

PSEUDO-RHEOTROPISM IN FISHES

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(Received 10 September 1936)

(With Five Text-figures)

MANY species of pelagic fish tend to orientate their bodies so that their heads are directed upstream, and to maintain a fixed position in space although the surrounding water is in motion relative to the earth. As pointed out by Lyon (1904, 1909), it is impossible to attribute these phenomena to direct stimulation of the fish by the surrounding water, for they may occur under conditions in which there is no relative motion between the fish and its surrounding medium. Lyon showed that under normal circumstances certain fish orientate themselves by optical stimuli; if such an animal is moved passively—either by a current of water or any other means—it responds by movements which are so adjusted as to maintain a stationary optical field; in other words, any passive movement between the fish and its visual field calls forth compensatory movements equal and opposite to the passively induced motion. Although such phenomena undoubtedly occur in nature it is doubtful whether optical stimulation accounts for all the phenomena usually included under the term “rheotropism”. Both Steinmann (1914) and Schiemenz (1927) have shown that, in the absence of a moving visual field, fish show a marked tendency to maintain a fixed position in space when subjected to rotary movements on a turn-table. Steinmann rightly associated this behaviour with the activity of the semicircular canals of the labyrinth, but his interpretation also involves the belief that the relative motion of the fish and the water can be influenced by the motion of the water relative to the ground. This conclusion was very properly rejected by Schiemenz, who concluded that orientation was effected by an “*unanalysierte Fähigkeit die Drehung an sich zu perzipieren*”.

A re-examination of the behaviour of blind fish on a turn-table suggests that their behaviour can be interpreted in terms of normal labyrinthine reflexes common to many types of vertebrate animal. Before describing the responses of fish to passive rotation it is convenient to emphasize the fact that no response of any kind was detected when blinded fish were subjected to rectilinear acceleration along any one of the three main axes of the body. This observation is in harmony with those of Schiemenz (1927) and of Löwenstein (1932), and suggests that when such responses are observed in the intact animal they are elicited by visual stimulation as was the case in Lyon's experiments.

Löwenstein (1932) has shown that the goldfish responds to passive rotation about a fixed vertical axis by compensatory reflex postures, and the work of Löwenstein &

Sand (1936) makes it almost certain that these responses are controlled by impulses arising in the horizontal semicircular canals. The experiments to be described in this paper show that when passive rotation is combined with a horizontal curvilinear displacement, as when the whole fish is passively moved tangentially along a horizontal curve, the static responses, characteristic of a fish which is rotated about a fixed vertical axis, are replaced by dynamic reflexes of a well-defined nature.

The material used for most of these experiments was the gold fish (*Carassius auratus*), which had been blinded by section of the optic nerve or removal of the eyes several days before being subjected to experiment. Essentially similar results were obtained with sticklebacks. The response of such animals to passive rotation in a circular tank is divisible into two phases: (1) an orientation of the head to the direction of passive rotation; (2) a tendency to maintain a fixed position in space after the orientation of the head has been effected. It is convenient to consider first the tendency to maintain a fixed position in space.

THE TENDENCY TO MAINTAIN A FIXED POSITION IN SPACE

When a blind goldfish is placed in a rotating circular channel of water, such as is shown in Fig. 1, the animal rapidly attains a state of dynamic equilibrium such

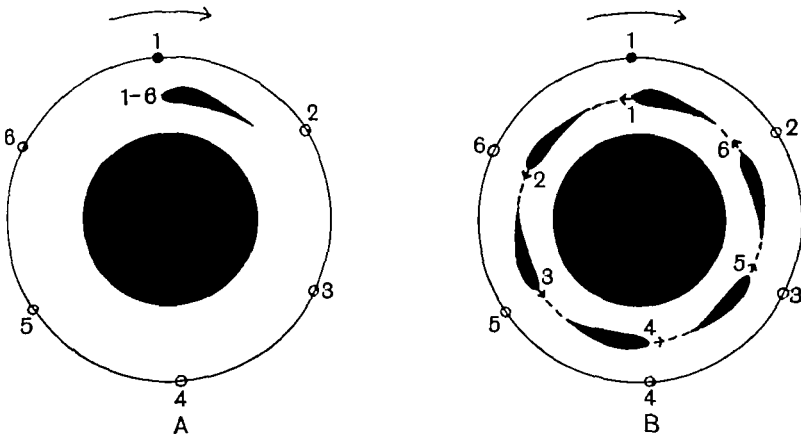
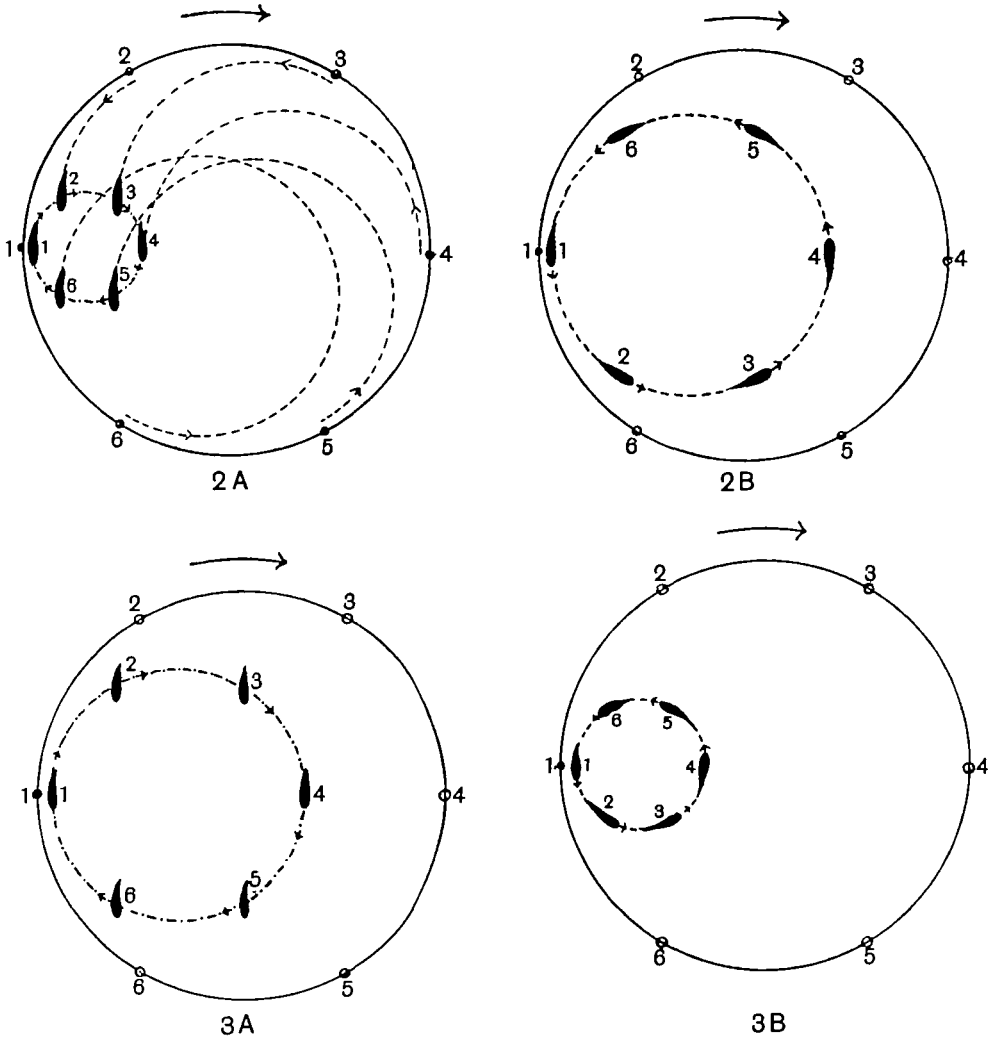


Fig. 1. Diagram showing the response of a blind goldfish to passive clockwise rotation at a velocity of approx. 120° per second in a circular channel of average radius 6 cm. The numerals on the outer rim of the tank show successive positions (relative to the earth) of the black dot seen at position 1. The numerals near the fish show the position of the latter relative to the earth in Fig. 1 A and relative to a point on the periphery of the tank in Fig. 1 B.

that it maintains a fixed position in space with its head facing "upstream", so long as the circumference of the channel does not exceed the maximum distance which the fish can swim forwards in the time required for one complete revolution of the tank. A similar phenomenon was observed by Schiemenz (1927) who used a small circular tank. It is obvious that the fish responds to passive displacement by swimming along a path relative to the tank which is equal and opposite to that of the tank relative to the earth. Movement of this type is effected by two simultaneous

reflexes, (i) normal forward locomotion, (ii) a compensatory turning reflex. As described elsewhere (Gray, 1933), the turning movement of a goldfish is due to an asymmetry in the intensity of the locomotory waves on the two sides of the body, the fish's track through the water being deflected towards the side displaying the more powerful contractions. The rate of angular rotation of the body (about a vertical axis) depends for any given degree of asymmetry between the two sides of the body, on the frequency of the locomotory rhythm so that the rate of angular rotation can be increased either by increasing the frequency of the rhythm or by increasing the asymmetry of the muscular movements. In the case of a fish moving in a circular channel, contact with the sides of the channel can only be avoided if the asymmetry of the body movements is such that the fish swims along a circular path whose radius is equal to that of the channel. If the radius of the fish's track is too large the animal comes into contact with the outer rim of the channel, and in turning away it automatically decreases its radius of movement; similarly, if the radius of movement is too small the fish comes into contact with the inner rim of the channel, and in turning away automatically increases its radius of movement. Freedom from tactile stimulation is only reached when the fish is moving along a path whose radius is the same as that of the channel. If the rate of movement of the fish (relative to the water) along such a path is opposite in direction but less in magnitude than that of the water relative to the earth, the fish is carried "backward" in the stream, and, being thereby rotated about a vertical axis, is therefore subjected to normal labyrinthine stimulation (see Löwenstein, 1932) which calls forth a reinforced forward locomotory reflex. On the other hand, if the fish's "forward" velocity is greater than the "backward" velocity of the tank the labyrinthine stimuli induced by the rotation of the tank is opposed by a contralateral stimulus due to active rotation in the opposite direction. Complete equilibrium can thus only be effected by the fish moving, relative to the surrounding water, along a path equal and opposite to that of the water relative to the earth. It will be noted that the ability of a blind fish to maintain a fixed position in space when rotated in a horizontal container depends partly on the form and size of the container and on the speed at which it is rotated.

If the container is large (e.g. 50 cm. in diameter), or if the rate of rotation exceeds a critical value, the fish fails to maintain its position in space and executes movements which are not easy to follow if considered, as in Schiemenz's (1927) figures, as displacements of the body relative to the earth. The movements are readily followed when considered as displacements of the fish relative to the tank; for this purpose cinematograph records are essential, but it is important that observations should be confined to periods during which the angular velocity of the water in the tank (as judged by the displacement of particles on the surface) is not substantially different from that of the tank itself. Figs. 2 and 3 show typical paths of such fish relative to earth and to the tank for varying speeds of rotation: it can be seen that in each case the fish responds to rotation by swimming, relatively to the tank, along an approximately circular track in a direction opposite to that in which the tank is being passively rotated. A survey of records of this type shows that the faster the



Figs. 2 and 3. Diagrams, constructed from cinematograph records, showing the response of a blind goldfish to passive clockwise rotation in a circular horizontal tank of 25 cm. radius. In Fig. 2 A the numerals near the fish show successive positions of the body relative to the earth during passive rotation at 120° per second, the dotted lines (---) running anti-clockwise show the track of the fish relative to the black dot on the edge of the tank, whose successive positions are shown by the numerals on the periphery of the tank. Fig. 2 B shows the track of the fish relative to the black dot on the tank only.

Figs. 3 A and 3 B show the effect of passive clockwise rotation at about 180° per second. Fig. 3 A shows the track of the fish relative to the earth and Fig. 3 B its track relative to the tank. Note that the radius of the fish's track relative to the tank decreases with increasing velocity of passive rotation. The fish is rapidly fatigued by rapid rates of rotation and the response is then of the type shown in Fig. 4.

animal is rotated the smaller becomes the diameter of the swimming circle, and it is obvious that this response tends to maintain an equality between the rate of passive rotation and that of the active compensatory movement in the opposite direction. Complete compensation to rotation, such as is shown in Figs. 1-3, enables the fish to maintain its longitudinal axis along a fixed geographical bearing, but this condition is lost as fatigue sets in or when the rate of rotation is increased. Under such conditions, the fish tends to drop back in the stream and, to a varying degree, rotates relatively to the earth. At still higher speeds of rotation or during severe fatigue the fish remains practically stationary relative to the tank, and responds

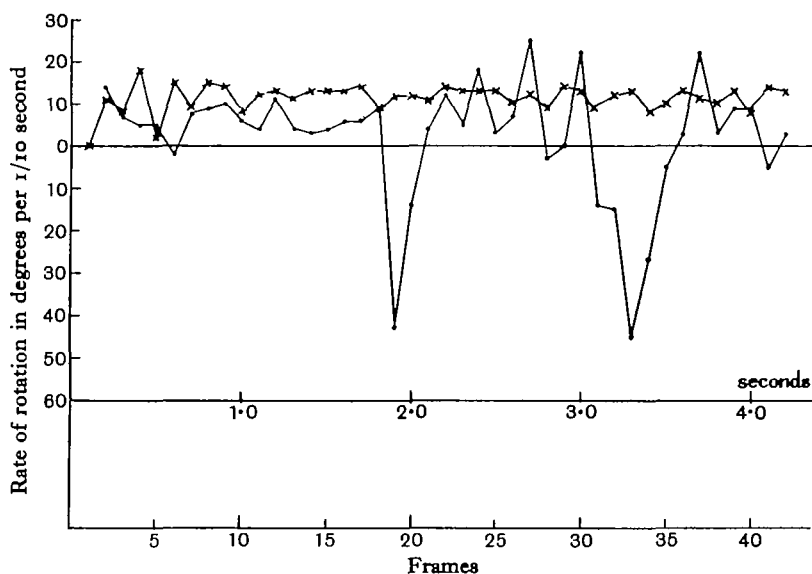


Fig. 4. Graph showing discontinuous and incomplete type of compensatory rotation shown by a fatigued goldfish when passively rotated clockwise at about 120° per second. Note that the fish moves passively with the tank but, periodically, makes a compensating turn of about 45° . \times = tank, \bullet = fish.

by periodic powerful flexions which rotate the head in a direction contrary to that of the tank (Fig. 4); in all such cases the compensation is very incomplete and the response is apparently the same as that described by Löwenstein (1932) when a goldfish, fixed in a holder, is rotated about a vertical axis. It will be noted that the behaviour of a blind goldfish on a turn-table can be interpreted in essentially the same manner as that of other vertebrates, viz. that passive rotation in one direction about a vertical axis elicits a compensating response of labyrinthine origin involving most of the muscles of the body. In the case of the common frog only the head may exhibit compensatory movements while the body remains stationary, but not infrequently the animal walks in a direction opposite to that of passive rotation (Tait and McNally, 1925). In *Xenopus laevis*, an aquatic type, the response is

precisely the same as in the goldfish, although the threshold of response is much lower than in the case of the fish.

It is of some interest to note that compensatory movements involving locomotion are not restricted to rotation about a vertical axis but also occur in response to rotation about a horizontal transverse axis as when a fish is rotated in a vertical container.

THE ORIENTATION OF THE HEAD TO THE DIRECTION OF MOTION

In the above experiments the fish is always so orientated that the passive rotation of the tank tends to move the fish in a posterior direction relative to the head of the animal; in other words, the fish is always facing "upstream". In order to see how this orientation is attained it is convenient to use a circular channel whose width is approximately equal to the length of the fish. It is possible to orientate a fish in a stationary container of this type so that it can be rotated either forwards or backwards; that is, with the head "upstream" or "downstream". If the container is rotated in such a direction that the head is upstream, the response of the fish is of the type described above, but if the direction of rotation is such as tends to move the fish head first in the direction of rotation the response is different. At first the fish may move passively with the container or may swim for a brief period in the direction of passive rotation, but within a few seconds it suddenly rotates its longitudinal axis through 180° by turning in a direction opposite to that produced by the passive movement of the container (Fig. 5*a*). This response is produced by violent contractions of the muscles on the side of the body towards which the animal is actively rotating and therefore on the opposite side towards which the animal is being passively rotated. As soon as this sudden turn has been effected, the behaviour of the fish follows the course described on p. 96. Precisely similar phenomena were observed in the case of *Xenopus laevis* (Fig. 5*c*). It is, however, important to notice that the abrupt rotation of the body, so characteristic of a fish being passively moved head first in a narrow channel, has only been observed when the experimental conditions are such as allow the fish to come into contact with a solid boundary. If a fish, lying near the centre of a large circular container, is slowly rotated "head first" the fish moves rapidly obliquely forwards until it reaches the edge of the container where it then exhibits the rapid 180° turn described above. The path (Fig. 5*b*) followed by the fish towards the edge of the container is not rectilinear but forms a curve whose concavity is on the side opposite to the passive rotation, and there can be little doubt that this phase of the movement is essentially compensatory in the sense that the fish is, whilst in active motion, actively rotating the longitudinal axis of the body in a direction opposite to that produced by passive rotation. Confirmation of this is readily obtained by using blind specimens of *Xenopus laevis*. In this case the animal can be arranged at or near the centre of a large container (50 cm. in diameter). As soon as the rotation reaches the threshold value, the animal swims rapidly towards the side of the vessel along a path which is deflected away from the direction of passive rotation. On

coming into contact with the edge of the vessel *Xenopus* turns abruptly through 180° and proceeds to swim upstream. These observations suggest that so long as the animal does not come into contact with a solid surface, the response to passive rotation is the same whether the animal is being rotated head first or not, namely,

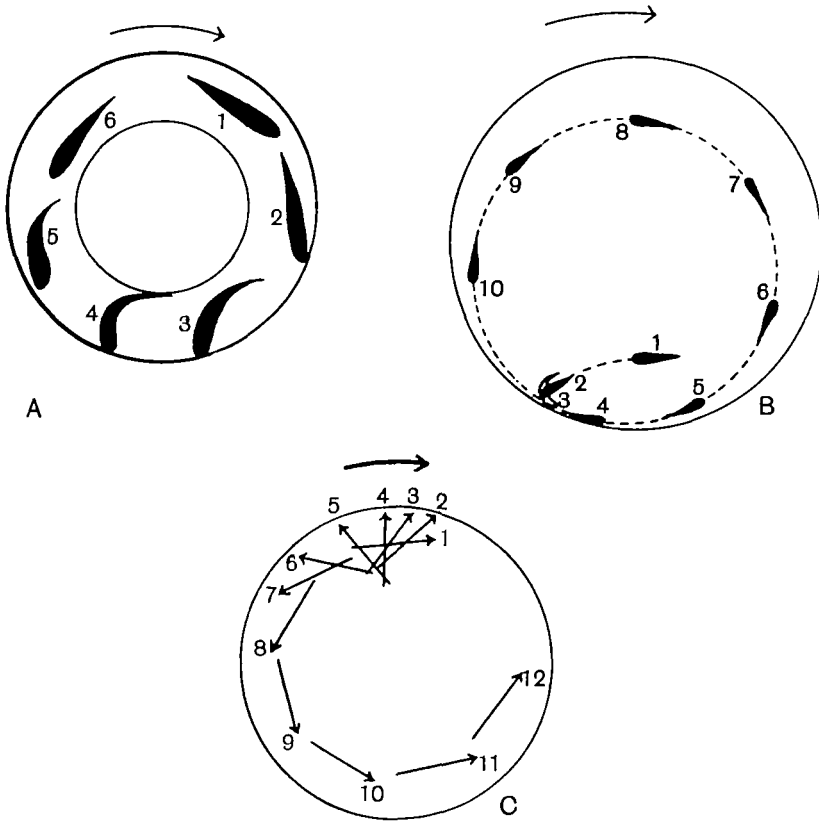


Fig. 5. Diagrams, derived from cinematograph records, showing the response of blind goldfish and *Xenopus laevis* to rotation head first in a clockwise direction. Fig. 5 A shows the movements, relative to the earth, of a goldfish in a circular channel. The fish is, at first, carried downstream, then rapidly turns contralaterally through 180° and finally behaves as in Fig. 1 A. Fig. 5 B shows the track, relative to the tank, of a similar fish originally facing downstream (position 1) in a large container. The fish swims obliquely outwards, away from the centre of the tank; at the rim of the tank it turns contralaterally and continues to swim along an anti-clockwise curve as in Fig. 2 B. Fig. 5 C shows, relatively to the tank, the successive positions of a blind *Xenopus laevis* originally orientated head first in the direction of passive rotation. Note the abrupt turn "upstream"; the animal moved from position 1 to position 12 in approx. 1 sec.

forward progression along a circular path in the opposite direction to the direction of passive rotation. It has been mentioned that as soon as the head of a fish or *Xenopus*, which is being rotated head first, comes into contact with the rim of the container the subsequent rate of compensatory rotation is very high until the animal is facing "upstream"—considerably greater than the rate of passive rotation. It would be interesting to know whether the response of the horizontal canals (see

Löwenstein & Sand, 1936) is affected by horizontal displacement of the head (either backwards or forwards) along a curved path as well as by the rate of change of rotary movement about a vertical axis.

It is of interest to note that the response of a blind eel to "head-first" rotation was somewhat different to that observed in the goldfish of *Xenopus*. The eel's response to "backward" rotation was similar to that of the other types, viz. the animal swam "upstream", but when the eel was rotated "head-first" it came to rest with the side of the body in close contact with the side of the container and passively rotated with the latter without making any active response. Reversal of the direction of rotation quickly elicited forward "upstream" swimming. An unblinded eel, when rotated head first, abruptly changed its direction by a contralateral turn through 180° and swam "upstream" as soon as it had encountered the edge of the tank.

It is obvious from these experiments that considerable caution must be exercised when comparing the ability of a fish to orientate itself in space under the experimental conditions imposed by a turn-table with that which exists under natural conditions. So far as these observations go it appears that a fish would automatically compensate any rotary movement exerted on the body by a stream of water, but there is no evidence that labyrinthine stimuli automatically cause the head of a fish to turn upstream under such conditions as are likely to occur in Nature.

THE NATURE OF THE "RHEOTROPIC" STIMULUS

Since well-defined compensatory movements occur under conditions in which the body of the fish is situated at a considerable distance from the walls of a container, it seems certain that tactile stimulation plays no essential part in eliciting these movements. The work of Löwenstein (1932) and of Löwenstein & Sand (1936) provides extremely strong support for the view that the responses of fish to passive rotation about a fixed vertical axis are brought about by excitation of the horizontal canals of the labyrinth. Numerous authors have shown that the frog, when deprived of these canals, fails to respond to rotation about a vertical axis. Since both fish and Amphibia only respond to passive movements which exhibit a definite rotary component, it seems safe to attribute such responses to the semicircular canals.

From the evidence given in this paper, it would appear that a current of water can only elicit a response from a goldfish, stickleback, eel or *Xenopus* (all in the absence of a visual field) if the current tends to rotate the animal about one of the primary axes of the body. There is no evidence of a response to rectilinear displacements and no evidence that the fish is directly stimulated by the surrounding medium. It may be that the so-called "rheotropic" responses observed in Nature are of a similar nature, but it is conceivable that further search will reveal a type of fish whose labyrinth resembles that of some of the higher animals in being sensitive to rectilinear accelerations. In such cases the animals would be able to maintain their positions in a linearly flowing stream in the absence of light, a feat which, in the case of the goldfish and similar forms, is not possible.

SUMMARY

1. Blind goldfish, sticklebacks, eels and *Xenopus laevis* are insensitive to rectilinear displacements, but respond to all passive curvilinear movements which involve rotation about one of the major axes of the body. In all cases the response is of a dynamic compensatory type in which the animal moves along a curved path, the curvature being in a direction opposite to that of the passive rotation.

2. The ability of blind fish to maintain a fixed position in space when placed in a rotating mass of water is the result of asymmetrical reflex locomotory activity whose rotary and translocatory components tend to be equal and opposite to that induced by the water. This response is almost certainly determined by the semi-circular canals of the labyrinth.

3. When a fish is displaced head first by a rotary current of water, marked over-compensatory rotation occurs as soon as the fish comes into contact with a solid surface. A solid surface does not have this effect when the fish is orientated with its head upstream.

4. In the species examined there is no evidence of true "rheotropism".

REFERENCES

- GRAY, J. (1933). *Proc. roy. Soc. B*, **113**, 115.
LÖWENSTEIN, O. (1932). *Z. vergl. Physiol.* **17**, 806.
LÖWENSTEIN, O. & SAND, A. (1936). *J. exp. Biol.* **13**, 416.
LYON, E. P. (1904). *Amer. J. Physiol.* **12**, 149.
— (1909). *Amer. J. Physiol.* **24**, 244.
SCHIEMENZ, F. (1927). *Z. wiss. Biol. Abt. C*, **6**, 731.
STEINMANN, P. (1914). *Verh. naturf. Ges. Basel*, **28**, 212.
TAIT, J. & McNALLY, W. J. (1925). *Amer. J. Physiol.* **75**, 140.