EYE MOVEMENTS OF THE DOGFISH
SQUALUS ACANTHIAS L.

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INTRODUCTION

The eyes of a dogfish can be caused to move by bending the body of the fish in the absence of labyrinthine stimulation (Lyon, 1900). The labyrinthine system of the dogfish has provided a preparation that has often been used in studies of the labyrinthine control of eye movements (e.g. Maxwell, 1919). As the head of the dogfish is not stabilized, but swings from side to side during swimming so as continually to excite the labyrinthine organs, it seemed of interest to investigate the interaction of labyrinthine reflexes and body movements as they affected eye movements during swimming. In this study the eye movements of free-swimming dogfish have been recorded and classified, and various experiments have been carried out in order to determine the origin and the functions of some of these movements.

MATERIAL AND METHODS

Trawled Squalus acanthias L. of from 1 to 9 lb. weight were kept in the large outside-sea-water tanks of the Portobello Marine Station until required.

The eye movements of free-swimming fish were recorded by means of a 16 mm. cine camera. The fish had small Perspex rods glued to each eye, and swam along a 25 ft. x 2 ft. x 1 ft. squared canvas trough suspended in a large open-air sea-water tank.

The rods were 1 cm. x 0.15 cm. in size, mounted on small concave Perspex bases. The bases were circular with two large segments removed so that fish with rods attached retained sufficient fore and aft vision to avoid the sides of the trough. Eastman 910 adhesive was used to attach the rods. This adhesive is 2-cyano-methyl-acrylate, a substance which rapidly polymerizes when spread in a thin film in the presence of water.

Fish were lightly anaesthetized by a brief (10-30 sec.) immersion in 1% urethane. The eyes were rinsed with fresh water and then dried with cotton wool before the rods were attached. Each rod was held in place for 30 sec. to allow a firm set.

The camera was hand-held. Errors of parallax were minimized by keeping the camera directly above the fish. Graphical records of eye and body movements were later constructed by making a frame-by-frame analysis of the film to determine the angles made by the rods with the reference lines on the tank. Measurements were normally found to be reproducible to within ±1°. Eye positions were measured twice,
to the nearest 0.25°, measurements differing by more than 1° being rejected and the frames re-examined. That vibrations of the hand-held camera caused serious errors in the records of eye movements is thought unlikely because of the smoothness of the records of head positions.

Fish whose eighth nerves were to be sectioned were anaesthetized by a 10 min. suspension in 1% urethane, and allowed 3 hr. to recover after the operation. A flap of skin was turned back on each side of the head at the level of the spiracles, the underlying cartilage and the otoliths were removed, and the two branches of the eighth nerve were cut through and removed for a few millimetres of their length. The resulting cavities were filled with cotton wool impregnated with petroleum jelly, and the skin flaps were glued back into place. The fish were stabilized and thus enabled to swim by clipping an appropriately sized cork to each dorsal fin. Fish of more than about 4 lb. weight could not be stabilized by this method, and were unable to swim without excessive rolling.

Other records were made from fish held by spiked clamps on the snout and back under running sea water in a rectangular tank. Threads were attached to the eyes by glueing or sewing them to the cornea, and tensions were recorded with resistance strain gauges and a pen-recorder. When body movements were to be recorded the anterior part of the fish was rigidly held by two clamps on the body muscles forward of the anterior dorsal fin, one above the gills and the other above the pectoral fins, with another clamp holding the snout. A fine rubber band was attached to the body of the fish just in front of the anterior dorsal fin, about 5 cm. behind the clamps, and tensions created in it by movements of the fish were recorded with a strain gauge. A thread attached to the posterior part of the body restricted tail movements to within an arc of 20 cm. If this were not done the fish struggled violently. With the tail restrained a lively fish would carry out synchronized swimming movements for as much as an hour, and if rendered spinal, for several hours.

The visual field was mapped by measuring the angles at which the lens, which could be seen protruding through the iris, changed in appearance from black to transparent. This method provided no more than a rough approximation of the limits of the visual field, and no check was made of its validity. The results of these measurements give the maximum extent of the visual field—i.e. the minimum blind area and the maximum binocular area.

**RESULTS**

(1) *Eye movements of free-swimming fish*

Fig. 1 is a graphical reconstruction of the eye and head movements of a free-swimming fish. The eyes do not fully compensate for the lateral swinging of the head which occurs during normal swimming. While the head moves through about 25°, the eyes turn only 10° relative to the head so that they move with the head through a part of its arc.

It has proved convenient to consider five categories of eye movement.

(a) *Compensatory eye movements.* These are the component parts of the overall eye movements due to static labyrinthine reflexes. Their importance during normal swimming was analysed in three experiments.

As mentioned above, while the head swung through an arc of 25°, the eyes turned
Fig. 1. Head and eye movements of a free swimming fish. Top: One complete swimming movement followed by a turn to the right. The arrow marks the beginning of the turn, and the synchronous turning eye movements. Trace (1) is formed by subtracting trace (3) from trace (4), to show the movements of the right eye with respect to the head. The eye moves in its orbit through about $10^\circ$ in a direction tending to compensate for the swinging of the head. As the head is rotated to the left the right eye moves backwards in its right orbit, and as the head turns to the right the right eye moves forwards in its orbit. Traces (2) and (3) show movements of the left and right eyes with respect to the trough, i.e. an external plane of reference. The eyes move through about $15^\circ$ while the head moves through about $25^\circ$. (Fig. 5 shows the effects of this movement in terms of the direction of regard of the fish.) The arrow shows where a synchronous turning eye movement (left eye forwards, right eye backwards) marks the beginning of a turn to the right. On the left half of the diagram the measured eye positions have been joined together in a speculative manner assuming complete synchrony of movement; on the right half of the diagram they are joined by straight lines. Trace (4) shows the angles made by the head with respect to the trough. Note that this trace does not directly correspond to the direction of linear progression of the fish. Bottom: Two normal swimming movements. Trace numbers as in top diagram. Time scale, 1 sec.; scale of angles made with guide lines, $10^\circ$. Film speed in both diagrams was 64 frames per sec.
through 10° in a direction which partially compensated for the head movement. If the eighth nerves were cut and the fish, stabilized by corks attached to each dorsal fin, was allowed to swim, then this compensation disappeared. In fact the eyes moved through a greater arc than did the head (Fig. 2). Thus this compensation was labyrinthine in origin.

![Graph](image)

Fig. 2. Head and eye movements of a fish with eighth nerves cut. Trace (1) shows movements of the left eye in its orbit. The graph was formed as in Fig. 1, by subtracting trace (2) from trace (3). As the head swings left the left eye moves backwards in its orbit; as the head swings right the left eye moves forwards, i.e. movements are in the opposite sense to those of an intact fish. Trace (2) shows movements of the left eye with respect to the trough. The eye moves through an arc of about 45° while the head moves through an arc of about 30°. Trace (3) shows movements of the head with respect to the trough. These movements are of greater extent than in a normal fish, indicating that labyrinthine reflexes play a part in controlling the swinging of the head during swimming. Film speed, 16 frames per sec. Time scale, 1 sec.; scale of angles made with guide lines on trough, 20°.

Compensation was by no means complete, and, to examine the possibility that eye movements were restricted anatomically, a record was made of a fish whose head was being passively swung through an arc of 40° (Fig. 3). In this case, although compensation was not complete, the eyes moved through 25° relative to the head indicating that the failure of a free-swimming fish to achieve full compensation was not due to the limits of movement of the eyes.

A further possibility was that the labyrinthine reflex apparatus was in some way inefficient in providing complete compensation, although it was fully responsible for the eye movements seen during normal swimming. However, a free-swimming spinal fish, stabilized in the same manner as the fish in which the eighth nerves had been cut,
moved its eyes so as to achieve virtually complete compensation for head movements (Fig. 4). Thus the failure of the intact fish to achieve full compensation was not due to inadequacies of the labyrinthine apparatus. Some active process had therefore to be postulated.

(b) Swimming eye movements. The component part of the overall eye movements due to the active process opposing labyrinthine compensation caused the eyes to move backwards and forwards in an arc of about 15°, relative to an external plane of reference. So as not to prejudice interpretation of its function the name ‘swimming eye movement’ is proposed for this motion. Fig. 5 shows how the resulting eye movements are related to the fish's swimming movements.

This active process can be seen in its pure form in the record of the fish with both...
eighth nerves cut (Fig. 2). Here the eyes turned in the opposite sense to compensation so as to move through an arc greater by about $15^\circ$ than that moved through by the head. As a swimming spinal fish showed almost complete compensation for the lateral swinging of the head, it seems that the influences opposing compensation depend on the functional connexion of brain and spinal cord.

The eye movements of free-swimming fish can be considered as the algebraic sum of compensatory and swimming eye movements. If the head movement is $+25^\circ$ with respect to the environment, then the compensatory movement is $-25^\circ$, and the swimming eye movement $+15^\circ$, giving an overall eye movement of $+15^\circ$ with respect to the environment (Fig. 1). If the compensatory component is removed by cutting of the eighth nerves, then the overall movement is $+25^\circ + 15^\circ = +40^\circ$ (Fig. 2). If the swimming eye movement component is removed by spinal section, then the overall movement is $+25^\circ - 25^\circ = 0^\circ$ (Fig. 4).

These calculations are oversimplified to the extent that head movement actually is greater in fish in which the eighth nerves have been cut, indicating that an additional factor, that of labyrinthine control of head movement, should appear in the equations.

(c) **Turning eye movements.** Dogfish swimming in the aquarium could be seen to flick their eyes in the direction of a forthcoming turn immediately before changing direction. In Fig. 1 a turning eye movement is indicated by the arrow. A synchronous
movement of both eyes through about $10^\circ$ precedes a spontaneous turn by the fish. When turns were made more abruptly, so as to avoid obstacles in the path of the fish, the turning eye movements were of greater extent, a typical recording showing an excursion through about $20^\circ$ to be made within $0.2$ sec. (Fig. 6).

(d) Fine eye movements. Fine movements through a few degrees of arc were superimposed on each trace made of eye movements. As they generally seemed synchronous, and appeared on the record of the motionless fish with its head passively turned (Fig. 3), it is likely that they were not due to turbulence about the rods attached to the eyes. However, the possibility of their being artifacts cannot be excluded.

Fig. 5. Relation between eye and body movements during swimming. The lines represent an arbitrary visual axis, so as to define the position of the eye. Line $a$ shows the position of the eye when the fish was at the right of the diagram. When the fish had reached the middle position, the eye had turned in its orbit so as to be in position $b_1$. The result of this eye movement was to fixate the point $(a,b_3)$. If the eye had not moved in its orbit, it would have been in position $b_2$ when the fish reached the middle position. If there had been complete compensation, the eye would have been in position $b_1$, and only points at infinity would have been stabilized. While the fish was moving from the middle to the left hand position the right eye was stabilized in a manner similar to the preceding stabilization of the left eye. Distance scale, 1 ft.

(e) Protective eye reflex. This reflex has been described in detail as it occurs in a clamped fish (Bell & Satchell, 1963). In contrast to the other patterns of eye movement shown by the dogfish it is monocular, and bears no direct relation to swimming movements.

The protective eye reflex was readily provoked in free-swimming fish by gently touching the snout with a rod. This caused a brief abduction of the eye on the side touched. If the fish turned as a result of the touch, it could be either towards or away from the rod. The turning was always preceded by a binocular turning eye movement.
In Fig. 6 two monocular phasic retractions of the right eye can be seen to follow a binocular turning eye movement. The fish was turning to avoid the side of the trough, and the retractions coincide with its closest approach to the trough wall.

(2) Eye movements seen in clamped fish

The eye movements of fish with their heads rigidly clamped were recorded by means of threads attached to strain gauges. Clamping the fish in this way prevented eye movements from being affected by labyrinthine stimulation.

\[\text{Fig. 6. Turning eye movements and the protective reflex in a free-swimming fish. Traces (1) and (2) show movements of the left and right eyes. Trace (3) shows movements of the head. A synchronous turning eye movement (left eye backwards, right eye forwards) precedes by 0.12 sec. an abrupt turn of the head to the left. This is followed by two monocular retractions of the right eye as the fish makes its closest approach to the side of the trough. Film speed, 24 frames per sec. Time scale, 1 sec.; scale of angles made with guide lines, 10°.}\]

(a) 'Swimming' fish. Unanaesthetized fish in good condition produced a caricature of swimming if held by a nose clamp and one or two clamps in the body muscles above the gills, with movement of the tail restricted by means of a thread. Although the labyrinths were not stimulated many fish showed powerful eye movements in time with the 'swimming'.

If the fish was curarized the eye movements ceased before the body movements, showing that the eye movements were genuine and not artifacts transmitted along the flexible body of the moving fish. Other control procedures, such as passive movement of an anaesthetized fish, were also employed.
Eye movements of the dogfish

Fig. 7. Eye and body movements of a fish with its head clamped. Top: Although the labyrinths were not stimulated, eye movements appeared in time with 'swimming'. Both traces have been selected to emphasize the active nature of the eye movements and to show that they are not artifacts due to the method of recording. In the second trace, fast 'swimming eye movements' did not begin until active swimming had been initiated by passively moving the body. The fine movements are due to respiration. Time scales: both 10 sec. Bottom: Body positions of clamped and free-swimming fish correlated in terms of eye positions. The common factor in the body positions is seen to be the position of contracting muscles (denoted by shaded areas), rather than the bending of the body.
Because of the unnatural conditions of the experiment it is not valid to consider the eye movements as being 'compensatory' or otherwise without further evidence. Taken in conjunction with the eye movements described in section (1) however, these eye movements seen in a fish with its head clamped and tail restrained are considered as being identical to swimming eye movements, and in the opposite sense to compensatory eye movements. Fig. 7 shows the eye movements and attempts to fit them into the pattern of swimming of a free fish. If the eye positions are correlated, the common

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**Fig. 8.** Turning eye movements and swimming eye movements in a clamped swimming fish. The peak of each backward swimming eye movement of the right eye is shown as a small bar on the record of body movements. The peak of each turning eye movement, both backwards and forwards, is shown as a large bar above or below the line of the body movement record. Trace (1) shows an unusually frequent occurrence of forward and backward turning eye movements, while trace (2) shows a more typical frequency. From these two traces it can be seen that turning eye movements occur about 180° out of phase with swimming eye movements. Trace (3), taken at slow paper speed, shows the superposition of swimming eye movements and turning eye movements, and the prompt diminution of the extent of eye movements after injection of curare, before the body muscles were affected. Trace (4) shows passive movement of the body of a fully curarized fish as a control procedure for artifacts in the eye-movement record.
factor in the bodies of the fishes is seen to be the position of actively contracting muscles rather than the way in which the body is bent.

As well as swimming eye movements another type of eye movement could be seen in the clamped 'swimming' fish. This was considered to be the manifestation of a turning rhythm, discussed in detail in section 2(c). As shown in Fig. 8, this movement can be seen to reset the baseline on which the swimming eye movements appear. On a fast trace it appears to be out of phase with the swimming eye movements by about 180°.

(b) Clamped ‘resting’ fish. To start a clamped fish ‘swimming’, it was often necessary to move it by hand for a few minutes or to apply a painful stimulus. A number of experiments were carried out on fish passively ‘resting’ in their clamps.

Fig. 9. Turning and protective eye movements in a clamped fish. The three traces on the left show the effects of stimulating the right-hand side of the snout, and the three traces on the right show the effects of stimulating the left hand side. The top two traces show that a protective withdrawal of the right eye precedes body movement when the right side is stimulated, whereas when the left side is stimulated the right eye does not move until just before the body moves. The two middle traces show protective movements of the right eye preceding movement of the left eye when the right side is stimulated, and protective movements of the left eye preceding movements of the right eye when the left side is stimulated. The two bottom traces show records taken from the detached external rectus muscle of the left eye in order to obtain a more accurate measure of the time elapsing between eye and body movements. When the right side is stimulated, eye movement precedes body movement by 0–15 sec.; when the left side is stimulated, so as to evoke the protective reflex, eye movement precedes body movement by 1–24 sec. Time scale, 5 sec. All records, except the bottom right, are to the same scale.

A touch with a glass rod, or mild electrical stimulation applied to any part of the fish, would cause it to take up a new body position. The resulting attitude depended on the site and intensity of stimulation and on the position of the clamps, and often was tonically held for some seconds. Otherwise ‘swimming’ movements might ensue, often dying down after a few strokes. For each position of the body a characteristic new position of the eyes was assumed. Because of the positioning of the clamps the
final body position, and the resulting eye positions, were normally seen as in Fig. 7.

A stimulus applied to one side of the snout caused the eye on that side to retract, due to the protective reflex. The contralateral eye did not move until just before the body moved. Needle electrodes inserted at the level of the thread recording body

Fig. 10. The effects of stretch of the extra-ocular muscles and of anaesthetic on the frequency of spontaneous eye movements. The arrows show the direction in which the threads attached to the strain gauges were pulling the eyes. The small movements are due to respiration. Further discussion in text. Time scale, 1 min.
Eye movements of the dogfish

position showed that the body muscles were activated at the same time as the contralateral eye, although the recording system did not register body movement for from 0.1 to 0.3 sec. after the contralateral eye movement (Fig. 9).

On cessation of the stimulus to the snout both eyes moved synchronously, and on occasions where the stimulation had been light, such as low-frequency electric stimulation, movements of the ipsilateral eye synchronous with those of the contralateral eye could be seen beneath the superimposed reflex abductions.

![Fig. 11. The effects of asymmetrical lighting and of body position on the form of the spontaneous eye movements of a clamped fish. The eyes move slowly in one direction and then flick back in the opposite direction. With the light shining on the right eye, or with the fish's body bent to the right, the fast movement is right eye back, left eye forwards, as if the fish was turning to the right. With the direction of the light or the body bending reversed, the fast movement of the eyes is right eye forwards, left eye back, as if the fish was turning to the left. The eye movements are synchronous, the right eye moving back as the left eye moves forwards. The fine movements are due to respiration. Time scale, 1 min.](image)

(c) Spontaneous eye movements. If a fish was rigidly clamped so that no body movements were possible, eye movements still occurred (Fig. 10). Similar eye movements were shown by fish resting on the bottom of the aquarium.

The eyes moved backwards and forwards with a steady rhythm. The frequency varied from between two to eight times per minute, normally appearing faster in small fish. Typical values are 7/min. for a 2 lb. fish and 2/min. for a 10 lb. fish. In a relaxed lightly clamped fish in good condition the rhythm was very regular, the eyes flicking in one direction and then in the other at equal time intervals.

The frequency of this rhythm was affected by the recording method used, and normally appeared faster when timed in a fish with no threads attached to its eyes. As recording was almost isometric its effect upon the frequency of the eye movements indicates a possible contribution of stretch receptors in the extra-ocular muscles.

The frequency and regularity of the rhythm could be affected in a number of other ways. Pouring water into the tank, slamming a door, placing a piece of strongly
smelling decomposed fish in the tank, or switching the room lights on and off, all these affected the rhythm in an irregular manner. In all cases both eyes moved synchronously.

Other types of stimulus affected the eye movements in a regular and reproducible manner. If a white board with a light shining on it was placed on one side of the fish and a black surface on the other, the eye on the light side tended to be held back, and the eye on the dark side to be held forwards, and movements took the form of a low-frequency rotatory nystagmus, the fast movement being towards the light side (Fig. 11). After changing the direction of the light a minute or more passed

![Diagram of eye movements](image)

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Fig. 12. Swimming eye movements in clamped resting fish. The first two traces show high-frequency movements of the eyes resulting from ablations; in the second trace as a result of cutting the eighth nerves, and in the top trace as a result of transecting the brainstem anterior to the medulla. (At the time of taking this record respiratory movements had ceased; they returned later.) The third trace shows high-frequency movements resulting from an increase in the general level of excitation of the nervous system caused by turning the lights on in a previously darkened room. The fine movements are due to respiration. Time scale, 1 min.

while the eye movement pattern was reset. No visual stimuli were found that had any immediate effect on the eye movements. On no occasion was any eye movement seen which could in any way be considered a visual fixation. This was also true of the eyes of fish observed in the aquarium. Although spontaneous eye movements could be seen in dogfish lying on the bottom, they did not bear any relation to the movements of other fish in the tank. (Dogfish in good condition did not normally lie on the bottom when the tanks were lit, but swam continuously. Lying on the bottom occurred only after 2 or 3 days of colliding with the walls of an inadequately sized tank).
Eye movements of the dogfish

If the body of the fish was bent the fast movement of the eyes was towards the side towards which the bent tail was making the fish 'turn' (Fig. 11).

After administration of an anaesthetic (Tricaine MS222, 0.33 g./kg.), the regularity of the movements was enhanced.

Transection of the brainstem anterior to the cerebellum, or high spinal transection, left this slow spontaneous rhythm intact. It also persisted during 2 hr. in a photographic darkroom, as might be expected from its survival of transection of the brainstem posterior to the optic lobes. It will be suggested in the discussion that these spontaneous eye movements appear as turning eye movements in the free-swimming fish.

For an hour or two immediately after transection of the brainstem anterior to the medulla, or after cutting the eighth nerves, the eyes of a rigidly clamped fish moved with a frequency approximating to that of swimming eye movements (Fig. 12). Intact fish were sometimes observed after clamping to maintain eye movements with a rhythm matching that of swimming.

DISCUSSION

(1) Dogfish behaviour

The spiny dogfish, Squalus acanthias, spends its life in shoals ranging over the flat sandy bottom of the continental shelf, feeding on crabs and other bottom-living invertebrates. Its swimming is primitive in that the whole body moves, even the head being only partially stabilized so that it swings from side to side as the fish progresses. It does not possess a swim bladder, so that it cannot stop to look at anything, for if it should stop swimming it would sink. To examine an object it must swim round it in a circle.

Certain well-defined swimming patterns were apparent in the dogfish kept in the large outside tanks at the Portobello Marine Biological Station. The rate of swimming varied with the age and the state of the fish. It was of the order of thirty swimming movements per minute, moving the fish about a foot every second, roughly three-quarters of a mile per hour.

The fish did not swim in a straight line, but in a zig-zag, turning slightly every three or four strokes. The turning frequency varied from one fish to another, from five to ten times per minute, but it was fairly constant in any individual. The turns were more distinctly obvious in young fish. Le Mare (1936) has noted a similar pattern of swimming in Scylliorhinus.

In the open central area of the tank the direction of turning normally alternated regularly from one side to the other. On a bright sunny day with large contrasts in light intensity in the tank the fish, when attempts were made to catch them, tended to keep in the shadowed areas and to turn away from the bright ones. This behaviour was accentuated if a cover was glued on one eye, so as wholly or partially to obscure vision. In this case all turns tended to be towards the 'dark' side, particularly when the fish was frightened, so that on placing it in the water it swam in circles until it calmed down.

Two other patterns of behaviour were commonly observed. One consisted of the fish relaxing its body and stopping swimming. This caused it to glide in a straight line, losing height until it was a foot or so above the bottom of the tank, when it started
swimming once more. The other, when the fish was excited, was to swim very quickly, in a straight line, violently shaking its head from side to side. In this case the fish could not avoid rising, and, in the tanks, rapidly reached the surface.

Except for the glide these patterns were accentuated when the fish were feeding. Excited by dissolved substances released from the food (in this case chopped-up fish) they as much as doubled their rate of swimming, and both the amplitude and the frequency of the turns were increased. Turns were now as much as ninety degrees and occurred at every other swimming stroke, or sometimes twice in rapid succession. They could still be in either direction, the fish moving in a rather random fashion but tending to stay in the neighbourhood of the food.

Swimming in a straight line and shaking the head sometimes occurred when the fish had a mouthful of food. This may have some function relating to killing the prey, or perhaps it helps the teeth to penetrate a large object so as to bite off a piece that the fish can swallow. Examination of mouth contents showed that very large chunks were removed in a single bite at a dead fish. It also occurred when fish were very frightened—it was because of this that the fish were lightly anaesthetized before gluing rods to their eyes.

(2) Visual functions of eye movements

(a) Compensatory eye movements. Compensatory eye movements are normally said to be ‘designed to maintain the visual field constant in spite of the movements of the animal’ (Duke-Elder, 1958). Such eye movements have generally, for experimental convenience, been examined for stationary animals which have been passively rotated (e.g. Benjamins, 1920) but not moved linearly.

Bauer (1924) inferred from casual observation that dogfish eyes moved so as to compensate completely, with respect to a plane of reference moving with the fish, for the swinging of the head during swimming.

On occasions where there is sufficient light for vision the dogfish is continually moving. Thus compensation in the sense defined above would mean at very least some form of optokinetic nystagmus, so that the eye was able to have some stable plane of reference—say the bottom over which the fish was passing, against which it could judge relative movement. The functioning of an all-rod retina has been described for the frog (Lettvin, Maturana, McCullough & Pitts, 1960), and it is emphasized that optic nerve fibres generally responded to relative movement against a fixed background—moving the background as a whole did not produce a response in units which responded to slight movement of a small object. (How far the retinas of dogfish and frog can be considered similar is debatable—certainly the dogfish is much less dependent on vision than is the frog).

Two types of movement which might serve to fix the eyes on objects passed have been described for the dogfish. Swimming eye movements move the eyes through an arc of $15^\circ$ every second. When the fish is moving at its normal rate of 1 ft./sec. these eye movements serve to fixate points of reference about 3 ft. away from the fish in the horizontal plane (Fig. 5). The locus of points so stabilized is the surface of a vertical cylinder, 3 ft. in diameter, rising above and descending below the fish. The only part of this hypothetical surface that is likely to correspond with a real surface is the circular line in which it cuts the sea bottom over which the fish ranges in its search for food.
Eye movements of the dogfish

This may in some manner help to define the movement of objects relative to the sea floor, and might also serve as a form of altimeter, as the position of the stabilized line on the retina would depend on the height of the fish from the bottom. The fish in the outside tanks of the marine station normally swam between 1 and 3 ft. from the bottom, regardless of the depth of water maintained in the tanks, to the limit that when the water level was drastically lowered their fins constantly broke the surface of the water.

Swimming eye movements stabilize only one eye at a time; the one on the side towards which the head is swinging. If the fine eye movements described in the swimming fish are real and not artifacts of the recording process they may serve to break up the period of stabilization into smaller units. No study was made as to whether an optokinetic nystagmus could be produced in a motionless dogfish, and it was not possible to determine how much effect the obscuration of vision caused by the rods had on eye movements. It was clear that the fish retained sufficient vision to avoid obstacles in their path.

According to Rochon-Duvigneaud (1943), 'spontaneous' movements of the eyes of fish are monocular, and so the movements of the eyes of the dogfish can be regarded as compensatory within the scheme of classification he proposes.

As can be seen from Fig. 5, eye movements providing full compensation for the lateral swinging of the head during normal swimming would actually be of disservice to the fish by stabilizing only points at infinity. If there was no compensation at all, the eyes being fixed in their orbits, points very close to the fish, less than a foot from the eyes, would be stabilized.

The lack of stabilization of more distant objects probably offers no disadvantage. The low light intensity, and the general lack of background other than directly below (and possibly above) the fish (fishermen say they are never caught over rocky ground), mean that detection of movement serves a useful function only in regard to objects close to the fish. At a distance from the fish any object would be of possible significance, and its detection perhaps rendered more likely if its image moved across the retina. Pirenne (1958) found that good vision in man at low levels of illumination required relatively large eye movements, sufficient to shift the image from one receptive field to another.

(b) Scanning eye movements. The eyes of the dogfish are set on the sides of the head with their line of vision directed slightly forwards, so that they are about 20° out of parallel. This arrangement gives the fish a large binocular field in front, above, and below it, as well as almost panoramic vision (Fig. 13). The bulge of the pectoral girdle, as well as the slight disalignment of the eyes, creates a blind area behind the fish, extending about 20° above and 60° below the fish. At its maximum extent, 20° below the tail of the fish, the blind area extends some 35–40° in the horizontal plane.

As the fish swims the 15° of scanning produced by the swimming eye movements means that first one eye and then the other is placed in a position in which it reduces the vertical extent of the blind area down to 10° above and 35° below the fish, as well as reducing its maximum width in the horizontal plane to about 20°. (Shown in Fig. 13 by a white line on the black 'blind area').

Complete elimination of the blind area requires a further rotation of the head and eyes. This requirement is met by the zig-zag pattern of swimming with its associated
turning eye movements. During quiet swimming the turns are of a degree more than sufficient to eliminate the blind area. Further possible functions of these eye and body movements include enabling the fish to see where it is going as it turns, and enabling it to cover greater areas of sea bottom during its search for the bottom-living crustaceans which form a large part of its diet.

Fig. 13. The form of the visual field of the dogfish, as projected on to an imaginary sphere. The shaded area is the binocular field, and the black area the blind spot. The white line inside the blind area shows the extent to which the blind area is reduced as a result of swimming eye movements. The measured angles are only approximately correct.

(3) Mechanisms controlling eye movements

(a) Labyrinthine compensation. Loeb (quoted by Maxwell, 1923) was the first to describe compensatory movements of the eyes in dogfish. The eyes move to compensate for rotation of the fish in the longitudinal, transverse, and vertical planes, and this compensation is dependent on the integrity of the labyrinths. The semicircular canals, sacculus, utriculus and lagena all appear to be of importance in this compensation (Maxwell, 1919). No quantitative study of compensation appears to have been made in fish, with the exception of Benjamins's detailed measurements of the degree of compensation for rotation about the transverse axis in teleosts (Benjamins, 1920).

(b) Tonic neck and body reflexes acting on the eyes. In so far as the dogfish can be said to have a neck the swimming eye movements might be considered as being analogous to the effects of tonic neck reflexes in higher vertebrates (Barany, 1907;
Bauer, 1924). Since, however, these eye movements are not compensatory, but in the opposite sense to compensation, the analogy breaks down.

Lyon (1900) described the effect of bending the body of a dogfish with its head firmly held as being to produce compensatory eye movements. The eye on the concave side moved forwards and that on the convex side moved backwards. He also claimed

Fig. 14. The relation of eye movements to the positions of contracting body muscles during swimming. The eye positions are defined by lines, and contracting body muscles by the shaded areas beside the fish. The diagram is discussed further in the text. A turning sequence is also shown, and discussed in the text. Body positions are taken directly from a 16 mm. film. Eye positions have been added in accordance with the records from fish with rods glued to their eyes. (For these records, a telephoto lens was used so as to show only the head.) Time scale, 1 sec.; distance scale, 1 ft.
that, when dogfish lay on the bottom with their bodies bent, their eyes were held in compensatory positions. It was possible to repeat Lyon’s observations without accepting his interpretations.

First, the dogfish does not appear naturally to assume a position with only one convexity and concavity while swimming. Second, the position assumed by the eyes when the body is passively bent depends not only on the position assumed by the body but also on whether or not the fish attempts to resist the bending. That is, as mentioned previously, the eye positions can be correlated with the pattern of contracting body muscles. The eyes are affected by maintained body position only in their pattern of low-frequency movements rather than in any static sense.

It is possible to predict the position of the eyes of a dogfish during any part of the swimming cycle (Fig. 14). This can be done by considering the lateral rectus of an eye as participating in the state of relaxation or contraction of the anterior ipsilateral swimming muscles. In Fig. 14 it can be seen that an eye reaches the fullest forward extent of its movement just before the body muscles of the ipsilateral side begin to contract in the region of the pectoral fins. As more and more of the ipsilateral body muscles contract, so does the degree of excitation of the lateral rectus increase, and the eye moves backwards with respect to the environment. When the eye has reached the backward limit of its excursion the ipsilateral body muscles begin to relax. A corresponding relaxation takes place in the lateral rectus and the eye begins to move forwards. The extra-ocular muscles of both eyes are reciprocally innervated, so that eye movements are synchronous. The backward and forward movement of the eyes described here is with reference to the environment. With reference to the head it is in the opposite sense (Fig. 1), because of the opposing action of labyrinthine compensation. If the eighth nerves are cut, then these eye movements are of greater extent, and take place relative to the head as well as to the environment.

Whether the correlation of contraction of lateral rectus and body muscles is more than a convenient method of working out the position of the eyes at any moment and has significance in the interpretation of embryonic development or evolutionary sequence provides an interesting subject for speculation. Goodrich (1930) summarizes a mass of controversial and conflicting evidence to conclude that the extraocular muscles of elasmobranchs develop from the body somites, the lateral rectus being derived from the third body somite, and the other extraocular muscles from the first and second somites.

(c) Turning eye movements. The mechanism causing the fish to swim in a zig-zag is thought to be the same as that producing spontaneous eye movements in a clamped or resting fish, and these spontaneous movements are thought to be identical to the turning eye movements of a free-swimming fish.

The reasons for this suggestion are as follows:

(i) The frequency of turning matches the frequency of the spontaneous eye movements.

(ii) The spontaneous eye movements bear no relation to visual stimuli any less gross than contrasting light and darkness on opposite sides of the fish, and in cases where they do show a response to visual stimuli the response (low-frequency nystagmus) is matched (turning) by the free-swimming fish.

(ii) The regular spontaneous movements can be altered to the form of a low-fre-
Eye movements of the dogfish

*quency rotatory nystagmus by bending the body of the fish into the position held during a turn.

(iv) Turning of a free-swimming fish is preceded by a fast movement of the eyes in the direction of the turn.

(v) A clear distinction can be drawn between turning and swimming eye movements in a motionless clamped fish indicating that these movements are not graded versions of the same process but are related to two different processes.

Fig. 14 shows the body positions assumed during a turn, and shows that they can be explained by assuming a reversal of the pattern of onset of the next part of the swimming sequence. If there was a concurrent reversal of the pattern of onset of the next phase of the swimming eye movements a turning eye movement would result. The eye having much less inertia than the body, the eye movement is manifest sooner than the body movement, and so precedes the turn, as in the experiments where a painful stimulus was applied to a resting clamped fish. In these, electrical recording from concentric needle electrodes showed that eye and body muscles were activated at the same time (±0.01 sec.).

It is not clear from the present study whether a spontaneous turn (as apart from an avoiding reflex turn) can be initiated at any part of the swimming cycle or only at one part suggested by the 180° phase relation of turning eye movements and swimming eye movements in the clamped fish. Turning results in the phase of the swimming cycle being completely reset, with the time of initiation of the new swimming wave depending on the extent of the preceding turn. As it appears to a casual observer, a slight turn involves only the anterior portion of the fish while a sharp turn involves the whole body.

Lissmann (1947) has described how the swimming rhythm of a spinal dogfish can easily be reset by quite slight stimulation, and his observations probably apply to the controlling of turning in an intact fish. In his study, a weak local stimulus modified local posture, the two parts of the body then re-integrating to form a new swimming wave. A more intense stimulus caused the rapid spreading of a reflex posture over the whole body. These two extreme cases can be considered analogous to the initiation of a slight turn, involving only the anterior swimming muscles, and to the initiation of a turn through an acute angle, in which the reflex posture induced by the turning mechanism affects all the swimming muscles.

Distinct species differences in the ability to control turning appeared between the various elasmobranchs commonly kept at the Portobello Marine Station. *Squalus acanthias* had not nearly the same degree of control as had the smooth hound, *Mustelus antarcticus*, or the school shark, *Galeorhinus australis*.

Gray & Sand (1936) found that hemisection of the spinal cord of a dogfish (*Scylliorhinus*) prevented it from being able to turn towards the injured side, although it could swim normally. This finding is in keeping with the idea that the influences affecting the fish in such a way as to cause turning normally originate in the anterior portions of the central nervous system—as would be expected from the many connexions this part of the nervous system has with the exteroceptors and teleceptors.

(d) The central excitatory state. The spinal cord of the dogfish is unusual in that it appears to be in a continual state of subliminal excitation (Gray & Sand, 1936). Cutting the spinal cord initiates spinal swimming, which may continue for days.
The release of regular and co-ordinated swimming eye movements by cutting afferent pathways or ablating parts of the brain suggests that a balance of excitatory and inhibitory influences impinging on some central co-ordinating agency has been upset by a partial removal of inhibition. Adding to the excitation may similarly upset this balance, as in Fig. 12 where an increase in light intensity caused the eyes to resume a frequency of movement resembling that of swimming, or as where a painful stimulus or moving the body from side to side released swimming in dogfish with its head clamped and its body free to move.

![Fig. 15. Eye movements during spinal swimming. Turning eye movements, shown by the heavy lines, are in phase with body movements, although the parts of the nervous system controlling body movements have been separated from those controlling eye movements. This indicates that the frequency of the eye movements is being modulated by impulses from stretch receptors (forward of the point of spinal section). Time scale, 10 sec.](image)

After their release the maintenance of rhythmic movements is probably helped by re-excitation from the periphery (Lissmann, 1947). Turning eye movements in a spinal fish with its head clamped, although retaining their original frequency, were in phase with the body movements produced by spinal swimming (Fig. 15). As the parts of the nervous system maintaining eye and body movements were separated by the spinal transection, the turning rhythm must have been modulated by afferent nerve impulses from areas of the body passively affected by the swimming movements.

Lissmann (1947) described the effect of stimulating a resting spinal dogfish as being first the assumption of an undulatory posture, and second the propagation of that posture along the body. He emphasized that the posture was assumed as a whole unit.

The results of this present study suggest that this 'whole unit' reflects a central excitatory state (CES) which is itself a whole unit. Thus eye movements and positions reflect the intended body position, as defined by the pattern of contracting body muscles, rather than the existing body position. The CES may be subliminal, as in a resting fish, and in such a case it can be made manifest by removing some inhibition or adding some excitation.

The close relation of eye and body movements make it seem a not unreasonable hypothesis to suppose that the eyes of a resting fish are affected by the influences that subliminally excite the central nervous system with respect to body movements, the difference being that this excitation need not necessarily be subliminal with respect to the eyes. Thus the influences, which when manifest in a swimming fish produce turning, evoke eye movements in the resting fish. Influences altering the CES with respect to turning behaviour, will, when the CES is in a reduced state, influence only
Eye movements of the dogfish

eye movements. If the fish is in a high state of subliminal excitation, bordering on the initiation of active swimming, then the eyes will tend to move with a frequency resembling that of swimming.

This CES is not intended to be defined as being in any way a static entity, but more akin to Lissmann's 'moving sites of nervous integration, continuously excited from within or without the nervous system', although as its manifestations in a resting fish may be of a rhythmic nature, sometimes with a frequency resembling that of swimming, it would be better to say 'affected by' rather than 'ruled by' co-ordinating patterns of afferent impulses.

That there may be eye movements with the frequency of swimming movements or of turning movements, in the absence of manifest swimming or turning—and further that these eye movements are affected by stimuli which in the presence of swimming would affect swimming or turning in the sense in which they affect eye movements—all these occurrences are suggestive, but by no means conclusive, of the common origin of the eye movements of a resting and a swimming fish. Certainly the eye movements of a swimming fish appear to be linked with body movements via a 'CES'. The CES 'causes' body movements, and it 'causes' eye movements in phase with these body movements. If the body movements are passively interfered with, then the eye movements reflect the intended body position rather than the passively induced one.

Whether it is the 'same' CES which produces the eye movements in the absence of body movements cannot be answered at present—and perhaps requires the arguments of a philosopher as much as those of a physiologist.

SUMMARY

1. A method for recording the positions of the eyes of a free-swimming dogfish is described.
2. The eyes of the dogfish do not compensate completely for the lateral swinging of the head which occurs during swimming. The labyrinthine apparatus and the extraocular musculature are capable of providing complete compensation, but this compensation is opposed by influences from the spinal cord.
3. Full compensation during swimming would stabilize only objects at infinity. Partial compensation serves to stabilize a plane of reference close to the fish.
4. Eye movements, allied with the normal zig-zag progression of the fish, serve to eliminate the blind area behind the fish.
5. Other movements of the dogfish's eyes are discussed, and arranged in five categories.
6. Spontaneous movements of the eyes of resting dogfish are described, and related to the eye movements of swimming dogfish. The spontaneous movements are suggested to be manifestations of an otherwise subliminal central excitatory state affecting turning and swimming.
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REFERENCES


GOODRICH, E. S. (1930) Studies on the structure and development of vertebrates. London.


