frogs, whether with or without labyrinthine lesions, one comes to classify their outstanding postures under three headings.

(1) *Symmetrical.* Between the fully prone and the fully up-squatting attitude as extremes, the frog may assume any intermediate symmetrical position. In these attitudes each participant muscle of one side is in the same state of elongation as its partner of the opposite side.

(2) *Lateral Curve.* With its spinal axis bent laterally, either to right or to left, the prone animal has its head pointing in a compass direction different from that of its pelvis. In this case the pairs of oppositely situated trunk muscles and those that adjust the limb girdles one to another are in a state of unequal elongation.

(3) *Spinal Torque.* In this type of taxis, which includes all the " diagonal " positions, the " diagonal forward " or the " diagonal backward," with right-sided or with left-sided inclination as the case may be, the head is twisted with respect to the pelvis. Here the extent of skeletal and muscular asymmetry is greatest of all, because, in addition to the axial asymmetry, the Magnus and de Kleyn rule with respect to concomitant flexion or extension of the limbs also invariably obtains.

In making this enumeration we have concentrated rather on the effect upon the axial skeleton, ignoring the occurrence of all minor differences in position of the individual limbs. One reason why it is incumbent to single out these attitudes as entities (even though the two asymmetrical forms often combine one with another) is that it is characteristic of horizontal canal stimulation to induce lateral curve and of asymmetrical vertical canal stimulation to induce spinal torque. Of special interest is the fact that any sideward lean of the head (relative to the plane of the substratum) invariably involves spinal torque.

Destruction of Both Labyrinths

Observers have vied with each other in attempting to describe the disabilities of movement associated with this operation in the frog. From our present point of view, the outstanding fact is that its ability to hold any stationary posture is untouched.* Manipulate the animal into any attitude within the range of ranine accomplishment. Having posed it to satisfaction, leave it alone. The frog of itself holds and may long continue to hold the imposed attitude. Whatever be the role of the labyrinths during movement, it is plain that they are not necessary for maintenance of a given posture. Basing our deductions upon the work of Sherrington on mammals, we should infer from this experiment that it is the muscle receptors of the frog that are involved in holding its different assumed postures.

The Beritoff Experiment

Since the time of Goltz (1870) and especially of Ewald (1892), it is well known that a frog with a unilateral labyrinthectomy adopts an asymmetrical posture, in which the head leans down on the operated side, the jaw-limbs being in extension and the cranium-limbs in flexion. Both de Kleyn (1914) and Beritoff (1928) have sought further to analyse the phenomenon. By section of dorsal nerve roots in the cervical region, the former established that the persisting labyrinth exercises a primary action on the neck musculature of the frog, and that the bodily asymmetry is secondary to the torque of the neck. He also found that so long as the neck is held straight by means of the fingers, the bodily asymmetry disappears, to recur as soon as the artificial restraint on the neck is removed ; whence he inferred that the single labyrinth maintains a steady tonic action on the muscles of the neck. Beritoff, however, showed that when once the head of the unilaterally delabyrinthized animal has been artificially set straight, it will continue for a time to keep its symmetrical position, provided the restraining fingers are very gently and slowly withdrawn. As, in this state of the frog, any extraneous (*i.e.*, non-labyrinthine)

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* This statement is subject to one qualification. The head is more slackly supported than usual and with droop of the head is conjoined less rigid support of the body by the fore-limbs.

stimulation is usually followed by an immediate resumption of the previous body-lean, Beritoff concluded that the influence of the single labyrinth is not of itself sufficient to induce asymmetry. In his conception, the labyrinthine influence requires to be reinforced by special activity occurring in regions of the nervous system other than those apportioned to the mere labyrinthine reflex arcs.

What Beritoff failed to note is that the symmetrical posture is maintained only so long as the head keeps motionless. The whole art of relinquishing hold of the animal so that it will maintain a symmetrical posture, is to withdraw the fingers without moving the head. Once the head suffers any effective displacement, whether by spontaneous activity of the frog or otherwise, the previous asymmetry is at once resumed.* Indeed, close observation shows that the one necessary condition for resumption of the old posture is head movement or head displacement, and no sensory stimulation that fails to cause head displacement is adequate to disturb the temporary symmetrical posture.

These facts throw a new light on the experiment. It is precisely the labyrinthine proprioceptors that are liable to stimulation by movement of the head. As we have already seen, experiments with the totally delabyrinthized frog show that the muscle receptors themselves are adequate to hold any posture that has once been successfully imposed. Consequently, in the present instance, we have no need to go beyond the labyrinth in searching for the cause of the inevitable, final reversion to asymmetry. It is a displacement of the head, whether of passive or of physiological origin, that conditions a labyrinthine reflex, with, as its effector result, assumption of spinal torque. As a corollary to this conclusion we also infer that, so long as the head remains motionless, no labyrinthine reflex and no labyrinthine excitation occurs.

Before we leave the Beritoff experiment, one other remark may be made. By his finger manipulation Beritoff brought the posture of the unilaterally delabyrinthized animal back merely to symmetry. By the same means as it can be undone, the original asymmetry can be over-corrected, and the frog will then retain for a time a posture in which it actually leans to the intact side. This striking fact provides further evidence that, when once the labyrinth has settled to rest, it ceases to signal.

Receptors for the Gravity Reactions

If a frog is both delabyrinthized and blinded, it gives no invariable reaction to gradual tilting of the surface on which it rests. Usually, at some high inclination of the substratum, it merely falls off, without having made any previous movement. Should it have been incited to move, its new skeletal adjustment is as often inappropriate as not. If the frog is delabyrinthized without having been blinded, it does, at high angles of inclination, carry out truly compensatory adjustments. If the

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* There are certain exceptions to this statement. Contrary to Beritoff's own assertion, deep inspirations (by which the head is visibly caused to move) fail as a rule to precipitate the assumption of spinal torque. The frog may even croak vigorously and still retain its symmetry.

animal is blinded without being deprived of its labyrinths, its compensatory reactions to gravity disturbance are so precise that only under special circumstances, into which it is unnecessary to enter here, can one detect any difference in its behaviour from that of an intact animal.

Regarding the receptors concerned in dictating those comprehensive skeletal adjustments, we may consequently draw the following conclusions. In themselves the muscle receptors of the frog are entirely inadequate for the purpose. With the added help of vision the frog may react against imminent danger of unbalance. The most important gravity receptors, however, lie in the labyrinths.

Outstanding Features of the Labyrinthine Gravity Reactions

It would be tedious to attempt to describe in detail the different adjustments of the frog, by forward, backward, sideward or diagonal body displacement to simple gravity disturbance—especially as many of the facts have already been recorded and illustrated by Tait and McNally (1925). Instead, we shall deal with the principles involved.

As already affirmed, the reactions are identical whether elicited by slow inclination on the tilt-table, by centrifugal force or by application of linear acceleration at right angles to terrestrial gravity. By each relevant movement of the animal two notable effects are achieved. First, the plane of the head (ordinarily horizontal) is brought to a position normal to the momentarily acting acceleration. Secondly, the centre of gravity of the body is shifted, so that a line drawn through it in the direction of the momentarily acting acceleration falls more securely within the base of support. It is also noteworthy that the animal does not react in a smoothly continuous way to progressively increasing change of the relation between the plane of the substratum and the acting acceleration. Its adjustment to increasing gravity change takes the form of separately executed moves. The discontinuous nature of these adjustments is most noticeable when compensatory body displacement in a lateral direction is demanded. In this instance head movement and body movement occur together, and the total number of successive shifts is small. On the other hand, when the animal has to react in a simple forward or backward direction, movements of its body do not necessarily accompany each head movement. When they do occur, the movements of the body are then as abrupt and sharp as those in response to lateral inclination on the tilt-table. Meantime the successive head movements may be so numerous as almost to give an impression of continuity.

If we make the assumption that each observed movement of the animal is the reflex result of some momentarily occurring utricular stimulation, we should conclude that the utricular receptors are more sensitive to tilting about a transverse horizontal than about a longitudinal horizontal axis.

The Tilt-table—In order to facilitate examination of the postural reactions of frogs, we designed the special table that is illustrated in fig. 1, Plate 21. Three main improvements were incorporated in the design. (1) A semicircular protractor, graduated in degrees (from zero to ninety in one direction and from zero to ninety in the other), is centred on the horizontal axis of the tilt-table. The protractor is adjustable, and can be rapidly set to zero with the help of a spirit-level placed on the table-top. It is then clamped in the proper angular position, and is now fixed relatively to the base of the table. (2) By means of a worm-gear and small, handled wheel, the table may be made to tilt at any desired slow rate. When faster rates of tilt are necessary the clutch for this attachment can be at once disconnected, and the table tilted by hand. (3) The table-top is circular and may rotate about a central axis (usually vertical), which is normal to the plane of the table-top. Thus the tilt-table may also serve as a turntable. The axis of the turntable consists of a slightly tapered rod, which fits into a correspondingly tapered bearing. By selecting a lubricating oil of the proper viscosity, it is a simple matter to have this bearing sufficiently firm to prevent any undesired rotation (as when the tilted table is unequally loaded) and at the same time to have it sufficiently loose to allow of ready rotation by hand. The table-top, 20 cm in diameter, is covered with a disc of thick, soft, red rubber, whose surface is precisely aligned with the radiating graduations of the protractor. This composite table, which serves both as a tilt-table and as a turntable, has an incidental quality worthy of mention. If required, it permits of examination of a frog during circular rotation, not about a vertical axis merely, but about any oblique axis as well.

Head Translation accompanies Spinal Torque—In speaking of the posture named "spinal torque," we mentioned that the frog can lean its head to one side only by twisting its spinal axis. When (for example, by continued lateral inclination on the tilt-table) the frog with intact labyrinths is made to assume successive stages of this special posture, its head and fore-body, with each new movement, also undergo a certain amount of lateral translation, and in a direction that leads up the table. Finally, in its utmost lateral-lean position, the frog on its inclined plane has the well-known extreme attitude of a frog with a unilateral labyrinthectomy. Yet because of the translatory movement associated with each new increment of torque, even the compass direction of its head has at the finish considerably altered (say, by 20°). The body is no longer parallel to the axis of rotation of the table. Without any movement of progression, the animal has swung itself into an attitude in which it is partially ready, as it were, to climb up the table. Similarly, if a frog deprived of its right labyrinth has been artificially postured in a symmetrical attitude with its head pointing due north, its head will point to the east of north as soon as the animal resumes the attitude characteristic of a unilateral labyrinthectomy. The lateral translatory movement occurs by an angular displacement about the rump as an axis.

The Angle of Adequate Stimulation—We had expected that the angle at which the frog first reacts to lateral tilting would prove to be fairly consistent and regular.

Actually it is subject to great variation, and by no method of testing could we arrive at uniform results.

Though different procedures were used to obtain these angular measurements, one usual method was to lift the frog out of water, place it on the horizontal tilt-table and, by slow revolution of the table-top about a vertical axis, give the animal, if need be, a correct compass orientation. When, by gradual inclination of the table to one side or the other, the frog now reacts, it is removed and replaced in water. After the table-top has again been set level, the same process is repeated.

Table I, which refers to a temperature experiment, will give a fair idea of the variability to which we refer. Each vertical line of figures represents the angle at which the frog successively reacted during a consecutive series of tiltings, first to the right (R.) and then to the left (L.). The experiment was carried out on one and the same day, the frog being first tested at a low temperature, then at a higher, again at a low, and once again at a higher. The temperatures specified are those of the water, and care was taken on each occasion that the frog's temperature should be at least close to the registered water temperature.

Table I

Temperature ..	7°—8°		27°—28°		7°—8°		27°—28°	
Direction of Tilt .	R.	L.	R.	L.	R.	L.	R.	L.
	29	21	17	30	36	29	24	20
	32	15	18	26	29	30	12	10
	25	20	19	40	45	34	16	17
	21	24	16	42	40	34	10	25
	27	25	15	37	39	36	12	37
	34	36	22	26	33	39	18	15
	34	25	30	21	31	38	22	20
	28	29	21	34	36	35	15	18
	40	33	25	25	41	39	15	11
	28	28	38	27	40	38	17	14
Average	29·8	25·6	22·1	30·8	37·0	35·2	16·1	18·7

In order further to illustrate the variability and to prevent the reader from concluding (more especially from the averages as shown above on the second heating) that the kind of change induced by the temperature condition is a simple one, let us cite the figures of two experiments carried out with two different frogs, subjected simultaneously to the same temperature circumstances. The animal, frog 1, from which the first series of figures was obtained is the same as that which provided the data of Table I. Each frog was first tested at a low temperature, then at a higher and then again at a low temperature.

TABLE II

	Frog 1					Frog 2				
Temperature ..	3°		23°		3°	3°		23°		3°
Direction of Tilt ..	R.	L.	R.	L.	L.	R.	L.	R.	L.	L.
	11	10	15	15	49	42	34	41	20	33
	8	7	28	16	28	33	39	39	18	39
	9	13	20	14	44	45	43	48	24	41
	12	11	28	14	22	30	51	48	27	39
	7	7	42	7	39	30	35	38	24	40
	14	9	30	21	54	32	39	35	24	54
	5	14	28	11	35	33	43	40	34	58
	7	10	43	25	42	41	48	44	33	48
	9	12	30	18	46	39	47	43	40	47
	8	12	32	23	51	29	48	39	34	45
Average	9·0	10·5	29·6	16·4	41·0	35·4	42·7	41·5	27·8	44·4

Inspection of Table II will show that frog 1, tested on this occasion at 3° C, is consistently more responsive than when it was tested on a previous day at a temperature of 7° to 8° C. With 20° rise of temperature it becomes less responsive and, on being cooled once more to 3°, it is least responsive of all; frog 2, on the other hand, more lethargic from the beginning, is not much disturbed by the temperature change.

These tables have been given, not to serve as any basis of further generalization, but simply to exhibit the kind of perversely erratic result that one encounters in seeking to accumulate practical data on the question. Not only may the average reactivity of a given frog vary from day to day, but, as we have seen, it may vary as the result of temperature change—and then not as any simple function of temperature—within a brief period of time. On the whole, too, it would appear that the labyrinths of some frogs are inherently more lethargic under gravity test than those of others.

One clear conclusion is that the utricular otoliths are not set, as one might, for example, set a piece of mechanical apparatus, to respond at particular fixed angles of inclination. This fact may be illustrated in another way. We sometimes used the following method of measurement. The frog is tilted first, say, to its right, until a response occurs; then in the leftward direction, until a reaction of an opposite kind is registered. One may thus obtain successive measurements of the total angle between responses. These, too, show considerable quantitative variation. What is more, a frog that has first reacted on rightward tilt may sometimes react in the opposite sense, before, by undoing of the first direction of tilt, the table has been brought level again. Because of these and other analogous findings, we have on many occasions been led to infer that the momentary responsiveness to a particular direction of lateral tilting depends, in part, upon the immediately preceding orientational history of the head. The mechanism at work within the receptors is at least not that of a simple downhill slip of the utricular otoliths on the inclined surface of their maculæ.

Reactions of an Ewald Frog to Slow Tilt

When a frog with a unilateral labyrinthectomy (which we may for convenience call an Ewald frog) has by the Beritoff method been once successfully posed with its head horizontal and its body and limbs symmetrical, its reactions to gradual inclination of the substratum may be examined as in the case of a normal animal. Whether it be tilted directly backward or directly forward, it tends at some stage to bring the longitudinal axis of its head to a horizontal position. Each head adjustment of this kind is liable, but not certain, to bring on its characteristic lateral lean. The reactions of most significance for our purpose are, however, those evoked by slow lateral inclination. These are found to differ according to whether the tilting occurs to the intact or to the operated side.

Tilting towards the Intact Side—When the animal reacts to tilting towards its intact side, the response is of one invariable kind. By torque of the spinal axis the frog resumes its previous Ewald posture. The anomalous feature is that the compensation is overdone. Had both labyrinths been present, the head would have been brought merely to the horizontal. Since the angle of inclination of the substratum sufficient to excite the reaction is always less than the final angle of compensatory torque of the head, the adjustment is an excessive or overacted one. The actual angle of table-top inclination necessary to evoke the reaction varies within fairly wide limits, say, from 2° to 30°.

If, notwithstanding its first extensive alteration of posture, one still goes on inclining the substratum towards the intact side, the frog may react a second (and sometimes a third) time. It all depends whether the head torque had been complete or extreme from the start or not. Where the first assumption of Ewald posture has been only partial, the frog may, by further steady tilt in the same direction, be induced at some new stage suddenly to screw its head with increased emphasis towards its operated side. For any second (or third) adjustment of this kind to occur, it is not necessary that the leaning head should have actually been brought back to the horizontal plane. A merely partial restoration of the head towards true horizontality may often suffice in these cases to evoke augmentation of the original reaction.

A similar experiment may be conducted by placing the frog on the horizontal table, without correcting its Ewald lean. Provided the degree of this original lean is not extreme, the animal, when well tilted towards its intact side, may react by suddenly increasing its head torque. It is true that the reaction occurs most commonly when, by the slow tilt of the table, the head has been brought near to or (better) just beyond the horizontal, but there is no strict rule about this matter. A head already inclined in Ewald fashion may frequently be made to increase its original lean during the course of a table rotation which is bringing, but has not yet brought, it back to horizontality.

Tilting Towards the Operated Side—When the artificially postured frog is slowly tilted towards its operated side, it may exhibit one or other of three different kinds of movement.

A common type is one that we fell into the habit of calling " body-lapse." This is a movement in which the musculature, especially of the shoulder-joints, yields to, instead of reacting against, physical circumstance. It begins to occur only when the angle of lateral inclination is moderately high. Suddenly the upheld fore-body, not collapsing, but moving parallel to the table-top, may slip a little in the downhill direction. Each little slip (as many as three or four may sometimes occur in the course of one single extensive tilt) ends as abruptly as it began. As a cumulative result the arms eventually become slightly askew with respect to the body. The fact that these body-lapses are individual and isolated, and not part of one continuous, plastically yielding motion, raised the question whether they are indicative of corresponding, discontinuous, labyrinthine alterations. We finally concluded that they are purely muscular events, having no necessary relation to happenings within the labyrinth. One reason for so thinking is that they also occur in a fully delabyrinthized animal.

Two features of body-lapse are worthy of passing mention. Its occurrence provides additional proof that of themselves the muscle receptors of the frog are insufficient to cause compensatory adjustments to gravity disturbance. In the matter of their negative influence on the remaining labyrinth, the head displacements associated with body-lapse resemble those associated with deep breathing or with croaking (see footnote, p. 246).

The second type of movement that may occur in the course of slow lateral inclination towards the operated side is full resumption of the EWALD lean. It is very probable, however, that this result is no direct effect of the tilting. It is an indirect effect, due to the prior, accidental intervention of some other form of head movement, whether (as sometimes does happen) by body-lapse, or by physical slip of the hands and feet over the surface of the table when it is highly inclined, or as an accompaniment of some sudden, intercurrent, spontaneous effort on the part of the frog.

The third type of movement is that which really represents the action of the single labyrinth when slowly inclined to its mesial side. This is a compensatory movement, in which the spinal axis undergoes a certain small but quite definite degree of torque in a sense opposed to that which prevails in the EWALD lean. In some cases it may not occur at all. It is always most readily elicited in an animal that has not by artificial posturing been previously placed in a symmetrical attitude. When it does occur, as it frequently does—and it may be exhibited more than once in the course of one single extensive tilt—it is, however, so unmistakable and so plainly compensatory, that one has to recognize it as a true effector action of the labyrinth.

What is here significant is the trivial torque effect of these responses as compared with the powerful torque action (of contrary sense) when the single labyrinth is tilted towards its lateral side. With two labyrinths present, it is reasonably plain that any final response to lateral inclination of the head, let us say to the right, would tend to exhibit rather the strong action of the right than the weak action of the left labyrinth. At the same time we are here far from having fully explained the give-and-take between the action of two intact labyrinths under conditions of slow lateral tilt. All that is really clear is that each static labyrinth is capable of signalling in two opposed senses, and that the signal of any one in response to one direction of lateral inclination has a stronger effect than when it signals in reply to the opposite direction of tilt.

Résumé

The ablatory evidence so far available indicates with tolerable certainty that the organs of the labyrinth concerned in reflex adaptation of bodily posture to the field of gravity are the utricular maculæ. It is clear nevertheless that their function cannot be the steady holding of posture. Their part is, presumably on the occurrence of some form of otolithic displacement, promptly to break up an existing postural set and as promptly to impose one that is physiologically more suitable to the changed inclination of the substratum.

While the two utricular maculæ are similarly or symmetrically disturbed by direct antero-posterior tilt of the head, they are, in virtue of their position, one on each side of the median plane, asymmetrically affected by lateral tilt. Examination of frogs with a unilateral labyrinthectomy shows that tilting of a single utriculus towards its lateral side tends to elicit a strong compensatory movement, whereas tilting of the utriculus to its mesial side elicits a less marked compensatory movement.

The precise angle at which one and the same frog reacts on different trials to lateral tilt is subject to great variation. The mechanism of the maculæ does not seem to involve any mere slip of their superposed otoliths in the downhill direction. There is evidence that the otoliths may, at different inclinations of the maculæ, take temporary positions of stability, about which (as a mean) they may be tilted, this way or that, through lesser angles without effective disturbance. An angular movement that is bringing, but has not yet brought, the maculæ back to the horizontal, may thus produce excitation of the maculæ, just as does an angular movement that increases an existing obliquity.

The least extensive (or comprehensive), compensatory, muscular adjustments evoked by the maculæ are the slighter adaptations of the head in response to antero-posterior tilting. It is also to antero-posterior tilt that the maculæ are most sensitive. Adjustments involving the assumption of an asymmetrical posture (as in response to lateral tilting) implicate the bodily musculature in a more far-reaching way. We may here call to mind that the work of Magnus and de Kleyn indicates that, in their gravity role, the utricular maculæ first effect a local action, which is then by chain reflex more extensively propagated.

Two Remaining Utricular Maculæ

In describing the effect of the special operations, in which either all the labyrinthine receptors except the utricular maculæ are rendered functionless, or all are preserved except the utricular maculæ, it is of advantage to employ a special terminology to designate the different kinds of frogs. In the sequel the following terms will be used :—

"bisoliutricular" = with only the two utricular maculæ remaining ;
"unisoliutricular" = with only one utricular macula remaining ;
"bi-de-utriculate" = deprived only of its two utricular maculæ ;
"uni-de-utriculate" = deprived only of one utricular macula.

The present section deals, however, only with the bisoliutricular animal.

Stationary Posture—While the frog is symmetrical, its stationary posture is distinctive. With chin well clear of the ground, with lungs distended and with abdominal wall tense, the frog rests most of its weight directly on its belly. Meantime, the limbs are laterally disposed, the humeri and also the femora projecting more than usual, see fig. 2, Plate 21. While this is the invariable posture on land, in shallow water the hind-limbs are again gathered close to the body. We have not quite succeeded in referring the outstretching of the limbs to its precise variety of receptor loss. The posture is never seen in the simple absence of the four vertical canals, nor is it necessarily present in a frog that has been deprived of all six canals.

Behaviour during Movement—As soon as the animal begins to move, it exhibits the rhythmic pendular movements of a frog deprived of four vertical canals, which McNally and Tait (1933) ascribed to undesignated receptors other than canals. As a fully delabyrinthized frog behaves quite differently, the pendulation obviously depends on the presence of the utricular maculæ. In the absence of canal check, the ungoverned maculæ impel the lurching body hither and thither, until such time as the head again succeeds in coming to rest.

A spell of pendulation can at any time be stopped by providing, with finger or paper-knife blade, some temporary support for the downward moving chin. The pendular swing once checked, the utricular otoliths apparently come to rest. The animal then holds the pose present at the moment of interruption. The experiment clearly shows the operated animal to be self-excitatory, while the observation also connects the self-excitation with head movement.

The bisoliutricular animal exhibits other disabilities of movement that are not observed in a frog deprived simply of its four vertical canals. Frequently it commences to circle and may keep continuously clock-circling in lumbering, jolting fashion either to the right or to the left. This manifestation of disorder is due to the absence of its two horizontal canals, for, as we have otherwise determined, simple ablation of two horizontal canals without any additional labyrinthine damage, forthwith deprives the animal of ability to progress for any distance in a consistently forward direction. In the absence of both horizontal canals the type of body-taxis that we have called " lateral curve " may at any moment set in. Should it momentarily become dominant, the frog, in attempting to progress, is condemned to move in clock circles, invariably to that side to which its body now happens to be curved.

In addition to its spells of clock-circling, the bisoliutricular frog manifests another abnormality as compared with one deprived simply of four vertical semicircular canals. In the course of any pendular movement it may suddenly swing its head and fore-body through a great arc about a vertical axis that passes through the pelvis. This additional degree of freedom (or additional lack of control), which greatly complicates any attempted description of its total variety of movements, is again due to absence of its horizontal canals. Unlike the up-and-down oscillations of the head associated with absence of vertical canals, these great swings are, however, erratic and unpredictable, not rhythmic or pendular.

Gravity Reactions—The gravity reactions of the animal are preserved intact. There are, however, certain complications, ascribable to lack of the usual vertical canal check upon the utricles.

When the frog is tested on the tilt-table, any primary movement of compensation is liable to be followed by pendulation. Thus, if it is tilted laterally, it first compensates and may then exhibit prolonged lateral rolling of the body. If it is slowly tilted either forwards or backwards, it may at some stage develop fore-and-aft pendular plunging.

Subjected to simple linear acceleration—for this purpose the frog is set on a flat board that may be slid to and fro on the smooth surface of a table—it reacts on each occasion in the same sense as an intact frog. That is to say, by each movement of compensation the frog thrusts its body in advance of the momentary position of the travelling board. If it is being accelerated in a forward direction, its head is lowered and its body goes further forward (with respect to the board). If it is accelerated in a backward direction, its head and forebody rise while its pelvis is thrust further backward between the hind-limbs. If it is subjected to acceleration in either lateral direction, the animal leans over towards the forward moving side. To elicit any of these reactions, the horizontal acceleration applied must be of an order appreciably comparable with that of gravity—*i.e.*, at least a few feet per second per second. On deceleration (negative acceleration) all these reactions are reversed. Throughout these various acceleration displacements there is no onset of pendulation, and at the finish the frog sits motionless in its last adopted position. Here, owing to the changing rate of acceleration, the utricles are evidently under mechanical constraint throughout, and once this constraint subsides the animal simply stays at rest.

The absence of vertical canal-check begins to manifest itself only when the applied acceleration, positive or negative, is high. The compensatory movements then become exaggerated. To take two extreme cases by way of example : if the frog is rapidly pulled in a lateral direction, it may turn completely over, rolling from the prone to the supine position over that side which travels in advance—that is, rolling, as it were, uphill ; if acceleration in the caudal direction is high, the frog may leap into the air and somersault backwards. From these and similar circumstances—for the intact frog does not behave thus—one infers that the original head rotation elicited by utricular stimulation is so sudden that, if vertical canals had been present, they would have controlled or interrupted the excessive head rotation.

Body-righting—When laid supine the bisoliutricular frog may right itself by rolling either to the right or to the left. While body-righting is often prompt, the animal may sometimes struggle for a time before the appropriate reaction sets in. In deep water it may be seen that the frog's hold on its prone orientation is rather precarious, for it frequently turns turtle. Having become supine in deep water, it may either right itself immediately or it may continue for a time to float supine. When it does right itself in water it does so with a conspicuous jerk.

Rapid Tilting—A very interesting feature of the bisoliutricular frog is the nature of its responses to rapid tilting. Tilted suddenly in any given bodily direction, it is incited to move in precisely the opposite way to that in which it responds to slow tilt of a similar kind. This can only mean that the utricular maculæ, unlike the canals, have two distinct servations. Under slow tilt (" first mode " of stimulation) they bring about a static compensation, in which the centre of gravity of the body has been so displaced as to give better bodily stability. Under rapid tilt (" second mode " of stimulation) they throw the centre of gravity in an opposite direction. By this curious action the stability is more than ever imperilled.

Let us consider the matter in another relation. Slow tilt is an inadequate form of stimulation to the semicircular canals, for whose excitation a certain threshold value of angular acceleration is needed. Therefore, by gradual inclination of an intact frog, only its utricular maculæ stand to be stimulated. The kind of skeletal adjustment then elicited is, however, like that which the canals themselves would have brought about, had the angular acceleration been greater. When the rate of tilting comes well within the range in which canal stimulation would occur, the utricular maculæ enter into action in a new way, their reflex effect being now antagonistic to that of the canals. Thus we see that under conditions of quick tilt in the intact animal the canals and the utricular maculæ work in some form of complementary association.

As to the bodily adjustments due to pure macular stimulation under conditions of rapid tilt, there is little need to go into detail, for McNally and Tait (1933), in reporting the behaviour of animals with lesions of the vertical canals, have in effect stated the outstanding facts. Removal of any particular vertical canal merely uncovers (to a rapid tilting test) the real action of the utricular maculæ. In other words, all the " disabilities " now observed are positive effects of utricular stimulation. It will be made plain, too, in the sequel that if a bisoliutricular frog, on rapid tilting in one particular direction, exhibits a certain complex reaction, precisely the same reaction is evoked by canalicular stimulation, provided merely that the direction of rapid tilt is reversed.

We previously concluded that the response of the utricular receptors cannot well depend on any mere slip or " downhill " displacement of their otoliths relative to the subjacent maculæ. We shall here briefly record our inferences as to the physical happenings connected with their second form of receptor activity.

When a frog is tilted through a certain angle on the tilt-table, its head describes an arc of a circle. The farther the head is distant from the axis of rotation, the longer is this arc. Theoretically, a rapid arc displacement of the head gives a possibility of relative *translatory* movement of the otolith upon its macula, which might conceivably constitute the effective stimulus. So far as ready elicitation of this reflex goes, one finds, however, that it is a matter of indifference whether the rapidly tilted animal is near or far away from the axis. Moreover, whether the frog (with a certain compass direction) sits on this side or on that side of the axis, it always responds in the same way. These facts of themselves practically dispose of the supposition that effective stimulation involves a translatory displacement of the otoliths.

In order to eliminate the possibility of any otolithic translatory movement, we constructed a special underhung type of tilt-table, in which the table-top is 2 cm below the axis of rotation. This distance is about the usual height of the frog's labyrinths from the ground. When the animal, sitting with its two labyrinths in this axis, is now quickly tilted either forwards or backwards, it reacts as readily as before. Similarly, if it sits with its body parallel to, and with its head in the axis, it is just as responsive to quick lateral tilt. The only possible conclusion from this experiment is that the utricular apparatus responds in some way to rotation as such.

The mode of stimulation of the semicircular canals is by fluid flow. As it was possible that the same fluid movements that excite the cristæ of the canals may be responsible for the stimulation of the utricles under circumstances of quick tilting, we arranged to investigate this matter. In all the operated frogs with which we had worked, the canals and their cristæ were presumably still in perfect order, because the cristal nerves had been severed externally to the membranous labyrinths. We therefore began by cutting an arc out of particular canals with the object of interfering with the flow of endolymph through them. When once we had found that this operation produces disabilities almost equivalent to, if not absolutely identical with, severance of the particular cristal nerves, we then took some of our tested utricular frogs and removed segments from each of their six semicircular canals. The utricular reactions to quick tilt were in no way altered as a result of the damage inflicted on the canals. Consequently, we have formed the conclusion that the utricular maculæ, of their own inherent construction and independently of the fluid movements associated with canal flow, respond to rapid rotation about a horizontal axis.

If the utricular maculæ are stimulated in one way by slow inclination in a particular direction, and if they are oppositely stimulated by rapid tilt in the same direction, one would expect that at some intermediate rate of tilt they might escape stimulation. That this is indeed the case would appear from the result of swinging the bisoliutricular animal in harmonic fashion through wide angles at the natural rate of oscillation of our tilt-table. This has a period just under one second for a complete cycle. Thus treated, the frog remains flat on the table-top without either pendular swing or compensatory adjustment.

Chin-lift and Chin-drop Tests—Comparative examination of a bisoliutricular with a fully delabyrinthized animal shows that these tests, introduced by McNally and Tait (1933) for diagnosis of lesions of particular vertical canals, are positive only in the case of the bisoliutricular animal. Therefore they are essentially adapted to exhibit the residual action of the utricular maculæ, and would have no particular application in cases where the whole equilibrial labyrinth had suffered damage.

Because of its lack of vertical canals the head of the bisoliutricular frog is slack both to suddenly applied upward, and to suddenly applied downward thrust. (Because of its lack of horizontal canals it is similarly slack to any suddenly applied sideward thrust.) While the neck of a fully delabyrinthized frog shows the same tonelessness, the chin-lift and chin-drop tests are positive only in the bisoliutricular animal, because the suddenly communicated rotation of the head stimulates the utricular apparatus in its second mode of stimulation. The frog actively rears upwards (it may even leap upwards and somersault backwards) on sudden chin-lift, and collapses with great forward slew on sudden chin-drop. (To elicit the latter reaction in a still more striking way one may rap the head downwards with the finger instead of allowing it merely to drop.)

"*Irrelate*" *Reaction*—Under this name we shall include a certain connected range of effector events that in this frog supervene towards the end of any pronounced forward slew. Should the head rotation due to rapping of the head, to smart forward tipping on the tilt-table, or to forward slew occurring in the course of pendulation, have been of unusually ample range, the frog, towards the finish of the head movement, suddenly flings its hind-limbs straight backwards. At the same time it carries out a characteristic swift movement of both fore-limbs. The arms, which in this frog are already laterally extended, execute a rotation about their own axis, so that each palm is momentarily directed backwards.

The reaction proves to be merely a suddenly accentuated phase of the general limb movements in virtue of which the animal makes its forward slew. During this initial stage, before the hind-limbs are actually lifted and thrown backwards (this process also occurs in the course of simple forward linear acceleration on a board), both pairs of limbs may be seen to thrust. While we have not witnessed the backward fling of the limbs in a normal frog, it may nevertheless represent a reflex not merely pathologically conditioned by the operation and impossible of execution otherwise, but one which might well be of service in ordinary backward unbalancing. At its moment of occurrence the neck and fore-body are strongly ventriflexed. The arms contribute not only a downward movement of the fore-body but also a forward propulsive action. Even the sudden, free, backward throw of the hind-limbs must give a momentary forward impulse to the body.

Though the reaction often occurs about the time of impact of the chin with the ground, we have in a variety of ways been able to show that it is not due to sudden arrest of the original rotation of the head. It occurs just as well when all possibility of arrest by impact is eliminated.

In response to still swifter and more extensive rotational displacement of the head, the reaction takes on other striking characters. After their first catapult fling, the hind-limbs, beating the air, begin to be alternately flexed and fully extended in very rapid succession; at the same time the hands of the laterally extended arms make forward scrambling movements. In these actions, which may last for a second or two, the limbs of the two sides do not work simultaneously. Those of one side are in a different phase from those of the other, and the body rolls slightly from side to side in correspondence. The rate of the rhythmic movement is conspicuously high. It is as if the animal, in dire straits, were working to save its life.

As any sudden downward rap administered to the back or even to the occipital region of the bisoliutricular frog fails to cause an irrelate reaction, and as the head-rap that elicits the response must be applied well in front of the occiput, one would conclude that the effect is either of utricular origin or is a chain-reflex resulting from the sudden bending at the neck. Seeing that no irrelate reaction occurs when head-rap is applied to a fully delabyrinthized frog or to any animal that has been deprived of its utricular maculæ, the only conclusion is that the response is a direct utricular one.

In explanation, we ought to state that our original choice of name for the type of rapid reflex effect here described had reference especially to the final phase involving rhythmic action. As this came under observation at rather an early stage of our ablatory operations on the labyrinth, and as we were unable to ascribe any physiological purport to the manifestation, we called it "irrelate." Only at a later period did it become plain that the rhythmic stage is an extreme condition at the termination, so to speak, of a graded series of effects. For reasons of practical convenience, but nevertheless somewhat arbitrarily and illogically, we have here applied the name to that part of the series which begins at the point where the hind-limbs are actually lifted, *cf.* McNally and Tait (1933, p. 175). As we shall later discover, one important feature of interest of the irrelate reaction is that, whereas it here derives from utricular stimulation, it may in the de-utriculate animal equally result from appropriate stimulation of posterior vertical canals.

Rotation about a Vertical Axis—Rotation of an intact frog about a vertical axis may, according to circumstances, elicit one or other of two different forms of response. If stimulation of a horizontal canal occurs, the frog develops lateral curve and may circle. If the animal occupies a position not directly over or near the axis of rotation, and if the turntable, by a rate of angular acceleration inadequate to excite horizontal canals, eventually acquires sufficient angular velocity, the frog, by utricular stimulation, begins to exhibit gravity reactions.

Only the latter reactions can be elicited from the bisoliutricular frog, and, just as on the tilt-table, these are often accompanied by pendulation. Should the bisoliutricular animal sit directly over or near the axis of rotation, it fails to react even when the imparted angular acceleration is high. Similarly, if rotated supine, it makes no active movement. From these latter experiments we are scarcely, however, entitled to conclude that a single utricular macula is insensitive to spin. As both are here present, it might be that an actual effect registering itself in one is just balanced or neutralized by an equivalent effect occurring in the other. For a decision on the matter we shall have to await the result of similar experiment on a frog with only one remaining utricular macula.

Résumé

The foregoing experiments show still more clearly that the utricular maculæ are responsible for the bodily adjustments to simple gravity circumstance. Although they react to quite slowly occurring gravity change, they also, on the occasion of most of their responses, need the quickly acting control of the four vertical canals. When this control is lacking, bodily pendulation, which can however be arrested by artificial steadying of the head, and which is an exhibition of what an engineer would call " hunting," is liable to accompany any sudden head movement. As with the pendulating body itself, so, in the absence of vertical canal control, something of a rolling or swinging nature presumably occurs within the receptors responsible for the pendulation.

Besides reacting to slow tilt, the frog with only two utricular maculæ is also responsive to rapid tilt. Instead of being compensatory, the reflex response is now such that the centre of gravity of the body is actively moved in the physiologically wrong direction. There are thus two modes of stimulation of the utricular maculæ, namely, the ordinary gravity mode and a rapid-tilt mode. All the tilt-table disabilities of frogs with any mere vertical canal lesion (or lesions), also their peculiar behaviour under the chin-drop or chin-lift tests, are in reality manifestations of the rapid-tilt mode of stimulation of their utricular maculæ.

By removal of arcs of the membranous canals it can be shown that the rapid-tilt mode of stimulation of the maculæ is unconnected with the simultaneous fluid movements set up in the canals. Moreover, as the utricles are stimulated by rapid tilt when all possibility of simple translatory slip of their otoliths over the maculæ is eliminated, it would follow that the utricular receptors are in some way designed to respond to mere quick tilt as such.

While its maculæ are responsive to rapid tilt, any rate of spin of its two utricles about a vertical axis fails to cause a reaction in the bisoliutricular animal.

ONE REMAINING UTRICULAR MACULA

As the procedure for depriving the frog of all labyrinthine receptors except one utricular macula involves an operation on both sides, we shall here call that side on which the eighth nerve has been wholly divided the ut — side, the other side being correspondingly denoted the ut + side.

De-utriculate Asymmetry—The resting animal is asymmetrical. Its head leans downward on the ut — side, but not always to the same extent in one and the same frog. Sometimes the lean may be only 25°, at other times, say, 35°, and occasionally as much as 45°. As a rule, however, the degree of spinal torque is distinctly less than that of an Ewald frog.

McNally and Tait (1933) have shown that frogs with a simple lesion of vertical canals may frequently exhibit a temporary, or non-obligatory, decanaliculate asymmetry. Because the inequality of the operation in the present case concerns only the utricles, and because we shall later find the same kind of asymmetry in the uni-de-utriculate animal, we shall name it de-utriculate. It differs from any decanaliculate residual pose in the following respects. The asymmetry is greater, 15° to 20° of head-lean representing a maximum for decanaliculate posture. It is less easily undone and has strong marks of permanency. It includes, too, a greater range of gradation than the decanaliculate, being in its most exaggerated phase as pronounced as the extreme stage of asymmetry of an Ewald frog.

Two questions in relation to the de-utriculate asymmetry deserve comment. Firstly, the fact that the unisoliutricular frog exhibits different degrees of the asymmetry is to be correlated with the difficulty of obtaining regular or consistent figures, when a merely blinded animal or one with two utricular maculæ remaining is subjected to slow lateral tilt. Evidently the otolith of the unisoliutricular frog may attain stability at different degrees of inclination of its underlying macula. Secondly, the fact that the usual degree of spinal torque of the present is less than that of an Ewald frog is to be correlated with the presence of vertical canals in the intact labyrinth of the latter animal. This inference may be experimentally verified. After severance of the nerves to the cristæ of its two untouched vertical canals, an Ewald frog forthwith becomes, as far as posture goes, like the unisoliutricular animal, its average degree of torque being no greater and no less.

If the unisoliutricular animal has once adopted a position of strong spinal torque towards the ut — side, lateral pressure applied (or lateral support given) to the palm of the strongly extended ut + fore-limb will enable the animal to lean more than ever to the ut — side. The frog is willing under these conditions to rest on the ut — border of its fore-body, with the transverse diameter of its head now vertical. The same holds true of an Ewald frog. Thus it is plain that, if only the frog's anatomical arrangements permitted, it would as a result of unilateral utricular ablation, exhibit at times an even greater degree of spinal torque than the maximum ordinarily observed.

By digital manipulation the de-utriculate asymmetry of the unisoliutricular is more easily corrected (or over-corrected) than that of the Ewald frog. Indeed, the unisoliutricular frog may of itself sometimes come to rest in an upsquatting posture that is quite symmetrical.

In addition to the head lean with its corresponding (Magnus and de Kleyn) disposition of the fore-limbs, the de-utriculate asymmetry involves other features that are worthy of note. While the hind-limbs may be kept well flexed, they are not identically disposed. On the ut — side the heel is always higher than on the ut + side, and the astragalo-calcaneum segment of the foot has a marked degree of verticality. The abdominal wall on the ut — side is also in tonic contraction, whereas that on the ut + side is relaxed. As a consequence the lungs and viscera become pushed to the ut + side, and the paunch here exhibits a lateral bulge. Because of the lung displacement (these animals, like the fully delabyrinthized, are at all times somewhat bloated), the frog floats with a decided list to the ut — side and with the abdominal wall on the ut + side above water. Should it happen to float supine, the ut + side is again higher than the ut — because on this latter side the abdominal parietes still remain in tonic contraction.

Pendulation—When the frog begins to move, it is seen to be even more unstable than the bisoliutricular. To the accompaniment of strictly correlated limb movements, its head rolls from side to side, or plunges now in this direction, now in that. In this instance, however, the animal, possessing an original list to the ut — side, keeps the same list throughout any spell of pendulation-accompanied movement. In its lateral rolling, for example, the white of its belly frequently comes into view on the ut + side. While this may also occur even on the ut — side, its incidence is distinctly less frequent. When antero-posterior pendulation occurs, it is not of the usual log-sawing kind. Moving about a transverse (but not horizontal) axis at the neck, the snout swings conspicuously up and down without much corresponding body or limb movement. As with the bisoliutricular frog, so in this animal digital steadying of the head may at any moment stop heavy pendulation and allow the harassed animal to come to rest.

Moving in deep water the frog is also extremely unstable. There its head sways, swings, rolls and tumbles to the accompaniment of corresponding limb movements. Many a time in swimming it may drive its head and half its body out of the water. Sometimes it spirals, going from prone to supine with the ut — side lowermost, and from supine to prone with the ut + side lowermost. The promptitude with which it then flings itself from the one orientation to the other is conspicuous.

Circling—An interesting feature is the frequency with which, on any attempted progressional movement on land, the frog falls into clock circling. The circling, accompanied by great bodily instability, usually occurs in a direction away from the ut — and towards the side of the persisting utricular macula, though we have observed reversal of this all but invariable rule.

In thus circling to the ut + side the frog may violently roll from one side to the other, and in its rolling it comes near to upsetting. Thus, with each roll to the ut — side the hand and stiffly extended arm of the ut + side may be lifted quite off the ground and the white of the animal's belly becomes visible from above. While, from its general trim (*i.e.*, with a list to the ut — side) one would expect the frog to be least stable on the ut — side, in actuality it is almost as apt to upset over the ut + as over the ut — side. This is because, by a wild circular sweep of the ut — arm, the body is every now and then pushed through a great arc to the ut +

side. As the ut + arm, at the end of any such push is momentarily in flexion, the frog may then throw itself directly on its back. When it rights after a fall of this kind, it does so by reversing the direction of the original upset, now turning from the supine to the prone position by rolling again over its ut + side.

In deep and also in shallow water, when the body has hydrostatic support, the direction of clock circling for some reason becomes reversed. Under these conditions the frog is especially apt to turn turtle over the ut — side.

Righting Reaction—The frog may readily be induced to lie supine, for its power of righting is gravely deficient. When it does succeed in righting itself, it invariably rolls from the supine to the prone position with its ut + side lowermost. If one attempts passively to turn the supine animal in the opposite direction, it resists and refuses to right itself by turning with its ut — side lowermost. On the other hand, with digital help, it is rather readily induced to roll from the supine to the prone position with the ut + side lowermost. Often, after it has been thus assisted to right itself, by unaided continuation of the same direction of revolution it rolls over on its back again, now turning from prone to supine with its ut — side lowermost. These reactions show that, if once rolling is initiated, an isolated utricle may cause both a righting reaction and an upsetting reaction.

In deep water, as on land, the frog may long remain supine. As already stated, its ut + side then tends to float at a higher level than its ut —. When the frog rights itself, it does so by rolling from supine to prone with the more buoyant ut + side lowermost, just as it had originally turned in a similar direction of revolution from prone to supine with the ut — side lowermost. In water, too, it resists any digital manipulation that seeks to roll it from the supine position in the direction of its existing hydrostatic list, but readily yields to an opposite direction of finger manipulation.

As it is easy with the unisoliutricular frog to make observations on the order of events during both body-righting and upsetting on land, and as these events are of no small importance in the study of labyrinthine lesions, the process may be briefly described here. For successful accomplishment of overturning a sudden onset of spinal torque must be supplemented by particular limb movements. For the reaction of body-righting the hind-limbs are principally responsible ; for that of upsetting, both the hind- and the fore-limbs. In the unisoliutricular frog, whether prone or supine, the spinal torque always occurs in the same sense. That is why the animal may on occasion go on rolling.

Before upset, the spinal torque has induced the MAGNUS and DE KLEYN disposition of the fore-limbs, and one side of the body is lower than the other. The hand of the lowermost side, having been brought to the region of what, if the frog were a man, would be its opposite vest pocket, makes rapid, scratching, pulling movements on the ground ; at the same time both the uppermost fore-limb (jaw-limb) and the uppermost hind-limb actively thrust. Prior to body-righting, the stiffly extended jaw-limb now takes a position ventrally athwart the body. Here it is merely out of the way.

When the supine frog is about to right itself, the hind-limb of the side over which it is going to roll is suddenly thrown straight backward. This " long-splint extension " is merely a facilitating device. The other hind-limb contributes an upthrusting action to the pelvis. To this end, it is first thrown laterally and backward (" pre-thrust extension "), but never to its fully extended reach, because, in order to thrust, it must retain a certain reserve of elongability. It is mainly by the subsequent up-thrust of the femoral head of this limb that the animal, simultaneously twisting itself, is enabled to right. In the reaction of upsetting, the hind-limb of the side over which the animal is to roll is also frequently thrown into long-splint extension, while its opposite partner may then be seen to have the pre-thrust extension pattern. For a convenient snapshot illustration of the limb disposition involved in an upsetting movement, see McNally and Tait's (1933, p. 179) account of the posture, at the moment of landing, of a frog deprived of two vertical canals of the same side.

In order to make leisurely and deliberate observations on body-righting, one may treat the unisoliutricular frog in either of two ways. Having placed it in a supine position one may rock it gently by finger manipulation, or one may, by appropriate tilt of the horizontal platform on which it rests, cause its back to roll a little on the board. This light rolling movement will then excite pre-thrust extension of the hind-limb of that side away from which the animal is momentarily being turned. Nevertheless the frog can right itself only when it is rolled to the ut + side, for only then do the following events supervene: sudden onset of spinal torque, upthrust by the hind-limb that is already in pre-thrust extension, and (what is customary but not essential) long-splint extension of the lowermost hind-limb. If the body-righting is initiated by tilt of the underlying platform, the frog is now liable to keep rolling downhill. During this process one may, but with more difficulty because of its speed, make observations on the reaction of upsetting.

Slow Tilt—Under slow tilt, the animal's reactions, apart from the frequent concurrence of pendulation, are in general like those of an Ewald frog. Especially is its behaviour during lateral tilting a matter of concern, because of the interest in knowing how an isolated macula signals when inclined towards its lateral and towards its medial side respectively.

While we have many records of tilting experiments carried out at different times, it would only weary to quote any of these in detail. The chief results (concerning lateral tilting) may be condensed as follows. As in the merely blinded, the bisoliutricular, or the Ewald frog, compensatory reaction occurs at very different angles on different trials. The compensatory reaction on tilting the animal to its ut — side is always feebler than that which follows tilting to the ut + side. At the same time the ease with which a given compensatory result is elicited depends on the prior posture of the frog. Slow tilt of the artificially postured animal towards its ut — side is usually accompanied only by body-lapse. It is when the animal retains its original lean from the start that the mild compensatory movement on slow tilt to the ut — side may best (and then not always) be observed. On slow tilt to the ut + side this rule does not hold; if anything, it is reversed. More frequently there is no body-lapse, the first movement being simply an abrupt resumption, or increase, as the case may be, of the original de-utriculate lean. These observations may either be taken to mean that the responses of the animal to utricular stimulation are dependent on the existing state of its muscular bodily taxis, or, what is perhaps more likely, that the response of a single utricular macula to slow lateral tilt depends on its immediately previous orientational history.

Rapid Tilt—If the frog is first postured in a symmetrical attitude and then tipped smartly forward or backward, it immediately resumes its original lean to the ut — side. If the asymmetrical frog is similarly tipped forward or backward, its responses resemble on the whole those of a bisoliutricular animal. On quick backward tipping, however, the head is heaved conspicuously upward, especially on the ut + side so that the snout points almost vertically upwards. Simultaneously the toes and sometimes the foot on the ut + side are extended, and the hand of the extended arm on the ut + side may part company with the table-top. On forward tipping, the head is thrown smartly downwards and forwards. At the same time both fore-limbs may be laterally extended and, by a twisting action of the humeri, the forearms and hands are quickly rotated backwards. This means that a single utricle may exercise a symmetrical, or nearly symmetrical, bilateral effect on the arms. Sometimes the corresponding influence on the hind-limbs is of an equally distributed kind, for both may begin to beat rapidly. At other times a distinction may be observed. Thus, the hind-limb of the ut + side alone may be thrown backward, or that of the ut — side may pass into long-splint extension while the limb of the ut + side beats. By pendular action the first downward slew of the head is then followed by an upswing.

The responses to quick tipping in either lateral direction are perhaps of special interest. Reference to pp. 256 and 257 will show that in general the skeletal adjustment of the bisoliutricular frog to quick tipping in one direction resembles that to slow tilt in the opposite direction. As we already know how the unisoliutricular frog responds to slow tilt, we have here an opportunity of confirming or refuting our previous conclusion.

On the whole the result may be claimed as confirmatory. While quick tilt to either side brings about extension of the two limbs of the opposite side, *i.e.*, of the two limbs momentarily uppermost, and twisting of the head towards the lower side, the effect is by far the most marked when the sudden tilt is towards the ut — side. In this latter case the frog may frequently upset. In the overturning process no long-splint extension of the lowermost hind-limb occurs, and the animal merely rolls over a folded ut — hind-limb. The feebler reflex response to rapid tipping towards the ut + side is more constant in occurrence than the corresponding (" mild compensatory ") movement when the animal is slowly tilted towards the ut — side. In this case the torque movement, or rather the undoing of the already existing torque, is complicated by a simultaneous slew, or lateral translation, of the fore-body towards the ut + side, a feature which is not observed when the frog responds to slow tilt in the opposite direction. The gravity conditions in the two cases are, however, different. On the slowly tilted table the head, if it were to move laterally, would have to slew in an uphill direction. Under present conditions the slew is downhill. Sometimes when the frog is quickly tilted to the ut + side it may upset. At the moment of upset the hind-limb of the ut + side is in long-splint extension, but the arm of that side fails entirely to make those dragging movements that invariably occur when the upset is in the opposite direction.

Rotation about a Vertical Axis—Set directly over the axis of the turntable, the frog, whether (1) prone with de-utriculate asymmetry, (2) prone and symmetrical, or (3) supine, gives no response whatever to simple spin about a vertical axis. A utricular macula, in other words, is not designed to respond to rotation about a vertical axis, so long at least as the essential direction of gravity is not thereby changed.

From this one might go on to draw a further inference : Being sensitive to rotation about any horizontal axis, the maculæ, as we have frequently observed, work in close association with the four vertical canals. A horizontal canal, on the other hand, stimulated by rotation about a vertical axis, can have no corresponding functional relation with the utricular maculæ. Later evidence will support this conclusion.

Résumé

The posture of the unisoliutricular animal is one of spinal torque. Because of the very specific nature of its operation, its asymmetry is purely de-utriculate ; it may be considered as a rather fixed variety of residual pose. Though the degree of torque varies widely at different times, its usual amount is greater than any decanaliculate torque and, for reasons that may be satisfactorily analysed, less than the prevailing degree of torque of an EWALD frog. Large areas of musculature, including abdominal walls and hinder extremities, are involved in the de-utriculate torque.

During movement the unisoliutricular is even more subject to pendulation than the bisoliutricular frog. On land it tends to circle towards the side of its functional utricular macula, but in water this direction of circling is reversed. Laid supine or floating supine, it rights itself by rolling in one direction only, *i.e.*, with its intact utricle lowermost. The process of body-righting as well as of upsetting may be conveniently studied in this frog. Any act of overturning involves a sudden onset (or sudden increase) of spinal torque, always of the same sense, which must be assisted by appropriate limb movements.

The reactions of the animal to slow and to rapid tilting enable one to confirm the broad conclusion that the skeletal adjustment to quick tilt in a given direction resembles that to slow tilt in the opposite direction. By quickly rotating the frog about a vertical axis, one discovers that a utricular macula is irresponsive to spin, and that the maculæ cannot therefore have any close functional association with the horizontal canals.

Bilateral Section of the "Conjoint" Nerve

By the "conjoint" nerve is meant that part of the anterior division of the eighth nerve which supplies the utricular macula and the cristæ of the two anteriorly situated ampullæ. The frog with bilateral section of this composite trunk we shall call a "biconjoint" frog.

Posture—By its prevailing posture, which is one of axial ventriflexion, the animal at once attracts attention. With arms laterally extended, the fore-body is carried low, while the chin often touches the ground. If the frog is placed at the edge of a table with its head projecting outwards, the snout, being now unobstructed, may sink well below the level of the table surface, fig. 3, Plate 21. The unusual ventriflexion of the axial skeleton may also be observed in deep water. When after swimming the animal subsides to the bottom, there to rest for the most part prone but sometimes supine, its posture might suggest that a tight bow-string joined its snout to its pelvis, fig. 4, Plate 21.

Whereas the ventriflexed posture tends to supervene whenever the frog is handled or disturbed, it is not altogether obligatory. Left quietly to itself, the frog can bring its head to the horizontal level. It can also at any time be induced to do so by a slight artifice. If the water-tap of the sink in which it sits is turned on and the water begins gradually to rise, the frog will, by a succession of slight upward adjustments of the head (each associated with a forward pace or two) keep its nostrils just above water. While the attainable head and fore-body level does not go beyond the horizontal, one may, by very patient and persistent elevation of the chin, eventually, after minutes, succeed in bringing the animal into the upreared posture of an alert intact frog. Should the raising of the head at any point be abrupt, should the frog of itself make any intercurrent movement, the whole process has to be begun over again, for sudden movement of any kind merely precipitates immediate resumption of the original obstinate ventriflexion.

The reason for the peculiar behaviour of the animal may be given at once. The posterior canals are in unrestrained control. As they may be stimulated in any spontaneous movement, and particularly by backward rotation, they are at every instant ready to intervene, and their positive action is above all to ventriflex the spinal column and head. The proof of this statement is that, if the nerves to these canals are cut, the frog forthwith loses its axial ventriflexion, thereafter behaving like a fully delabyrinthized animal.

The posture is not always symmetrical. Two main deviations from symmetry may frequently be observed—spinal torque and lateral curve—with each of which some depression of the snout is always associated. In general the twisted postures of this frog, owing to absence of its utricles, tend to be more exaggerated than are any residual poses resulting from simple section of nerves to vertical canals.

Gait and Leaping—Keeping its hind-limbs closely gathered to the body and rarely allowing them to extend backwards, as does a normal frog in crawling, it moves its feet in a succession of little rapid steps, with which the fore-limbs keep time.

Progression in this hurried way may be either forwards or backwards. It is never rectilinear, for, from lack of horizontal canals, the animal constantly changes direction. Because of this, one may safely leave a number of them for a time together on the open floor and depend on finding them in the same approximate location on one's return. The natural prone position is on the whole well maintained. Occasionally a biconjoint frog, in executing an abrupt sideward bend, may throw itself on its back, but this is rare.

Children sometimes play a game of " wheelbarrow," in which one child of a pair acts as the barrow. His legs being grasped by a companion and held as barrow handles, while his arms do duty for the wheel, the " barrow " permits himself to be trundled by his fellow. The biconjoint frog can be similarly trundled in a forward direction, provided one lifts and pushes the animal not by its hind-legs but by its rump. In shallow water animals with this operation tend to rest on vertically held fore-limbs, the hinder body with its extremities floating free behind. Not infrequently they may now propel themselves gently forward by strokes of the hind-limbs, the fore-limbs meantime acting the part of the barrow wheel. This is almost the only occasion on which we have seen frogs of the kind spontaneously progress for a space in one consistent forward direction.

While the biconjoint is at all times chary rather than prodigal of movement, in which respect, as we shall later see, it resembles the bi-de-utriculate, it is never observed to hop. There is one exception to the statement. If one should have succeeded in manipulating an animal of the kind into an upslanting posture, it may, on being startled, effect a powerful leap. Often enough the attempted leap from a similar posture is cut short at the beginning and transformed into an abrupt nose-dive to the floor. This helps to explain why the animal left to itself, and whose head is never raised beyond the horizontal, is incapable of jumping. From absence of the anterior canals, too, it will be understood that simple falls of the head, particularly at one or other corner, frequently occur in the course of its irregular motor activity. Equally in semi-continuous circling and in sudden individual or isolated downward and forward movements—aborted leaps—the head, previously carried free of the ground, may smite the floor.

Both on settling to rest and also during movement, the head and fore-body are affected by a just perceptible tremor. With this manifestation of disability, which also occurs, in more varied fashion, in the bi-de-utriculate animal, we shall deal in a later section.

Swimming Activities—Placed in water, the frog, in sharp contrast with its general inactivity on the solid ground, becomes very active. It frequently begins by executing wild clock-circling movements, in which, while maintaining on the whole the prone position, it carries its alternately beating hind-limbs at an unusual angle. While the other segments of these limbs are in a position of extension rather than of flexion, the thighs are more in flexion than in extension. As a result the straightened hind-limbs, instead of being consistently behind the rump, are just as frequently in front of it. This gives an odd aspect to the rear end of the animal, for the body, instead of being continued behind into the Y-fork of the two elongated limbs, seems to end bluntly and abruptly in the projecting rump. A similar alignment of the beating hind-limbs is even more frequently seen in doubly delabyrinthized frogs. While the direction of the circling is a matter of accident, the frog having once begun to circle keeps rotating in the same sense. Reversal of direction occurs only after a stop, or as the result of some external intervention, as, for example, being seized between the fingers. During the circling movements the body is always ventriflexed and the nostrils are under water.

At other times the frog, by alternate movement of the hind-limbs, which are then more laterally extended than when the animal " backs " on the ground, may progress slowly backward in water. This action readily passes into backward circling. Still another evolution is ventral " looping the loop." The frog, driving onward with ventriflexed body, first forces its snout downwards, then by continuation of the movement becomes supine, and finally with upward glide of the head returns to its previous prone position. Diagonal-forward " looping the loop " also occurs. The animal begins the evolution with diagonal depression of the head and then rolls over more laterally than antero-posteriorly, returning at the finish to the normal prone position.

Floating at the surface in alligator position with their nostrils above water, the animals may also slowly drive themselves forward by alternate strokes of the hind limbs. Under these conditions the head, moving about a vertical axis that passes through the region of the occipito-spinal joint or of the intervertebral joint next to it, sways with each limb-beat from side to side through a small angle. Submerging, the frogs may make a fair show at forward progression for a very short distance. At any moment, however, they are apt either to lose their compass direction and to deviate laterally, or to lose their horizontal trim and to dive downwards. The water surface of a tank that contains a few of these frogs is frequently broken by the splash of their hind-limbs when they thus struggle in diving, and the manuscript of the observer who sits beside them taking notes is often splashed by the water they throw about. Their best attempt at direct forward movement is when they happen to smite their hind-limbs not alternately but synchronously.

Falling Asleep in Deep Water—At any odd time one of these frogs in deep water is apt to pass into a state of inactivity accompanied by cessation of respiration, by reduced excitability to stimulation, and by a characteristic posture, which we have been in the habit of calling the " drowned man condition"—see fig. 5, Plate 22. The back being arched with concavity ventralwards, the nostrils usually below water, the limbs extended and the eyes closed, the animal comes to rest in whatever position it happens to be hydrostatically stable. Sometimes it floats, more usually it sinks, and in this position it is carried passively along in any chance current of the water. Should it then collide with an obstacle, it is not necessarily aroused but drifts on like any piece of flotsam. Nor is the non-blinded animal, even though ordinarily shy and timid, then responsive to visual stimulation. Whether the optic nerves have been cut or not, the frog in this state has its eyes shut. One can only conclude that it has temporarily fallen asleep.

In water at 18° or 19° C these periods of somnolence may last for a few minutes ; in cold water they last much longer. They are interrupted apparently by need of oxygen, for the animal having opened its eyes becomes active at intervals and continues active until its nostrils again come above water, when its limb movements cease and it respires rapidly for a spell. Then, if not otherwise disturbed, it is apt to pass into the same soporific state as before.

The position of hydrostatic stability during sleep depends upon the temporary distribution of air within its body, which, it may be observed, does not undergo alteration during any single spell of somnolence. As a consequence the head may assume any orientation with respect to the field of gravity. If with two light rods appropriate coupling forces are now gently applied to the body or limbs, the submerged animal may be turned from the prone to the supine position and *vice versa* without evoking any movement by way of compensation or resistance. Should the animal, after tilting beyond a point of critical stability, begin at any stage to revolve with appreciable rapidity directly backwards, diagonally backwards, or even at times laterally, it is apt to receive stimulation from its posterior canals and so to be aroused. Short of this, however—and, be it noted, mere forward acceleration does not arouse—it may for the time being be manipulated at will, and may also at need be held in any orientation whatsoever.

As this slowly performed test appeared to be indicative of the absence of the utricular maculæ rather than of any particular canals, we selected for a similar test a frog with intact utricles but with the nerves to all six canals sectioned. While this latter type of animal will also (somewhat less readily) fall asleep in deep water, it is much more responsive to change of orientation. By no process could we succeed in rolling it about in the same fashion as the frog with bilateral section of the conjoint nerves. When its head had been swung into a slightly changed inclination, it opened its eyes and struggled. The illustrations in figs. 6 and 7, Plate 22, exhibit the difference between the two types of frog.

Other Gravity Reactions—To any form of passively imposed, slow inclination on the tilt-table the frog is irresponsive. As, in these circumstances, its low posture, often with chin resting on the table-top, might in some way interfere with the exhibition of a proper gravity reaction, we tried similar experiments with animals that had already been posed in an up-squatting attitude by the method previously described. When slowly tilted backwards, they simply fell backwards off the table. When slowly tilted in a lateral direction, they showed body-lapse but no compensatory movement.

Should the animal happen to leap from any slight height, or otherwise to propel itself over the edge of an eminence, it may strike the ground in any position. Instead of landing prone, as does a normal animal, it may first collide with the ground by its nose, by its side or even by its back. If, selecting two frogs, one normal, the other with a bilateral conjoint lesion, one proceeds to drop them from varying heights on the surface of a couch, the normal animal is found to possess the ability to right in the air—*cf.* BERITOFF (1928)—whereas the operated animal is unable to do so. As we shall later see, mere ablation of the utricular maculæ alone produces a similar disability.

Body-righting : Rotation about a Vertical Axis—The use of the double phrase in this heading is of design, for there is a connection between the two things.

To begin with body-righting. As the normal gravity reactions are abolished, it is of no little interest to find that the body-righting reaction is prompt and is expertly carried out. Only with careful manipulation can the biconjoint frog be induced to lie on its back. In this respect it is far less accommodating than the bisoliutricular animal. The righting may occur equally well to either side. When a normal animal is placed in a supine position on a slanting surface, it usually rights itself by rolling over downhill. Should it momentarily lie supine on a horizontal surface, lateral inclination of the substratum at once incites righting in the downhill sense. In these regards the biconjoint exactly resembles the normal frog.

If, on the horizontal turntable, the frog, momentarily lying supine, is subjected to smart rotation towards a given side, it rolls at once from supine to prone with that side lowermost. Should the rate of angular acceleration to the specified side have been insufficient to induce body-righting, the frog may, on sudden cessation of the rotation, right itself by rolling over the opposite side. As a delabyrinthized and even a bisoliutricular frog under similar circumstances remain wholly unresponsive, it is plain that some labyrinthine mechanism, retained in the biconjoint frog and destroyed in the other two, is responsible, and in a perfectly determinate and consistent fashion, for the righting of the rotated biconjoint.

That the mechanism in question is the pair of posterior canals is indicated by the following facts. As McNally and Tait (1933) have shown, prominent actions of a given posterior canal are (*a*) to cause spinal torque, (*b*) strongly to ventriflex the head on the opposite side, and (*c*) simultaneously to extend, or stiffen, the hind-limb on its own side of the body. When one watches the effect on the supine biconjoint frog of turntable rotation, say, towards its left, one notes that the spinal axis becomes torqued, that the right side of the head becomes strongly flexed on the abdomen and that the left hind-limb is thrown into long-splint extension. This points to effective stimulation of the left posterior canal.

Experiment proves the conjecture. If, by subsidiary operation, one severs in the biconjoint frog the nerve from its left posterior canal, it gives no response to leftward rotation when lying supine on the turntable. If, however, the rotational movement to its left is abruptly stopped, or if one begins by rotating the supine animal to its right, it recovers its prone position at once by rolling over its right side. If, apart from rotation, the frog is simply deposited on its back, it is now seen to have more trouble in righting itself than before its secondary operation, and may long lie supine. When it does right itself it does so by turning from the supine to the prone position with its right side lowermost. Finally, if the nerve to the single remaining posterior canal is severed, the frog, so far as body-righting is concerned, is reduced to the condition of a fully delabyrinthized animal.

If the posterior canals inverted are responsive to rotation about a vertical axis, we should expect that in their normal orientation they would be stimulated by similar rotation. When the prone biconjoint animal is subjected to rotation on the turntable it neither swings its head by lateral curve in a direction counter to that of the rotation, nor does it circle. Instead, it develops a spinal torque, in which the fore-limb on the side to which it is rotated becomes for the moment a "jaw-limb" and the opposite fore-limb a "cranium-limb." It retains this position of spinal torque so long as the attained rate of rotation keeps constant. When deceleration occurs, the animal subsides again into symmetry, or assumes a spinal torque of opposite sense. If one should grasp the vertical stem of the turn-table and by wrist movement make it revolve (through 60 or 70 degrees) alternately in one direction and then in the other, the frog's body keeps rolling in correspondence.

The rate of angular acceleration required to elicit the reaction is definitely higher than that ordinarily adequate to stimulate horizontal canals. In order to make the supine animal react to rotation about a vertical axis, a moderately fast rate of angular acceleration is also necessary. If the angular acceleration is very high (the frog being rotated, say, to its right), it may in addition throw the right hand out laterally and throw the left hind-limb into long-splint extension. Thus it gives the impression of being about to upset over its left side. By fast rotation in an opposite sense it may similarly be brought near to the point of upsetting over its right side. If the frog is set, not over or near the axis of rotation, but at the outer edge of the turntable, it likewise reacts in two different senses according to the direction of rotation. If it sits, for example, with its right side towards the turntable centre, on being spun in a forward direction it leans downwards and outwards, on being spun in a backward direction it leans inwards.

After severance of the nerve to a right posterior canal, the biconjoint prone frog no longer responds to rotation about a vertical axis to its right. Only on cessation of the rotation or when one begins by rotating the animal to its left, does it respond as before.* If the nerves to both posterior canals are severed, the animal entirely ceases to react when rotated about a vertical axis. Thus experiment finally shows that, whether the posterior canals are in the inverted or in the normal orientation, they may be stimulated by adequate angular acceleration about a vertical axis. The rule for effective stimulation is similar to that which holds for the horizontal canals, namely, each posterior canal responds only to a rotation towards its own side of the body.

The prompt body-righting of the biconjoint frog is now explicable. With its first struggling movement it stimulates a posterior canal. This sets the whole righting process in operation.

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* The animal reacts similarly, but more readily, when the axis of rotation is normal to the plane of its persisting canal. Thus, on quick diagonal backward tilt in the "plane" of the intact canal, it seeks at once to overturn, and although upset must now occur in the difficult uphill direction, the manœuvre often succeeds.

Sudden Backward Tip of Head—To any forward tipping the animal is quite unresponsive. So, too, head-rap applied to the upsquatting animal will bring it to the ground only if the degree of mechanical force therewith applied to the fore-body is sufficient. On the other hand, any direct backward tip of the head, whether by chin-lift or by table-tilt, immediately excites both posterior vertical canals. The response then elicited is the spectacular irrelate reaction. According to the degree of angular acceleration employed, the stimulated canals may evoke any grade of the reaction, ranging from an embryonic phase with mere forward thrust of the body and ventriflexion, to the final stage in which the frog, with scrambling arms and wildly beating hind-limbs, keeps its body oscillating in tempo with the alternate movement of its limbs.

The elaborate irrelate reaction may thus be elicited from two quite different kinds of labyrinthine receptors. Whether we stimulate an isolated pair of posterior canals by sudden backward tilt or an isolated pair of utricular maculæ by sudden forward tilt, the end result is the same. If we may change our phraseology, the case presents this unusual feature, that the final common path—see SHERRINGTON (1906)—for these two separately evoked reflexes includes more than the ultimate motor neurones that directly activate the participant muscles. The common pathway in this case obviously involves an extra part of the neuraxis as well. This additional stretch of common roadway must be neurones of the vestibular nuclei with axones in the vestibulo-spinal tract. It is on the anterior end of this bi-neuronal common route that the two sets of incoming Scarpa neurones converge. Each relevant neurone in the vestibular nuclei must therefore receive at least two synapsing fibres, one connected with a utricular macula, the other with the crista of a posterior canal.

It would be strange if the very precise type of relationship thus displayed, through the medium of the irrelate reaction, as existing between utricular maculæ in their second mode of stimulation and posterior vertical canals, were not of more general application. A similar relationship also seems to exist between the anterior vertical canals and the utricular maculæ. Though we cannot yet say, as we can of the canals, that the suddenly tipped utricular maculæ are stimulated by angular acceleration, further pursuit of this method of operative investigation should eventually make more plain the precise kind of functional relationship between the utricular maculæ and the four vertical canals. The whole co-operating receptive apparatus in question might well receive a special designation. We shall call it the " vert-utricular (receptive) mechanism."

Résumé

While the biconjoint animal has lost the use of its utricles, its more conspicuous symptoms—*e.g.*, axial ventriflexion, downward diving and " looping the loop " in water, retention of body-righting ability, development of specific torque on being rotated, supine or prone, about a vertical axis, rapid beat of its hind-limbs (irrelate reaction) in response to quick backward tipping of the head—may be said rather to exhibit the unrestrained influence of its posterior canals. The facts that its compensatory reactions to slow tilt are absent, that during stationary posture it may lean markedly to one or other side and that, when dropped from a height, it fails to land properly, are more direct indications of the loss of its gravity receptors.

Through the frog's serviceableness for the study of posterior canal function the following knowledge is gained. The posterior canals, whether inverted or in their normal orientation, can be stimulated by adequate angular acceleration about a vertical axis, the right canal being stimulated when the animal is rotated towards its right, and *vice versa*. The reflex result in each instance is assumption of spinal torque, leading in the supine animal to body-righting. Just as excitation of the isolated utricular maculæ by sudden forward tilt, so bilateral excitation of the isolated posterior canals by sudden backward tilt causes an irrelate reaction.

UNCOMPLICATED SEVERANCE OF BOTH UTRICULAR NERVES

With practice it became possible to sever the nerve to the utricular macula. The approach is the same as that used for severance of the nerve branches to the ampullæ of the horizontal and of the anterior vertical canals, though more bone is removed with the drill. The saccule being held aside with the help of the screw retractor, a free view of the whole utricular nerve is obtained as it spreads fanwise over the under surface of its macula. A hook, passed between the utricular chamber and this nerve of supply, is dragged along the base of the macula in a forward and lateral direction, first on one side of the expansion, then on the other, care being taken to move the hook in a direction exactly conforming to the under surface of the macula and to avoid ventral traction, which is likely to tear the more distal branches to the two cristæ. In this way the whole terminal expansion of the utricular nerve can be displaced so as to give a free view of the base of the macula. The completeness of the operation and the integrity of the cristal branches have also been confirmed by subsequent microscopic examination. When the operation is effected on both sides, the frog is then deprived of the use of its utricular maculæ without damage to any of the other labyrinthine receptors.

General Behaviour—On first observation the animal seems so little incommoded by its operation that one of our preliminary difficulties was to know just how it differs from a normal frog. Both on land and in water it keeps the prone position well, and its body-righting reaction is prompt and perfectly carried out. Its reactions to sudden tipping are also wonderfully good. As often as not it has a symmetrical posture, in which the limbs, unlike those of a bisoliutricular animal, are well gathered to the body. The horizontally kept head is then usually held low, and the back, which is straight and without prepelvic kink, is parallel to the ground—see fig. 8, Plate 22. The frog can crawl in natural fashion in a consistently forward direction and can also effect a short leap. In reality, however, its disabilities are numerous.

For one thing it is strikingly inactive and disinclined to move. After movement it may come to rest in a variety of extreme postures not usually observed in the intact animal. Thus, it may on occasion show a strong degree of EWALD lean to one or other side, or it may adopt a high symmetrical attitude with unusually up-pointed snout ; at other times it may maintain one of the diagonal backward postures. Should its head have been depressed with the finger, the frog will continue to hold the sharply ventriflexed posture that we have seen in the biconjoint animal. In other respects, too, as stated below, its behaviour is abnormal.

Tremor—Each spontaneous movement of the animal is seen to be accompanied by a curious tremor, in which especially the head is rapidly jerked up and down through small arcs. Another form that the tremor may take is an alternate rapid twisting of the body, first to the right then to the left, again through small arcs. The tremor is most conspicuous of all when the animal settles to rest after bodily movement. On landing after a leap, for example, it may persist for a second or two, and then die away gradually, just as the vibrations of steel ribbon die down.

Investigation by the method of secondary canal ablation shows that this tremor, associated only with bodily movement and involving particularly the head, is maintained by alternate stimulation of opposing vertical canals. If only one vertical canal is left to the bi-de-utriculate animal, the tremor does not occur. For tremor to occur, two or more must be present. As to its mode of production, let us suppose that the sudden stoppage of a spontaneous movement excites a particular vertical canal or pair of these canals. The first ampullary excitation causes a muscular response that jerks the head in an opposite direction. The reflex jerk, brief as it is, gives to the head sufficient angular acceleration to excite the canal or pair of canals antagonistic to that first excited. So the matter goes on for a space, like a " rally " in a game of tennis, but subject to a process of gradual extinction.

These observations and experiments point to two new conclusions. First, as the tremor is of vertical-canalicular origin, its absence in the normal animal must be due to some form of " damping " by the utricular maculæ. If the damping in these animals involves actual utricular excitation (which on the whole is the most likely supposition), we must infer that the utricular maculæ, like the semicircular canals—*cf.* McNALLY and TAIT (1933, p. 161)—are liable to be excited by any and every form of bodily movement. Secondly, we have to extend our conception of antagonism between canals. On the conventional view, the sole antagonist of a right posterior is the left anterior vertical canal, and *mutatis mutandis* for the other diagonal pair. Since, however, even the biconjoint frog shows a head-twisting form of tremor, it would follow that, in certain circumstances and in some respects, one posterior may act antagonistically to another posterior canal.

Because of this precise canal antagonism all the spontaneous movements of the bi-de-utriculate frog are, apart from the associated tremor, far better co-ordinated than those of a delabyrinthized frog. In any effort at continuous movement the delabyrinthized animal throws itself violently about, whereas in the present animal all these wildly erratic movements are eliminated.

Gravitational Disabilities—Like the biconjoint frog, the bi-de-utriculate makes no compensatory reaction to slow inclination of the tilt-table, nor does it retain the ability, when dropped from a height, to land properly. When by very slow increase of angular acceleration it is subjected to strong centrifugal force, it makes no movement of a compensatory kind. So, too, when subjected to simple linear acceleration, it fails to throw its centre of gravity in the direction of that acceleration ; instead it simply sits still, like a delabyrinthized animal.

Swimming Activities—In deep water, in which, by contrast with its behaviour on land, it may be very active, the frog swims for the most part in the prone position. Should it slowly paddle along the surface by alternate strokes of its hind-limbs, its head makes lateral swaying movements in tempo with these beats. When the hind-limbs beat simultaneously, the frog is liable to propel itself violently against the side of the tank. In rapid forward drives of this kind the alignment of its head with respect to its body may suddenly change. If the head bends symmetrically downwards, the frog goes to the bottom ; if it bends symmetrically upwards, the animal may, if the tank is full, throw itself over the edge on to the floor ; if spinal torque supervenes, the frog, spiralling, may turn supine for a moment and quickly right itself again. It never exhibits the regular pendular swaying of a frog deprived simply of four vertical canals. Instead, its movements in water are abrupt and jerky.

Thigmotactic Response—Another feature of its behaviour in deep water is its strong inclination to secure and maintain contact with a solid surface. Having arrived, in the course of its swimming, at the vertical side of the tank, it turns its body laterally through 90 degrees and coasts along with its belly against the side. If it touches bottom, it ploughs its way along the horizontal surface, maintaining contact all the time. Should it, however, find a chance to brace itself between two suitable objects standing in the water, it comes to rest at once. At a rectangular corner, for example, it will stop with one toe-tip touching bottom and a hand on each rectangular side. Whereas an ordinary frog moving through a wide or narrow channel between two objects may or may not use them as a resting place, the de-utriculate animal would seem instantly to become magnetized in such localities and to adhere to them. Moreover, any flat object floating on the water is immediately seized upon in order to provide muscular tension or cutaneous pressure.

Quick Tilt—On quick tilt the head is promptly adjusted by the vertical canals, so as to keep in a horizontal position. At the same time the lack of the utricles brings about certain deviations from the behaviour of a normal frog under similar circumstances. Perhaps one might best characterize the derangements in question by saying that, when the rate of tilting is high, certain limbs tend to be lifted clear of the substratum and thrown farther from the body.

When the animal is quickly tipped in a forward direction, its hands and feet may either maintain their position on the table-top or they may at a late stage of the tipping become displaced. In either case the forward pointing fingers rise off the table-top in momentary dorsiflexion and the toes spread laterally. Should the hands become displaced they are thrust forward. Meantime, by lateral spread, each hind-limb is thrust a little outward. While the table remains tilted the frog now keeps this buttressed position. As may be otherwise proved, the reaction whereby the limbs become spread, the arms anteriorly, the legs laterally, represents the real response to strong, simultaneous and equal stimulation of its anterior vertical canals.

When the direction of rapid tipping is reversed, the limbs are thrown at a much earlier stage and are also more easily displaced. The exaggerated reaction in this case is simply the irrelate reaction, of which all grades may be obtained according to the extent and rapidity of the tilting.

On quick lateral tilt, say to the right, both right limbs become laterally extended, while the left hind-limb is thrown straight backwards. The head and fore-body not only undergo torque to the left but are also laterally displaced towards the left. While these movements would indicate that the animal had, as it were, taken the first steps towards upsetting in the uphill direction, it never does actually overturn. The reaction, due to simultaneous stimulation of the two vertical canals of the right side, is similar to that evoked in the bisoliutricular frog when it is quickly tipped in the opposite direction, *i.e.*, towards its left.

When the frog is rapidly tilted in a diagonal direction, the limbs also respond in an unusual way. If the tilting is diagonally forward to the right, both right limbs are partially extended, while the left hind-limb is thrown backwards, but not quite so promptly and rectilinearly as in lateral tilt to the right. When the tilting is diagonally backward to the right, the two limbs whose movement is most marked are those that lie in the line of the axis of rotation, viz., the right fore-limb and the left hind-limb. Both are lifted and thrown to their full extent from the body in the line of this axis. While this is the broad effect, certain other movements also occur. The right hind-limb, though not lifted, receives thrust innervation, as is shown, for example, by slight movement of its foot, extension of its toes and slight lift of the pelvis on its side. The left fore-limb is moved forward and twisted so that its palm points laterally or backward. On the left side, too, the head is immediately lowered.

These reactions to quick diagonal tilt differ from any that we have hitherto described. The more distinctive and spectacular of the two, viz., that to backward diagonal tilt, when the two limbs that lie along the axis of rotation are at once spread straight in the line of this axis, is one that we have frequently used in the examination of uni-de-utriculate frogs. In these the reaction is present only when the backward diagonal tipping occurs to one particular side. Because of its use as a diagnostic feature and because of the insight it affords into the working of the vert-utricular mechanism, we shall give it a special name and call it the "axi-diagonal reaction."

Rotation about a Vertical Axis—As we are here dealing for the first time with responses in which horizontal canals play a part, let us introduce a terminology that is convenient in relation to the lateral curve produced by horizontal canal stimulation.

When the spinal axis, remaining horizontal, bends to one particular side, say, to the right, the left lateral border of the animal is convex and its right lateral border concave. This may be simply expressed by saying that the frog is convex to the left and concave to the right. Similarly, the left side is then its convex side, while the right is its concave side.

Whereas the biconjoint animal, on being rotated about a vertical axis, never exhibits lateral curve, the present animal invariably does. Its lack of utricular maculæ together with the presence of vertical canals may, however, permit of later imposition of spinal torque upon this underlying lateral curve. If one uses a low rate of angular acceleration, only a horizontal canal, namely, that on the side to which the frog is being rotated, may be stimulated. The first effect is to make the body convex on the side of the stimulated canal, the head meantime remaining horizontal. The next effect in an intact frog would be to cause circling, but in our experience it is difficult to get the bi-de-utriculate animal to begin circling to the concave side with head still horizontal. By the time circling commences, the spinal axis has also become twisted—and in the same sense in which torque occurs in the biconjoint animal when rotated about a vertical axis. That is to say, on the convex side the head and pectoral girdle become raised, while on the concave side they are depressed. On many occasions, even with rapid angular acceleration, circling fails to occur, though torque is always present.

On cessation of the original rotation the frog has an after-reaction in which the process is reversed. If the check to the rotation is not particularly abrupt, the animal simply swings its head through a wide arc to that side which was previously convex. At the same time it tends to develop spinal torque in a sense opposite to that which was present before. Circling to the now concave side does not seem to occur as part of the after-reaction. As the check to the original rotation becomes more and more abrupt, the after-reaction becomes by far the most conspicuous event in the course of these turntable experiments.

On stoppage of a rotation, let us say, towards the frog's left, the head, immediately swinging through a wide arc to the left, becomes slowly lifted on the right and correspondingly twisted to the left. For a moment the frog looks as if it were going to upset over its left side, for the left hind-limb is now in long-splint extension and the right hind-limb in pre-thrust extension. On sudden check of a still swifter rotation, the frog with rapidly moving limbs will actually upset and roll off the table. Because of this liability it is expedient to keep the rotated animal under a glass shade. Then it can be seen that in the course of an upset either the left hind-limb or (less frequently) both hind-limbs beat as in the irrelate reaction.

The whole behaviour suggests that the upset over its left side is due to stimulation of at least its right posterior vertical canal. While we shall not here delay to decide what part, if any, anterior vertical canals play in the process, let it be said that if the nerve to the right posterior canal has previously been severed, the animal on rotation to its left twists its head to the right as before, but on sudden stoppage of this leftward rotation entirely fails to exhibit the upsetting reaction just described.

When the bi-de-utriculate animal, laid supine, is subjected to rotation about a vertical axis, its mode of righting resembles that of a biconjoint frog. In other words, it invariably rights by rolling over that side towards which the rotation occurs.

Sense of Gravity Orientation in Water—In deep water some, but not all, of these animals show the same tendency to drop asleep as biconjoint frogs. In order to discover whether the absence of the utricular maculæ interferes with their ability under these conditions to reach the surface, we selected two which readily fell asleep in water for a special experiment. We filled a deep vessel with oxygen-free water at a temperature which ranged during the experiment from 28° to 25° C. In order that the sleeping animals should subside to the bottom, and that they should not receive much directional influence from air contained within their lungs, we began by expelling with our fingers most of this residual air. As a control a fully delabyrinthized frog was similarly treated. On being released, each animal would after slight activity subside to the bottom and stay there for a time asleep. At intervals they would become restless and start to swim. If a frog failed during the restless stage to obtain air, it would subside into somnolence for a period again.

While neither type of animal seemed to have any real " sense " of gravity direction, there was this great difference between the delabyrinthized frog and the bi-de-utriculate. The latter, in moving, could preserve on the whole one determinate direction and so stood a far better chance of arriving accidentally at the surface. A delabyrinthized frog, on the other hand, moves in an erratic, blundering way. As its direction of progression was thus subject to constant change, this frog never once succeeded in getting to the surface. While the experiment thus seemed to show equal loss of gravity sense in both types of frog, it also exhibited in a very striking way the extra control over bodily movement due to a full equipment of canals.

Résumé

As with the biconjoint, so the interest of the bi-de-utriculate frog lies less in the gravitational disabilities it displays than in the way its operation uncovers the true action of the semicircular canals. For one thing, they prove to be irresponsive to simple linear acceleration. The tremor that accompanies and follows the movements of the bi-de-utriculate animal is due to rapid alternate action of antagonistic canals. Its occurrence as a deficiency symptom would indicate that under normal conditions the utricles are brought into action in any bodily movement.

When the frog is subjected to quick tilt in any given direction, its reactions represent simply the positive effect of canalicular stimulation. Thus the bi-de-utriculate animal is a suitable one with which to demonstrate the result of simultaneous stimulation of two posterior, two anterior, or two vertical canals of one and the same side, and so on.

Under rotation about a vertical axis not only are its horizontal canals readily stimulated but also, with higher angular accelerations, its posterior vertical canals. By adequate stimulation of the latter the prone frog may be made to upset on the turntable.

Uncomplicated Severance of the Nerve to One Utricular Macula

De-utriculate Asymmetry—On the operated side the head leans downwards, but the average angle of dip, 25° to 30°, is less than in an Ewald frog, 30° to 45°. In deep water, too, an Ewald animal floats with a heavier list towards the side of the operation. In order to reproduce the Ewald posture in the uni-de-utriculate animal it suffices to sever the nerves to the cristæ of its two vertical canals on the side of the original operation. On the other hand, if in the uni-de-utriculate frog one should sever the nerves to the opposite two vertical canals, the head becomes more nearly horizontal than before (lean of 15° to 20°), fig. 9, Plate 22.

Spontaneous Movement—On the ground the frog is more active than a bi-de-utriculate. Unlike the unisoliutricular animal, which tends to keep circling towards the side of its intact utricle, this frog may abruptly change its direction of movement. It can both crawl and leap forward, yet in sustained forward movement it does distinctly deviate in circus fashion towards its intact side, thus exhibiting some mild degree of the clock-circling behaviour of the unisoliutricular frog. A further resemblance is that in water both types of animal tend to circle towards the side of the absent utricle.

The animal can make quite vigorous leaps without spiralling, but the Magnus and de Kleyn type of body-taxis persists during progression through the air, and is present at the moment of landing. While the frog may upset after a very vigorous leap, upsetting is by no means so common as in a frog deprived solely of two vertical canals of the same side.

Whereas in deep water the trim of the animal approximates to that of a unisoliutricular frog, its buoyancy is quite different. The unisoliutricular frog, becoming tightly filled with air which it cannot expel, is unable to submerge. The uni-de-utriculate frog, which can expel its "tidal" air at any time, usually goes to the bottom of the tank. It may either swim straight forward with simultaneous strokes or progress by alternate movement of its limbs. In the latter case it either circles continuously towards its operated side, or then, with long redoubling drives, moves as if coasting along the interior of a narrow rectangle. It also contrives to keep its prone orientation better than a unisoliutricular frog.

Its spontaneous movements are accompanied neither by tremor, nor by pendulation.

Righting Reaction—When the animal is placed in a supine position it promptly rights itself, but invariably turns from the supine to the prone position with its intact side lowermost. So, too, if by careful manipulation it should have been induced to remain momentarily supine on the horizontal turntable, the very first rotation of the turntable towards its intact side provokes immediate long-splint extension of the hind-limb of that side, followed by similar righting. By two methods, however, it may be induced to right by rolling with its operated side lowermost. One is to place it in a supine position on an inclined surface that slopes at least 30° downwards to the operated side ; the other is to rotate the supine animal on the turntable smartly towards its operated side. In the EWALD frog, on the other hand, in which the whole righting mechanism is confined to one side of the head, there is no exception to the rule that the intact side comes lowermost in body-righting.

These experiments exhibit two factors as contributing towards body-righting. Because the frog with one utricle absent usually rights by rolling to one particular side, one must acknowledge the general fact of utricular influence in the body-righting process. Because the same animal, in special circumstances, may also right itself by rolling in an opposite direction, we have renewed evidence that the canals are especially important for body-righting.

Quick Tilt—We obtain a new light on the relation between vertical canals and utricles by quickly tilting the uni-de-utriculate frog.

When the frog is quickly tipped in the diagonal backward direction towards its operated side it reacts like an intact animal. When the quick diagonal backward tipping is towards the intact side the response is the axidiagonal reaction of the bi-de-utriculate animal. If the tipping is very abrupt, both hind-limbs may beat for a little as in the irrelate reaction. By backward tipping towards any one side the posterior canal of that side is of course stimulated. If a utricular macula is present on the opposite side, the frog's response is normal ; if it is lacking on the opposite side, the response is abnormal. This can only mean that, under the displacement of sudden backward tipping, the right posterior canal of the intact animal works in association with its left utricular macula, while its left posterior canal works in association with its right utricular macula.

By sudden diagonal tipping in the forward direction, one can establish the existence of a similar functional relation between an anterior vertical canal and the utricular macula of the opposite side. Should the diagonal rotation in this case be towards the operated side, the frog reacts as well as any normal animal. When the diagonal forward tipping is towards the intact side, the frog behaves in the same way as the bi-de-utriculate animal ; that is to say, both limbs of the intact side are partially extended, while the hind-limb of the operated side is, after the briefest delay, thrown backwards.

These results enable us to anticipate one general principle with respect to the response to lateral tilt. If the sudden lateral tilt should occur towards the operated side, the frog, apart from its original asymmetry, should react on the whole like a normal animal. If the sudden tilt is towards the intact side, the rotational displacement should be much more disturbing to the subject.

The anticipation is confirmed on trial. Quickly tilted towards the operated side, the frog, without any undue spread or throw of its limbs, keeps its balance. Quickly tilted towards the intact side, it gives the same reaction as a bi-de-utriculate frog in similar circumstances, except for one slight difference. The tipping evokes no special increase of torque to the operated side, but instead the fore-body by lateral swing deviates decidedly towards the intact side. This deviation, absent in the bi-de-utriculate frog, may well be due to action of the remaining utricular macula.

Rotation about a Vertical Axis—We may dismiss the effect of the horizontal canals with the statement that, in whichever sense the turntable rotation occurs, the frog becomes convex on the side to which it is being turned and may likewise circle towards its now concave side. While, just as with the bi-de-utriculate animal, more marked effects occur on abrupt cessation than on ordinary initiation of the rotation, the striking and anomalous feature in the present frog is that the after-reaction is more pronounced on sudden cessation of a rotation towards its intact side than of one towards its damaged side.

When the frog is rotated towards its damaged side, its head is lowered on the intact side and becomes more nearly horizontal. As a result, the animal, apart from its lateral curve, is temporarily more symmetrical. Rapid deceleration, on the other hand, exaggerates the type of torque originally present. When the frog is rotated to its intact side, by increase of its existing spinal torque its head becomes more raised on that side. If the angular acceleration is high, the head may be so uplifted on the intact side that its transverse axis becomes nearly vertical. On sudden cessation of this rotation, the frog exhibits an irrelate reaction with beating of both hind-limbs and quick lateral alternate roll of the body. Finally, the animal lies with all four limbs extended. If the check to swift rotation is still more abrupt, the animal may upset over its intact side, whereupon it rights again by a reversal of this very unusual direction of roll, *i.e.*, by turning from the supine to the prone position with its intact side lowermost.

As may be shown by secondary ablation, the twisting effects and also the upset described are due to stimulation of posterior vertical canals. In each case, too, stimulation follows the specific rule that we already know from experience both with the biconjoint and with the bi-de-utriculate animal. That is to say, swift rotation towards the right and abrupt cessation of a leftward rotation stimulate only the right posterior canal, and *vice versa*. The anomaly here is that it is a posterior canal on the side opposite to that of the persisting utricle that brings about the upset. Plainly we are here confronted with conditions very different from those that obtain when the same frog is quickly tilted.

Apart from the primary fact that a utricular macula is not affected by mere spin, whereas it is affected by quick tilt, the only explanation of the anomaly that we would proffer is that, when a rotation to the intact side is suddenly checked, the frog's head is leaning strongly to the operated side. When it now begins, by excitation of the appropriate posterior canal, to be torqued to the intact side, a wide range of free arc is available to it. When, on the other hand, a rotation to the operated side is suddenly checked, the frog's head still leans slightly to that side. Thus, when active torque to the operated side sets in, its possible free range is much less. There is some evidence that the amplitude of sudden tilt to which a utricular macula is subjected is an important factor in its excitation; if so, then secondary utricular intervention might be marked in the one case but insignificant or absent in the other. Without further experimental analysis, however, it would obviously be unwise to lay much stress on the above explanation.

We have hitherto said little about possible stimulation of anterior canals by rotation about a vertical axis. If, after removal of a right utricle, the left anterior canal is put out of commission, the responses of the animal to rotation in either direction remain the same as before. Only with high angular acceleration, and then to the side of the absent canal, does one detect a slight difference in the degree of torque that is manifested, namely, a little less dorsiflexion of the left side of the head. This would indicate that, provided the angular acceleration is sufficiently high, an anterior canal may respond to rotation about a vertical axis towards its own side. The conclusion is confirmed by rendering all the labyrinthine receptors functionless with the exception of a single anterior canal. When a frog of this type is rotated towards the side of its remaining canal, it responds neither so markedly nor so readily as an animal with a single posterior canal. Yet, with very high angular acceleration towards the side of the persisting canal, it may be made to elevate its head on that side. To any degree of angular acceleration in the opposite direction it is irresponsive. Thus we conclude that, on rotation of a normal frog about a vertical axis, all three canals on that side to which the rotation occurs stand to be stimulated. As the angular acceleration increases, the successive order in which they come into operation is, first the horizontal, next the posterior vertical, and lastly the anterior vertical.

Résumé

By quick tilt of the uni-de-utriculate frog one discovers that under normal conditions the two vertical canals of one side work in association with the utricular macula of the opposite side. This crossed partnership obtains only in the case of tilting, not when the vertical canals are stimulated by rotation about a vertical axis.

By turntable rotation towards a given side the anterior vertical canal of that side may, with some difficulty, be stimulated.

Discussion on the Inner Mechanism of the Utricle

Of the two objects of this investigation, enumerated in the second paragraph of the "Introduction," only the second, that of establishing more clearly the reflex effect of utricular stimulation, has to any marked extent been realized. The résumés appended to sections cover not only this side of the work, but also certain principles respecting the interrelation of utricles and canals. We shall now attempt to deal with the presumptive mechanism of utricular action.

On two counts it would seem necessary to discard the prevailing idea that the utricular otoliths of the frog act like the sand-grains in the statocysts of *Palæmon*, *i.e.*, by simple sliding descent from a higher to a lower level. If this were their mode of action, experiment would compel us to suppose that the heavy otoliths sometimes slide uphill instead of downhill. Secondly, the attempt to harmonize the two modes of utricular stimulation by seeking to refer also the second to translatory displacement broke down.

Here, too, the only well recorded direct experiment on the actual utricular maculæ, that of MAXWELL (1923), should be kept in mind. Having freely exposed, in the dogfish, a utricular otolith from above, he gently displaced it, backwards, forwards or laterally, with the help of a light pledget of cotton wool held in forceps. To his surprise the effect of this displacement was exactly contrary to what might have been predicted on the KREIDL gravity hypothesis. For example, a forward displacement of the otolith, instead of making the eyes roll upwards, caused them to roll downwards, and so on.

It might be urged that the fact of two distinct modes of stimulation points to the existence of two different mechanisms within the utricular receptors. Against this idea the evidence, practically conclusive, is as follows. A bisoliutricular frog, subjected to linear acceleration in a forward direction, begins by giving the same gravity response as if it were being slowly tilted backwards. In other words, the case is one of "first mode" stimulation. By insensible gradation, however, the response to successive increase of this acceleration passes eventually into the most pronounced form of the irrelate reaction, which otherwise appears only in answer to the "second mode" of utricular stimulation. All other cases of response of the bisoliutricular frog to steadily increasing degrees of linear acceleration show a similar commingling of "first mode" and "second mode" effects, in which the one passes into the other without trace of discontinuity. The inevitable conclusion is that the utricular process corresponding to "first mode" and to "second mode" of stimulation is one and the same.

When we recall that first mode and second mode have reference only to rotations about a horizontal, and never to rotations about a vertical axis, it is plain that the fine interior displacement responsible for excitation of a utricular macula is a readjustment of the otolith or of its parts in conformity with gravity requirements. Having rejected the idea that the otolith is a simple weight that slides in a downhill direction, what other supposition involving a gravity control on the otolith is available to us? Might we, for instance, adopt the view that the parts of which the otolith is composed, viz., the individual otoconia, tend to preserve under the influence of gravity a vertical orientation like that of a buoy floating in water?

Regarding the finer structure of these otoconia, which in our decalcified preparations of the frog's labyrinth appear to be arranged over the macula in a shallow layer, not more than one or two deep, we can as yet say little. At the same time it is profitable to pursue the supposition that they may resemble buoys, not in being lighter than the endolymph* but in tending to arrange themselves vertically. Granted a behaviour of this kind, one could readily explain the "first mode" of stimulation. The question is, would it similarly account for the "second mode"

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* The centrifuge experiments of WITTMAACK (1909), and especially those of DE KLEYN and MAGNUS (1921), combined with the anatomical reports of DE BURLET and DE HAAS (1923)—see MAGNUS (1924), also DE KLEYN and VERSTEEGH (1933)—show sufficiently that the otoconia are of higher total density than the endolymph.

of stimulation, which in rapid tilt yields a reflex response of opposite kind to that evoked by slow tilt?

This matter may be explored with the help of a model. Celluloid sinks in water, and also in pure glycerine: by insertion of a fragment of cork into the excavated end of a short, solid, cylindrical rod of celluloid, one may obtain an artificial otoconium which, subsiding to the bottom of a spherical flask filled with either water or glycerine, assumes a vertical position. In the viscous glycerine the natural oscillations of the rod are better damped than in the water. Any smart rotation now communicated to the flask deflects the celluloid rod in the same sense (with respect to the flask) as a very slow rotation in the opposite direction.

The reason for the sudden deflection in the case of a rapid rotation is that the layer of fluid in immediate contact with the flask wall tends to move with the wall, while layers that are successively farther from the wall are less readily set into rotatory movement. Because of this fluid shearing action, the top, or head, of the celluloid rod tends to stay still while its base is rapidly carried with the flask wall. Its head therefore " nods " towards that region of the wall of the flask towards which it more slowly approaches when the flask is slowly rotated in the opposite direction.

While the model, with unattached otoconium, thus fulfils the primitive requirement demanded of it and would likewise harmonize with the MAXWELL experiment, it can at best provide only a suggestion as to the possible structure and mode of action of the utricular macula. Should the true mechanism be found to agree in some way with the model, one might perhaps make two additional remarks. First, any marked deflection from uniform curvature in the wall of the flask is liable to inhibit the response of the artificial otoconium to the second mode of " stimulation "; this may have a bearing on the configuration of the utricular chamber. Secondly, the natural period of oscillation of even the tiniest model otoconium may theoretically be adjusted to suit any requirement. (In the frog, as we have seen—p. 257; *cf.* also McNALLY and TAIT (1933), p. 159—this period should be of the order of one complete cycle in about four-fifths of a second.) The reason for this is that, if the artificial otoconium were for the moment horizontally instead of vertically oriented, the two coupling forces (themselves susceptible of variation) which restore it to verticality, are distant by an amount equal to that separating the true centre of gravity from that centre of gravity which the otoconium would have if it were throughout of the same density as the surrounding fluid. With progressive decrease of this distance the natural period of oscillation becomes slower and slower. Short of zero distance, and ignoring the implications of viscosity at small dimensions, there is no limit to this means of slowing the period.

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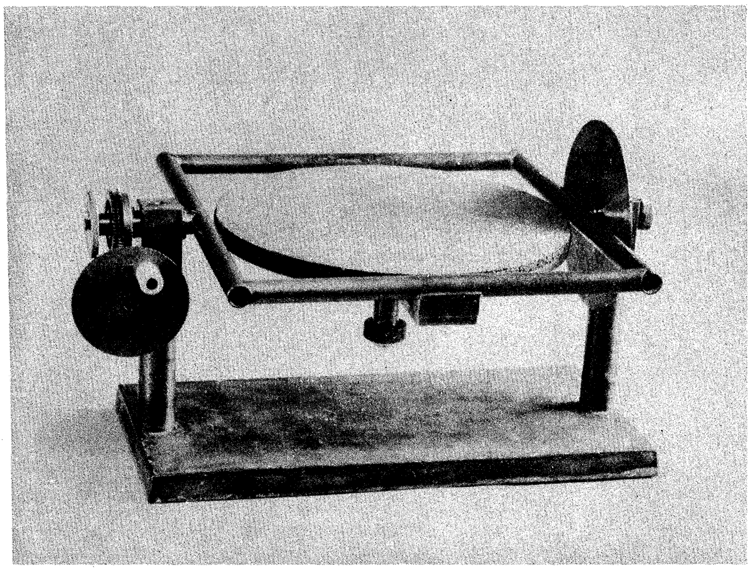
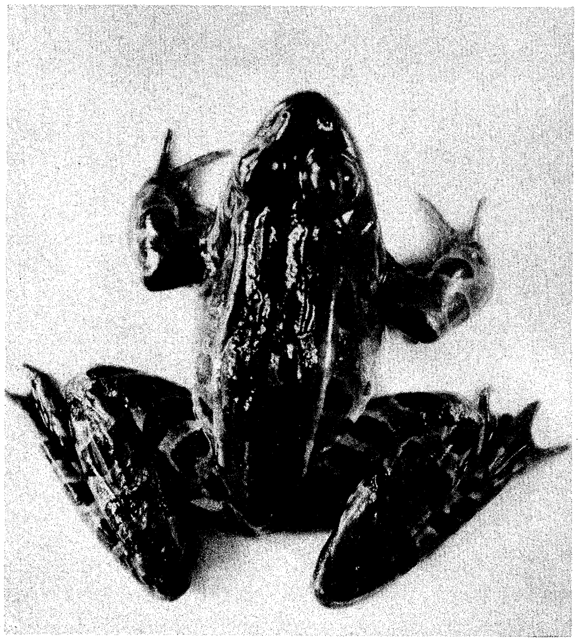


Fig. 1



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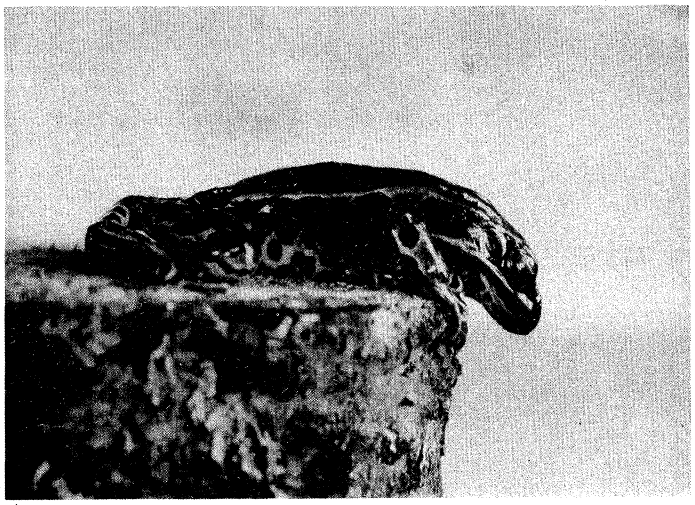

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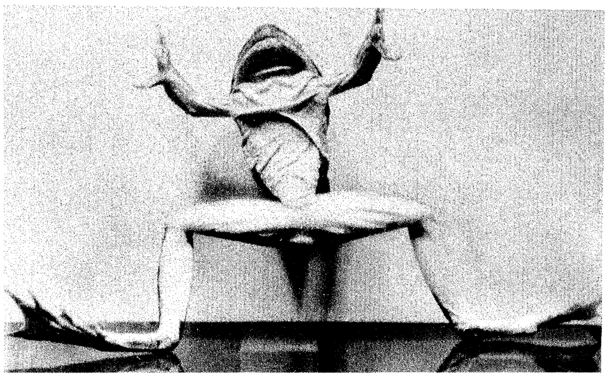

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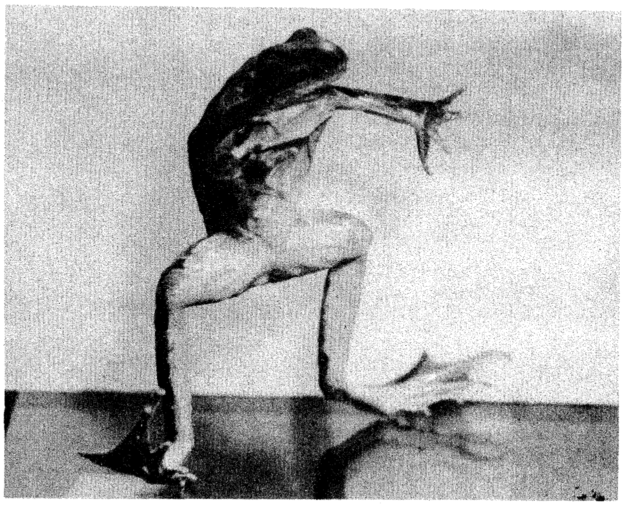

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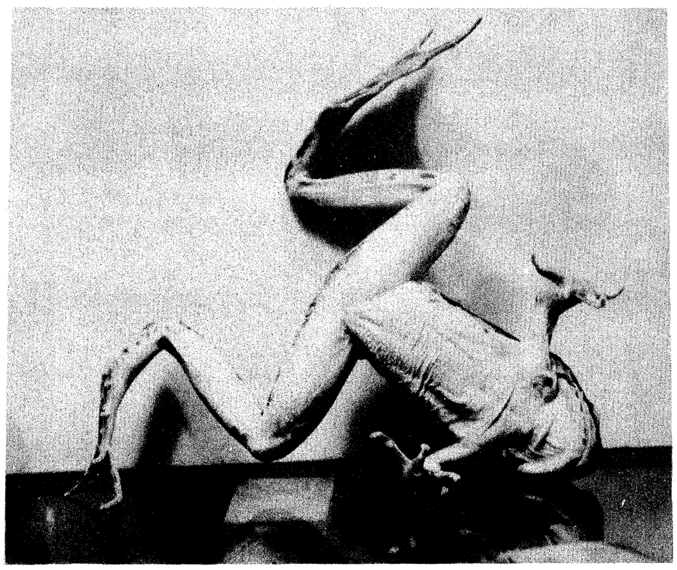

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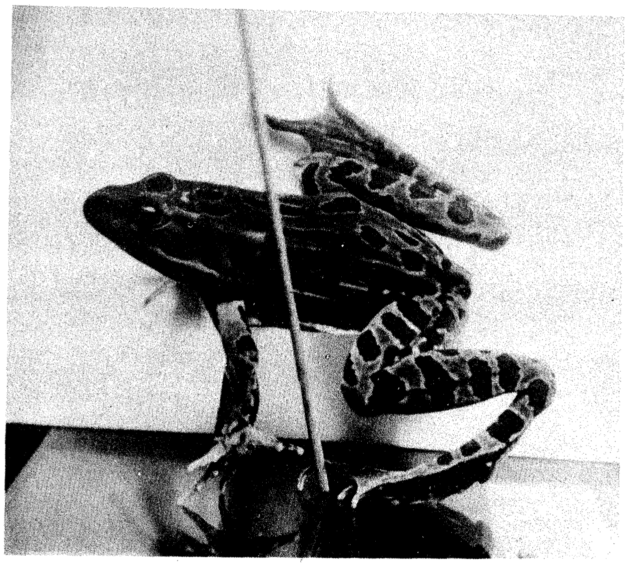

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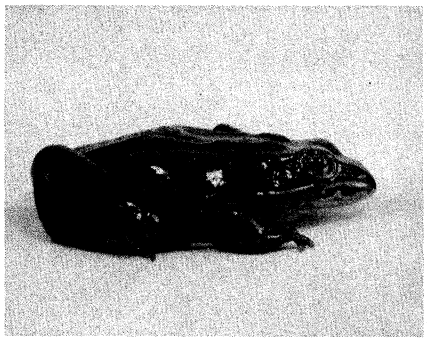
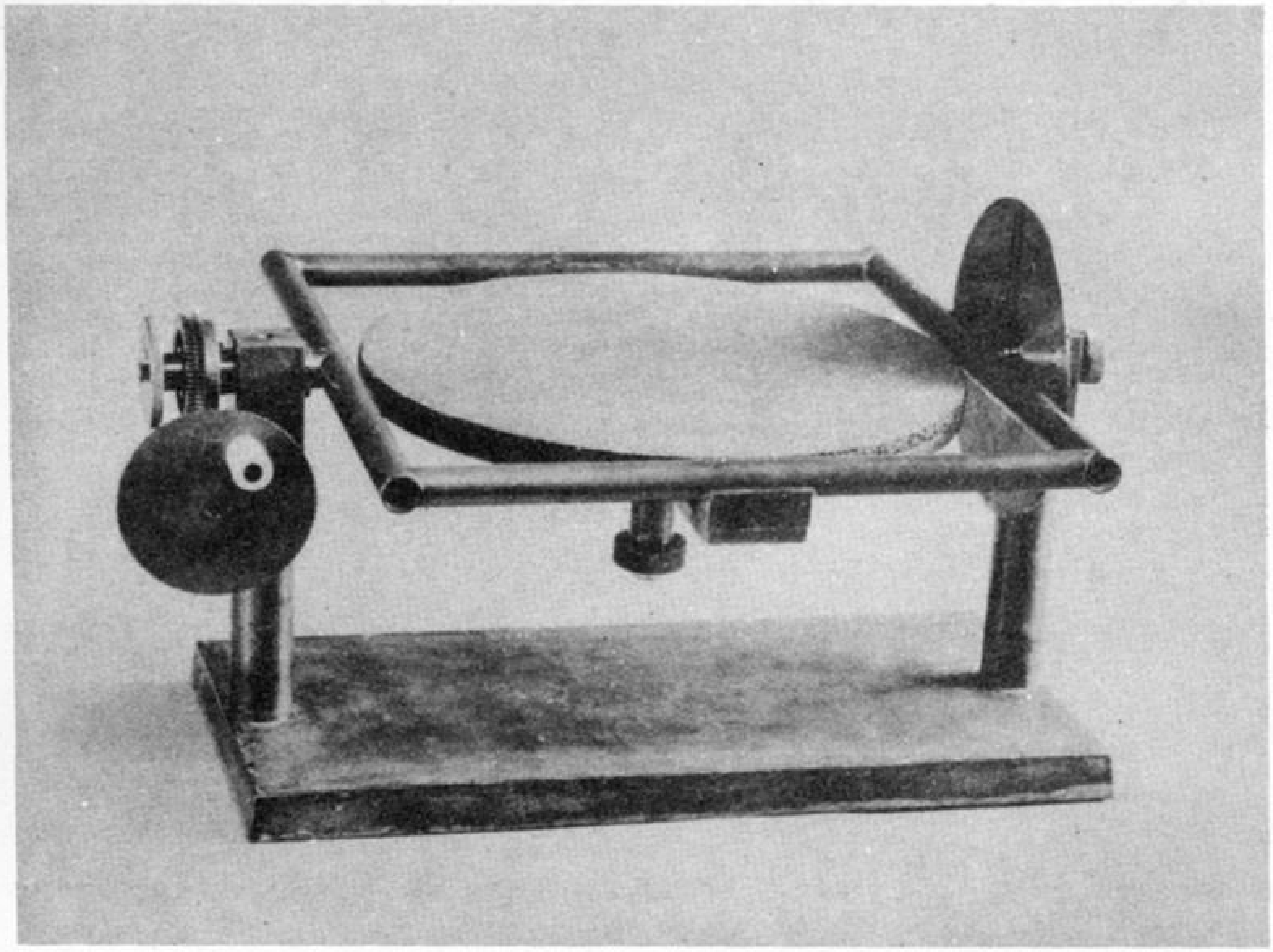


FIG. 8

FIG. 9



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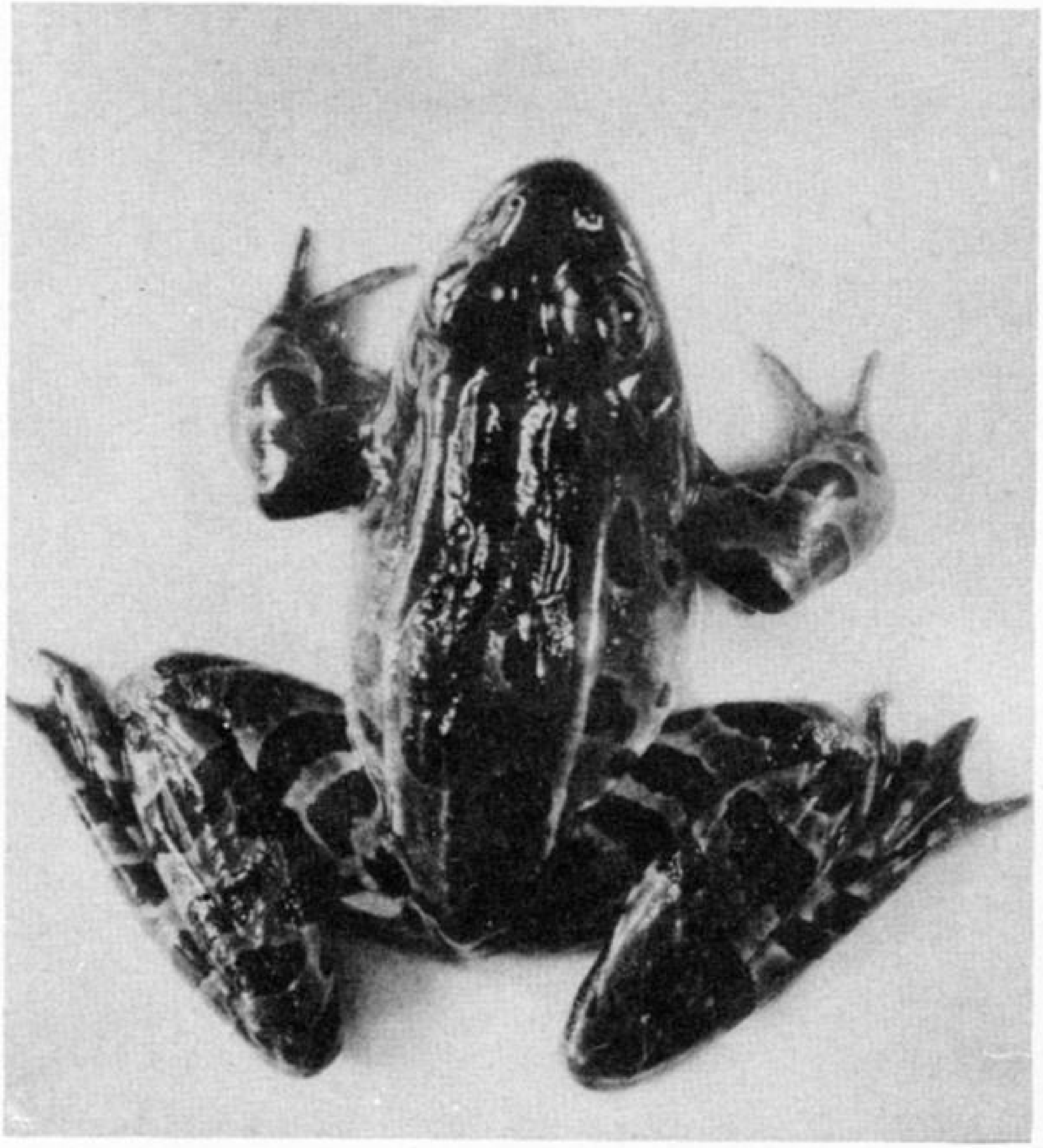

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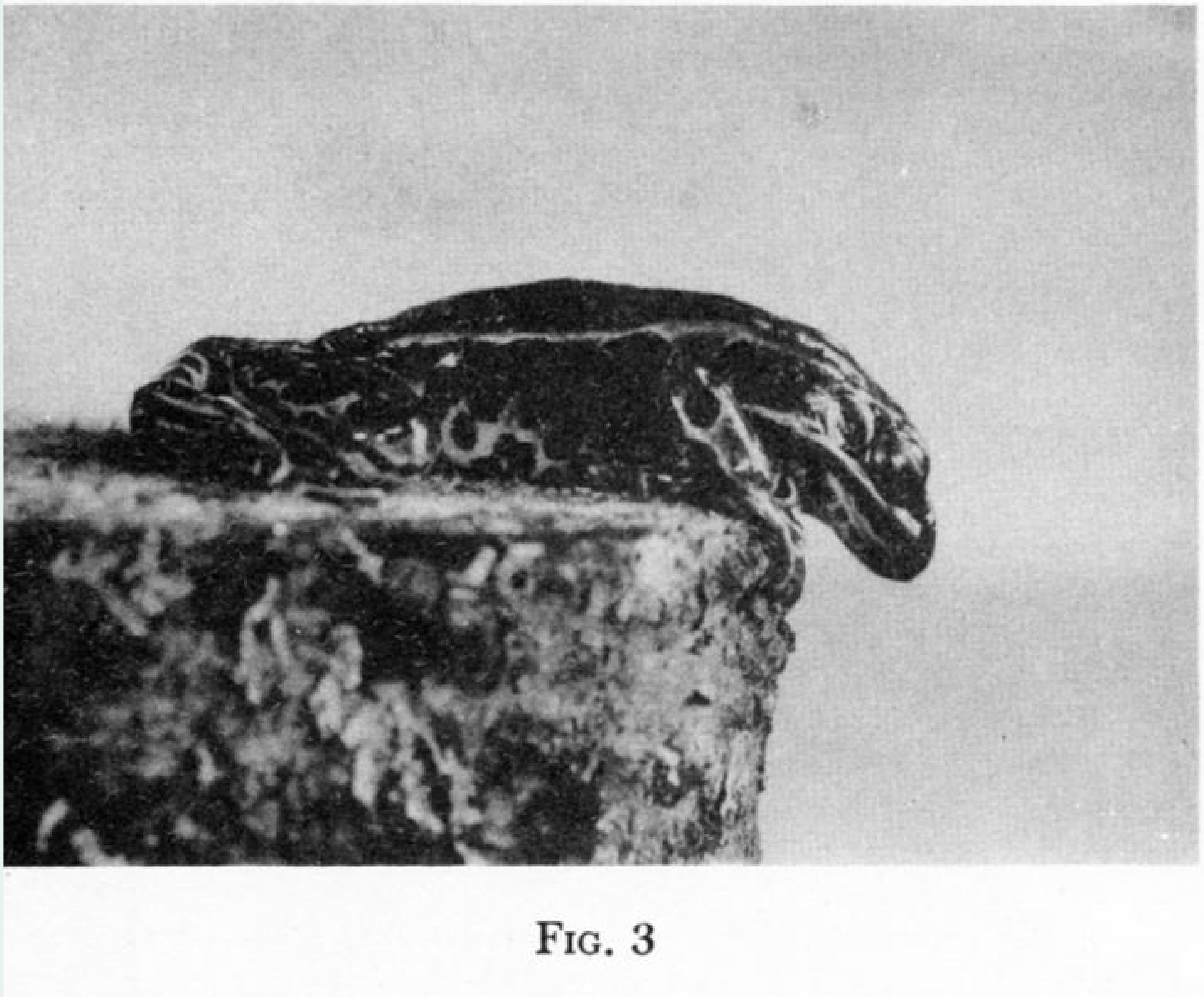

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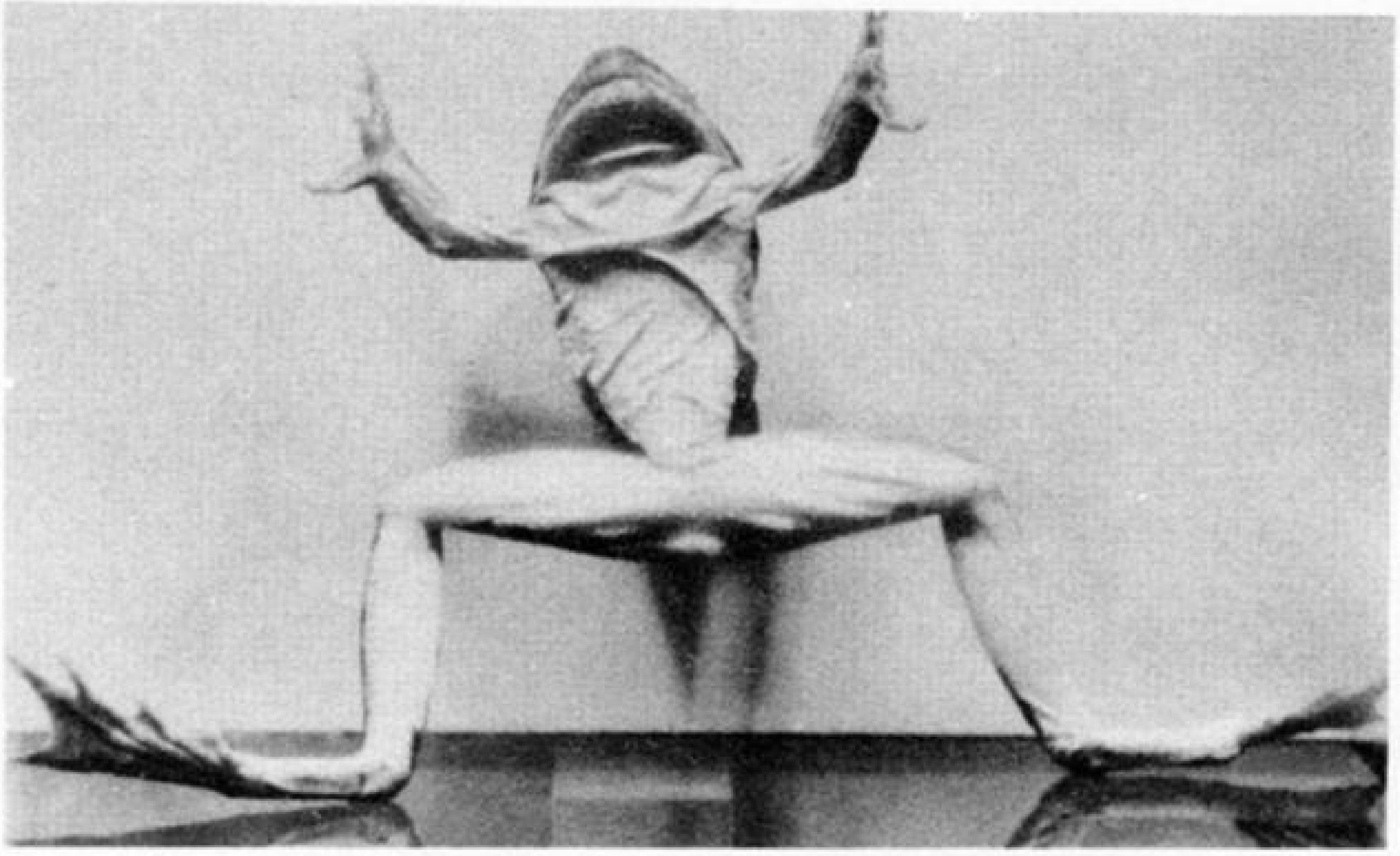

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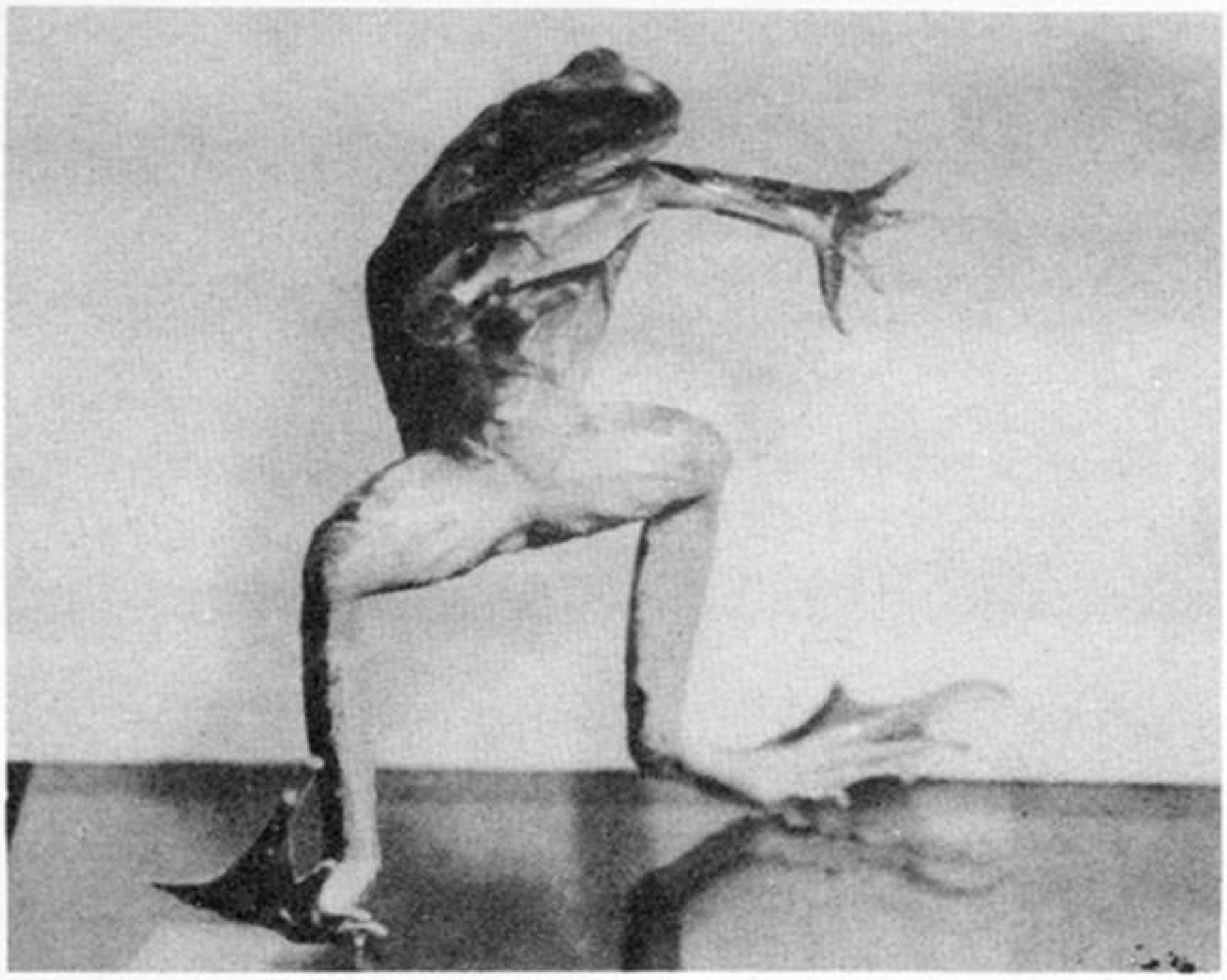

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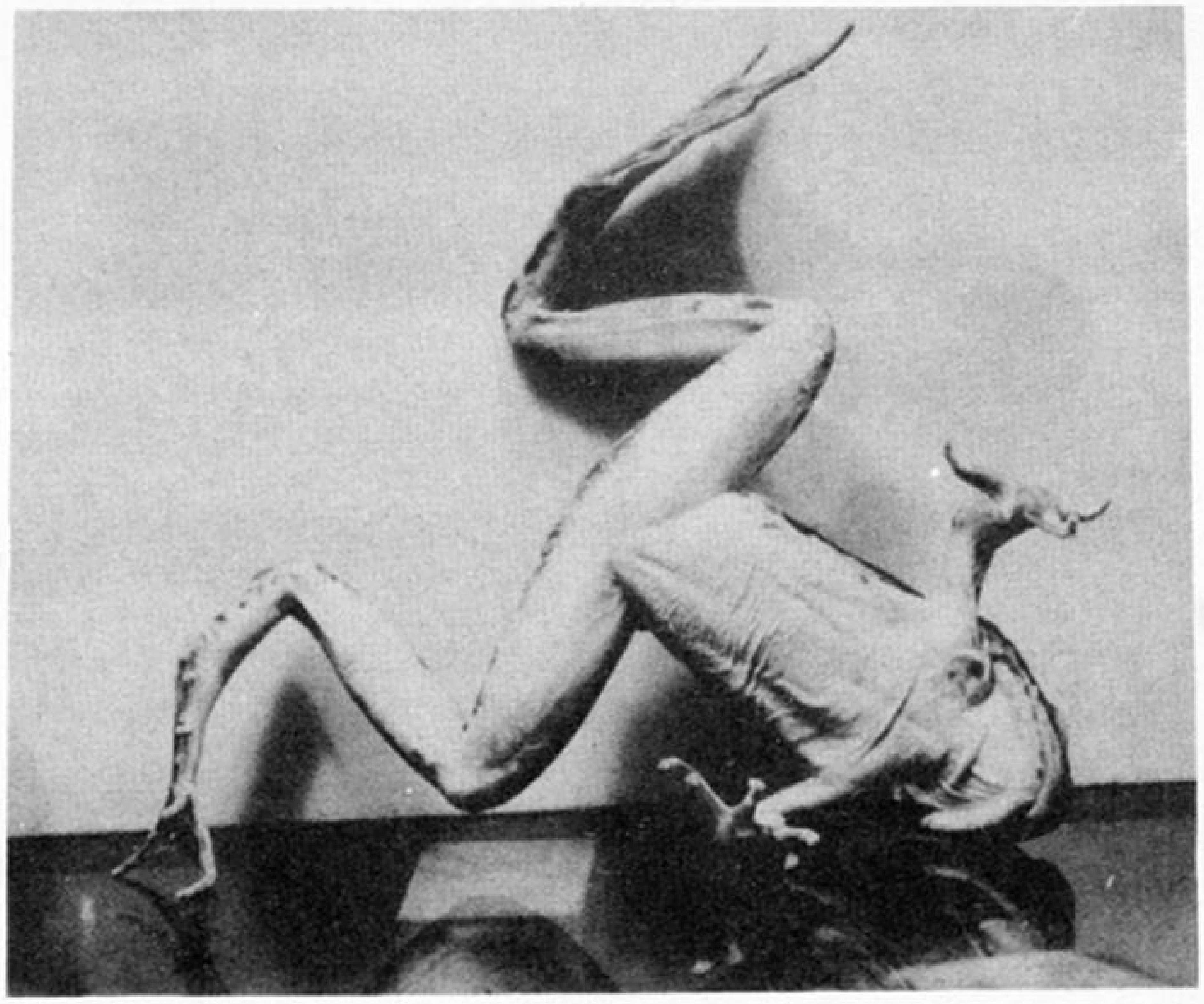

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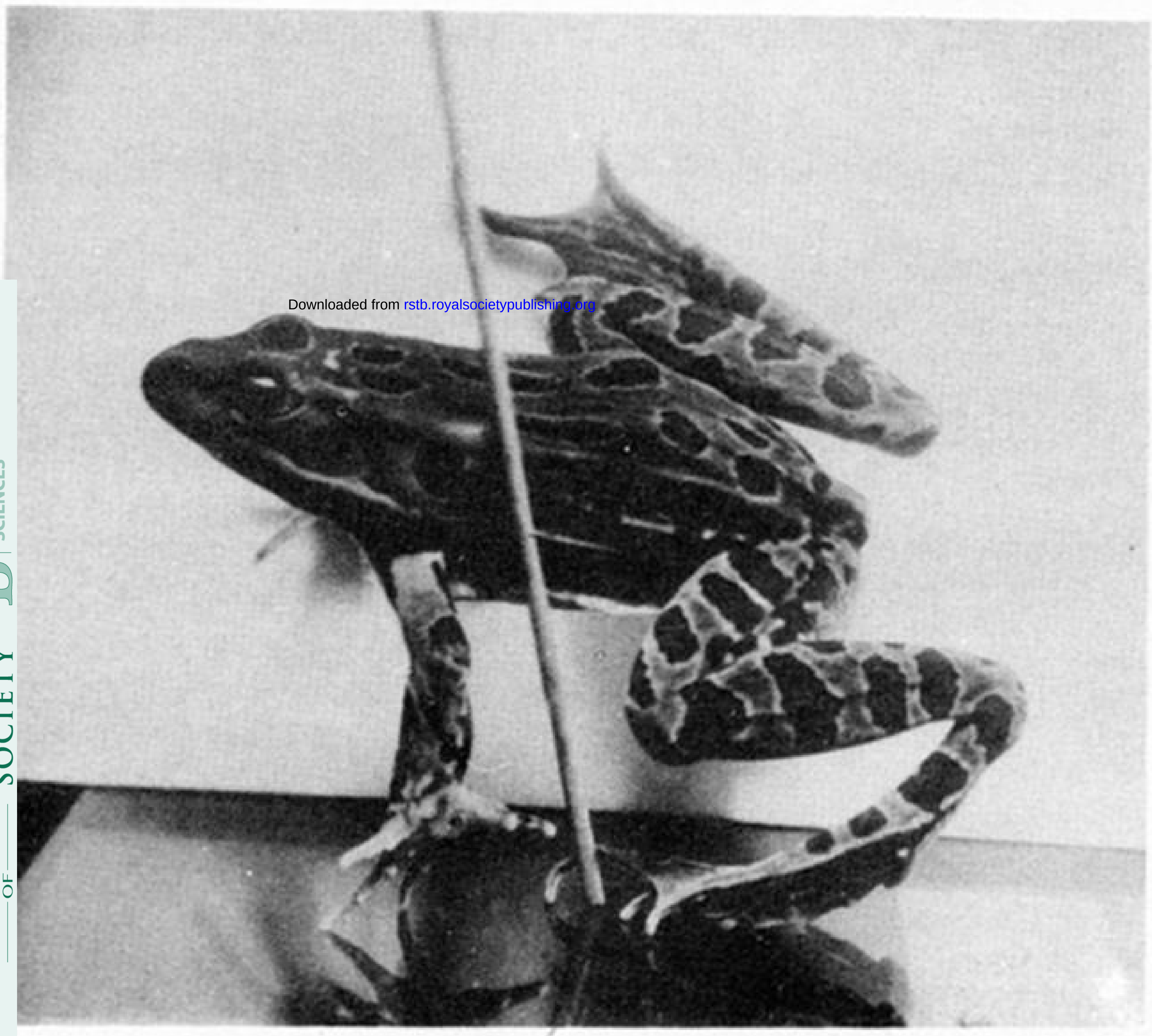

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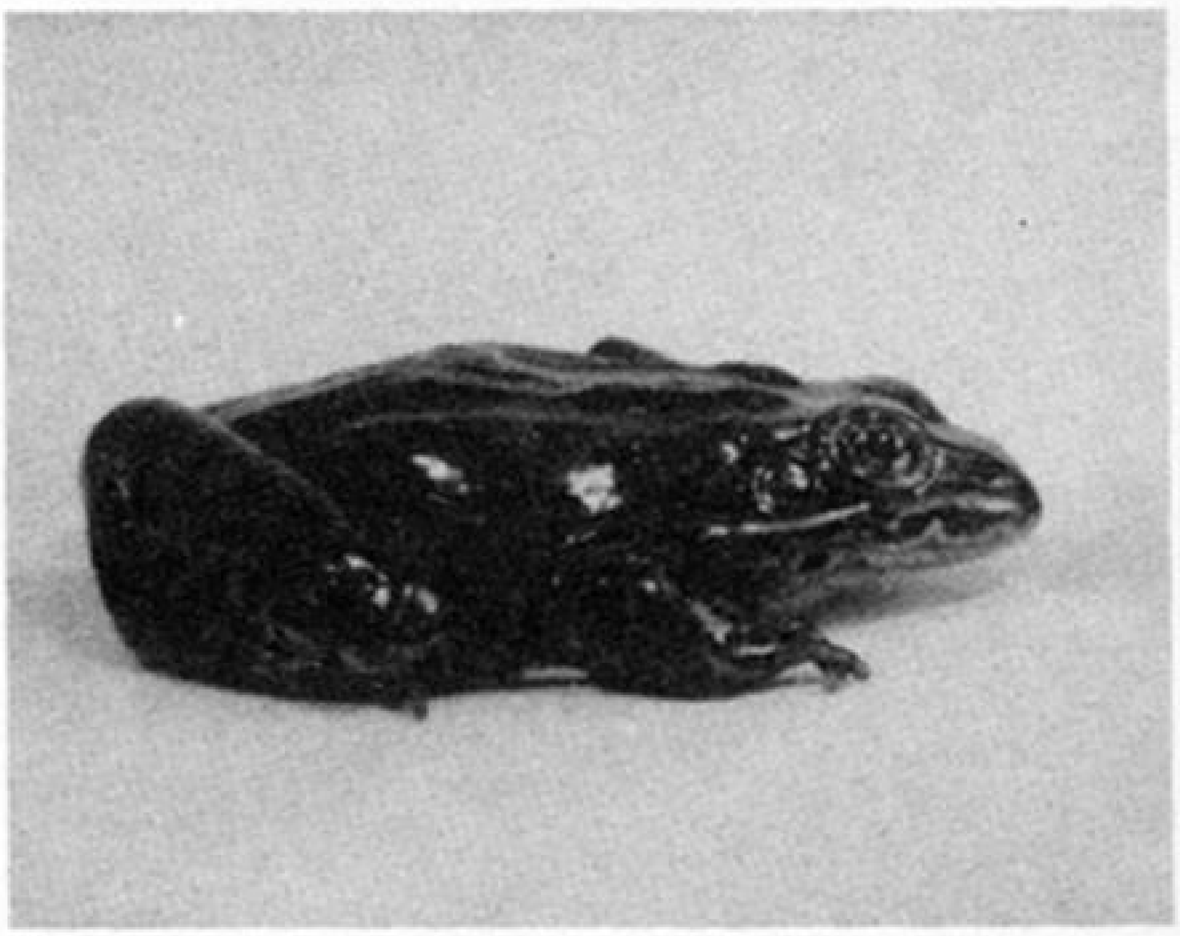

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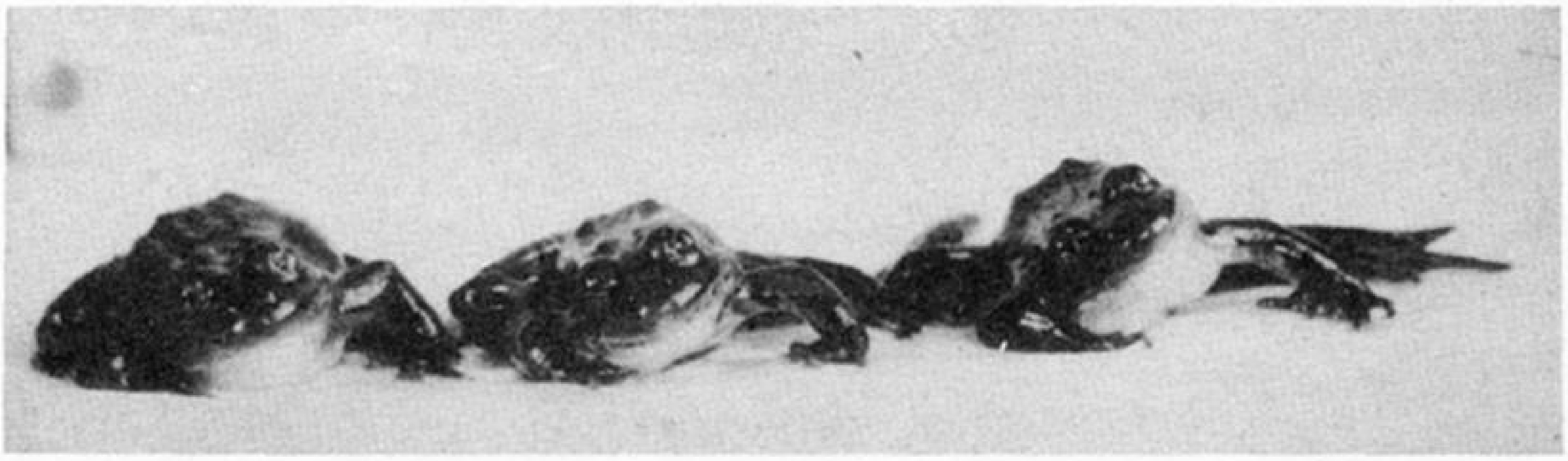

Fig. 9