

THE EFFECT OF LABYRINTHECTOMY ON THE
CO-ORDINATION OF LIMB MOVEMENTS
IN THE TOAD

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(With Plate 1)

If the limbs of an animal are to propel the body along a straight horizontal line the propulsive forces exerted by the right and left pairs of limbs must be equal and the vertical thrusts exerted by each of the four limbs must be such that their combined resultant is equal to the weight of the body and act through its centre of gravity (Gray, 1944). During the normal ambulation of a toad these conditions are not strictly fulfilled, for the body exhibits a slight but definite tendency to rotate about its principal axes (Barclay, 1946). Since all such movements are liable to induce compensatory reflexes of labyrinthine origin, it is of interest to know how far the normal level of co-ordination between the limbs is affected by labyrinthectomy. In all cases the operation has been performed from the dorsal side.

THE EFFECT OF LABYRINTHECTOMY ON AMBULATION

After bilateral labyrinthectomy a toad exhibits relatively little spontaneous movements on land and tends to remain at rest with its hindlimbs partially extended and its head depressed towards the ground. If, however, sharp pressure be applied simultaneously to the plantae of both hindfeet the animal frequently responds by ambulation, the progression of the animal being of the normal type. The limbs are protracted in diagonal sequence and the animal progresses along a rectilinear path. It is therefore clear that the labyrinths do not play a fundamental role in the maintenance of the normal diagonal rhythm of limb movements or in the ability of the limbs to support and propel the body; in the absence of the labyrinths, the co-ordination of the thrusts exerted by the limbs and the sequence of movements of the limbs are controlled by the proprioceptor mechanisms described in previous papers. In the intact animal, however, proprioceptor and labyrinthine responses are very closely associated with each other. This fact is well illustrated when a labyrinthectomized animal is set in motion in response to a tactile stimulus applied to one side of the body; in this case, the resultant ambulation takes place along a path which constantly curves towards the unstimulated side. If the stimulus be weak the radius of the track is usually large and the limbs retain their diagonal

sequence of movement; the limbs on the stimulated side take longer steps than those on the unstimulated side. If, however, the exciting stimulus is relatively intense, the head turns sharply towards the unstimulated side of the body and the animal proceeds to 'circle' actively without making any effective progress over the ground. The limbs on the stimulated side step forward in alternating sequence, whilst those on the unstimulated side step backward. The sequence in which the limbs are lifted from the ground is no longer diagonal but rotary (*RF, LF, LH, RH*). The physiological basis of this circling movement is by no means clear, but it is dependent on the integrity of the sensory nerves of the limbs. No circling, or other locomotory, movements ever occur if all the spinal nerves of the labyrinthectomized animal are de-afferented.*

After complete spinal de-afferentation a sharp stimulus applied to the right jaw of a labyrinthectomized animal elicits a typical monophasic response; the right forelimb is adducted, the right hindlimb is extended (with or without abduction) and the left hindlimb flexes. All these responses tend to move the animal away from the source of the stimulus. A similar stimulus applied to the jaw of a labyrinthectomized animal, whose sensory nerves are intact, elicits circling movements, whereas in the intact animal the initial turn towards one side is followed by rectilinear progression. Pending further experimental data it would appear that the response of the intact animal to a relatively violent stimulus applied to one side of its body consists of three components: (i) A monophasic response independent of both proprioceptors and labyrinths. (ii) A response dependent on the proprioceptors which, when unaffected by the labyrinths, tends to reproduce rhythmically the same mechanical effects as the first monophasic response. (iii) A compensating response due to the labyrinths which enables the proprioceptor rhythm to be transferred from the muscles involved by the initial response to those concerned with rectilinear progression.

The close association between proprioceptor and labyrinthine excitation is also illustrated by the effect of labyrinthectomy on the ability of a toad to use a de-afferented limb for ambulatory purposes. In the absence of the labyrinths a de-afferented limb frequently fails to exhibit any ambulatory movements, progression being effected entirely by the intact limbs.

* The 'circling' response to a strong unilateral stimulus is remarkably persistent in the sense that it continues for relatively long periods after the cessation of the stimulus. It is also remarkable in another respect: a stimulus applied to one side causes persistent circling which eventually ceases; if shortly afterwards a second stimulus is applied to the opposite side the direction of circling is not reversed but is resumed in the original direction. Only after a prolonged period of rest or after a period of 'hypnosis' does the direction of circling invariably occur towards the unstimulated side of the animal. The significance of these phenomena is obscure. Circling does not occur in a unilaterally labyrinthectomized animal. If the animal is gently pressed between two glass plates it can be turned with its dorsal side uppermost, without (in the case of the labyrinthectomized animal) exhibiting any tendency to struggle. The upper plate can now be very slowly raised until out of contact with the animal which then lies motionless on its back. In this position the toad may remain motionless for as much as 5 or 10 min., after which it rights itself spontaneously; if, however, during the 'hypnotic' state the toad is very gently stimulated it immediately rights itself. A similar phenomenon can be observed in intact animals after steady compression, in the inverted condition, between the palms of the hand.

THE EFFECT OF LABYRINTHECTOMY ON SWIMMING

If the labyrinth be removed from one side of an otherwise intact toad the phasing and frequency of the propulsive swimming strokes remains unaffected, but, sometimes, the amplitude and power of the limb on the operated side are reduced and the animal swims towards that side. If both labyrinths are removed all effective co-ordination between the two hindlimbs is lost and the motion of the body in the water becomes completely unco-ordinated; the frequency of the movements of the two hindlimbs not infrequently appears to remain the same, but the power of adjusting the strength and direction of thrust on the two sides of the body is absent.

As previously reported (Gray & Lissmann, 1946) a toad can swim after severance of the dorsal roots of all its spinal nerves; such preparations usually fatigue rapidly, but the level of co-ordinated movement is fully maintained so long as movement persists. On the other hand, all swimming movements are permanently lost if total spinal de-afferentation is accompanied by bilateral labyrinthectomy. If only one labyrinth be removed, the ipsilateral de-afferentated limb frequently fails to exhibit swimming movements, whereas the contralateral limb on the intact side remains active. These facts suggest that the maintenance of a well-sustained and well co-ordinated swimming rhythm is dependent on the integrity of the membranous labyrinths and of the proprioceptor mechanism of the limbs themselves. In the absence of the proprioceptor components of stimulation, the labyrinths alone can excite and control the motor centres of the limb musculature but cannot sustain a rhythm of activity for very long; in the absence of labyrinthine stimulation, the proprioceptors of a limb can sustain active swimming movements but cannot maintain co-ordinated movements between the two hindlimbs.

How far the swimming rhythm of a spinally de-afferentated animal is due to a rhythm of stimulation emerging from the labyrinths is uncertain, but the following experiment suggests that this may be the case. The hind region of a toad was mechanically isolated from the head by dislocation of the ilio-sacral articulations, and severance of all structures except the nerves and main blood vessels uniting the anterior and posterior regions of the preparation. The head and denervated body were then mounted on a cork and the preparation floated in Ringer solution; swimming movements of the hindlegs were readily elicitable so long as the cork was free to move, but as soon as the cork was rigidly fixed all swimming movements ceased. This suggests that, during normal swimming, the acceleration applied to the body by the hindlimbs excites the labyrinths which then reflexly induce movement of the hindlimbs. We have also frequently observed that swimming movements can readily be induced in totally de-afferentated animals by accelerating them quickly over a smooth surface.

THE EFFECT OF LABYRINTHECTOMY ON THE RIGHTING REACTION

Perhaps the most striking effect of bilateral labyrinthectomy on the toad is the failure of this operation to abolish the power of the animal to right itself when forcibly placed on its back. This confirms the observations of Beritoff (1927) on the frog.

The mechanics of the righting response in the operated animal are fundamentally the same as those of the intact animal although the process is usually slower. The mechanism, as determined by cinematograph records, is (for an animal righting itself by rolling towards its right side) as follows: (i) The left hindleg flexes and lies in contact with the ground, the plantar surface being held in a more or less vertical plane. The right limb is fully extended, and retracted, the posture of the forelimbs being variable but never fully flexed. (ii) The righting of the body is effected by the rotation and extension of the left hindlimb. Rotation of the limb's axis towards the ventral surface of the body raises the left hip, at the same time bringing the plantar surface into contact with the ground. In this way the mechanical axis of the left hindlimb passes well above the right side of the body and the left plantar surface forms a firm *point d'appui*. (iii) The extensor muscles of the left knee and ankle extend, thus raising and pushing the left hip towards the right side. In this way the centre of gravity is eventually displaced beyond and to the right of the bearing surface of the body. From this point onwards the body falls under its own weight—the fall being broken by the extended left forelimb. The process of righting is shown in Pl. 1. Beritoff concluded that the righting response of the labyrinthectomized frog is of proprioceptor origin, since removal of the skin and various other organs did not abolish the response. With this view we agree. A toad can right itself either by response to proprioceptor or to labyrinthine excitation, and under normal conditions the two sources of stimulation reinforce one another. The general relationship between the proprioceptor and the labyrinth is illustrated by the following experiment in which the proprioceptor organs of the hind end of the body can be made to operate with or against the labyrinths. Under ether anaesthesia, the body and forelimbs of an animal were completely denervated, the ilia were detached from the vertebral column, a circular transection was made to the body wall and skin, and the gut was removed. In this way the posterior limbs could be rotated independently of the anterior region of the body. The preparation was then allowed to recover from the anaesthetic. If the whole preparation was then placed on its back, the hindquarters immediately righted themselves and thereafter remained at rest. If the whole preparation were resting on its ventral surface, a sharp lateral tilt of the anterior region towards the right elicited only an extension of the right knee; if, on the other hand, a similar tilt was applied when the anterior region was on its ventral surface and the posterior on its back, the response of the ipsilateral hindlimb was much more active and the hindquarters righted themselves. These observations suggest that when a normal animal is placed on its back the righting response is due to a mutual reinforcement of labyrinthine and proprioceptor stimulation, either of which may be adequate for the righting of the body; under artificial conditions, however, the labyrinths may work with or against the proprioceptors.

SUMMARY

1. After bilateral labyrinthectomy, a toad can only walk normally if the stimulus which excites it to move is applied symmetrically on the two sides of the body. If the stimulus is asymmetrical, the animal's path curves towards the unstimulated

side; if the stimulus is relatively intense the animal 'circles' persistently towards the unstimulated side. The ambulatory response of a normal animal to an asymmetrical stimulus is dependent on both proprioceptive and labyrinthine activity.

2. After bilateral labyrinthectomy, both hindlimbs exhibit swimming movements when the animal is freely suspended in water but co-ordination between the two limbs is lost. Evidence is put forward which suggests that the swimming rhythm of the limbs may be dependent on rhythmical excitation of the membranous labyrinth. No swimming occurs when the limbs of a labyrinthectomized toad are de-afferented.

3. The removal of both labyrinths does not abolish the power of the limbs to right the animal when placed on its back. The mechanics of the righting movement are described.

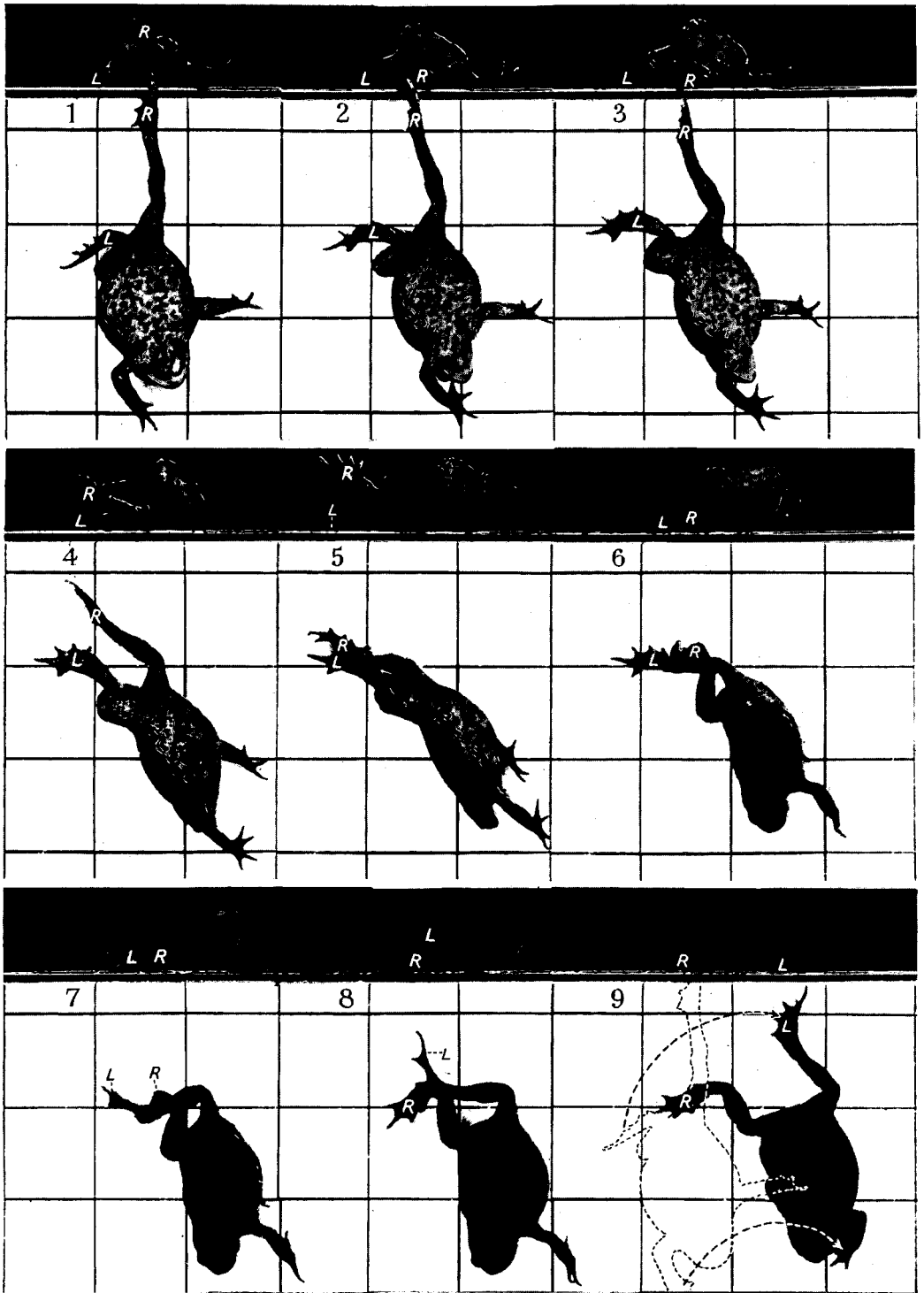
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EXPLANATION OF PLATE 1

Successive cinematograph pictures of the righting response of a normal toad; each figure shows a vertical view and a posterior horizontal view, the latter as seen in a mirror.

In phot. 1 the left hindlimb is flexed, the foot being in contact with the ground along its post-axial border. In photos. 2-5 the axis of the left hindlimb has rotated relatively to the body, thus lifting the left hip and bringing the whole plantar surface into contact with the ground. At the same time the left hindlimb extends and pushes the centre of gravity of the body over the surface of support which is provided by the right side of the body. From this point onwards (phot. 6) the latter falls under its own weight on to its ventral surface—the impact being broken by the right forelimb. *L* and *R*, left and right hindlimb respectively. In phot. 9 the original position of the animal as seen in phot. 1 is indicated by the outline figure.



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