

## SPATIAL ORIENTATION IN THE LAMPREY

### II. VISUAL INFLUENCE ON ORIENTATION DURING LOCOMOTION AND IN THE ATTACHED STATE

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#### Summary

The responses of attached lampreys to homogeneous visual stimulation and the role of visual stimuli in orientation during locomotion were investigated. Experiments were performed by video recording the responses of intact and lesioned animals to illumination. The following results were obtained.

1. In lampreys attached with their sucker mouth to the bottom of the aquarium, illumination of one eye evoked several possible motor responses (ordered after mean latency): (a) movement of the illuminated eye downwards, and the contralateral eye upwards; (b) rotation of the body around the longitudinal axis, with the illuminated side tilting downwards; (c) deviation of the caudal part of the anterior dorsal fin in the contralateral direction (away from the light); and (d) flexion of the neck and body towards the side of illumination.

2. Illumination of one eye in attached lampreys often resulted in detachment and subsequent movement in a direction away from the light source (negative phototaxis). This response was not related to the degree of roll tilt before detachment, so the negative phototaxis does not appear to be a consequence of the vestibular stimulation.

3. Negative phototaxis was also seen during locomotion: lampreys turned through 180° when they approached a brightly illuminated area. Photostimulation also affected their orientation in the transverse plane during swimming. Illumination of one eye from the side induced a roll movement, so that the illuminated side tilted downwards and the dorsum of the lamprey became turned towards the light. This is similar to the 'dorsal light response' of fish and shows that vision also plays a role in postural control in lampreys.

4. The behaviour of blinded animals differed strikingly from that of intact ones. Whereas intact animals preferentially swam close to the bottom, along horizontal trajectories, blinded animals showed episodes of continuous swimming upwards, near the water surface. During horizontal swimming, their orientation in the transverse plane remained normal, with the dorsal side up.

Key words: lamprey, locomotion, orientation, vision, postural control, *Lampetra fluviatilis*, *Petromyzon marinus*.

#### Introduction

The control of an animal's orientation in space during motor activity requires integration of information from several sensory modalities. Orientation in the gravity field is stabilized by the vestibular-driven control system (see Orlovsky, 1991; Platt, 1983; Wilson and Melvill Jones, 1979). For orientation relative to other objects, a multitude of sensory modalities (vision, audition, electroreception etc.) play important roles in different species (see Northcutt and Davis, 1983). The present study was carried out to elucidate the role of vision in the orientation of the lamprey, a primitive vertebrate that has been used as a model system in the study of motor control (Grillner *et al.* 1991). It is not a comprehensive investigation of visually guided behaviour in lampreys, but rather an attempt to characterize the basic features of the responses to

homogeneous visual stimuli. Such a description provides a necessary complement to studies of the neuronal networks responsible for visuomotor control and visuo-vestibular integration (Deliagina *et al.* 1993; Ullén *et al.* 1993a).

The lamprey has several photosensitive organs. The lateral eyes of adult lampreys are physiologically well-developed and typically vertebrate in structure (Kleerekoper, 1972; Rovainen, 1980, 1983). All the major retinofugal pathways, as well as a retinopetal pathway of mesencephalic origin, have been demonstrated anatomically (see Fite, 1985; de Miguel *et al.* 1990; Veselkin *et al.* 1980). Electrical activity can be recorded in the forebrain, optic tectum and medulla in response to a flash of light to the eye or electrical stimulation of the optic nerve (Veselkin, 1966; Karamyan *et al.* 1975). Lennon (1954)

suggested that vision may be important in prey localization, but the functional role of the visual system has not been studied since the first report by Young (1935*b*), who found that eye illumination evoked 'uneasy movements of the animal' and an alteration of the rate of breathing.

In addition to their eyes, lampreys possess dermal photoreceptors in the skin of the tail region (Steven, 1951; Whitear and Lane, 1981, 1983). The skin photoreceptors are innervated by the trunk lateral line nerves and mediate activation of locomotion (Ronan and Bodznick, 1991; Ullén *et al.* 1993*b*; Young, 1935*a*). The pineal complex has been shown to be involved in the control of the diurnal rhythms of, for example, skin colour change (Eddy, 1972; Young, 1935*b*), locomotor activity (Morita and Samejima, 1984) and ventilatory frequency (Joss and Potter, 1982). It also controls the onset of metamorphosis and the reproductive phase (Eddy, 1972), but it plays no role in the short-latency response to photic stimulation (Young, 1935*b*).

In the present study, the different motor responses induced by homogeneous visual stimuli (asymmetrical illumination of the eyes) were characterized. Negative phototaxis has been described previously (Ullén *et al.* 1993*b*), but was reinvestigated in the present study to determine whether it is a consequence of the changes of posture occurring before detachment and thus could be mediated by a vestibular reflex.

## Materials and methods

### *Animals*

The majority of the experiments were performed on adult river lampreys (*Lampetra fluviatilis* L., see Ullén *et al.* 1995). Fin reflexes were also studied in adult land-locked sea lampreys (*Petromyzon marinus* L., body lengths 35–50 cm), caught in the Great Lakes (USA), because of the larger size of their dorsal fins. The following lesions were employed [all performed under MS222 (Sandoz) anaesthesia] and approved by Stockholms Norra Djurförsöksetiska Nämnd: (1) spinalization at the level of segments 1–3; or (2) unilateral or bilateral enucleation of the lateral eye. White ligature markers were surgically inserted into the dorsal skin at the midline of some animals. Video recordings were performed either in a large, narrow aquarium (140 cm × 16.5 cm × 60 cm deep) or in a smaller aquarium (60 cm × 35 cm × 30 cm deep; Ullén *et al.* 1995).

### *Experimental paradigms*

The responses to illumination when the lamprey was attached to the bottom of the aquarium with its sucker mouth were studied in the following manner. An animal was transferred to the small aquarium where, usually within a few minutes, it adopted a stationary position, attached to the bottom of the aquarium. The eye was illuminated with an optical guide (diameter 8 mm, 90 W white lamp) held 1–2 cm away. The stimulus light remained on until recording of the response was finished. A period of at least 60 s dark adaption was allowed between each test with the same animal.

Different camera positions and frame sizes were used to record the responses.

Responses to illumination during locomotion and the role of light in postural control were studied in the large aquarium. As described in Ullén *et al.* (1995), the animal was initially placed in a cage positioned in the right-hand part of the aquarium. Locomotion was evoked by photostimulation of the tail dermal photoreceptors with a white 60 W lamp. During the study of the role of vision in postural control, a black paper screen was put along one side of the aquarium to give higher illumination from the opposite side and thus a weakly asymmetrical illumination. In some cases, a white 60 W lamp was positioned 20 cm from the aquarium to illuminate a restricted zone from one side. Negative phototaxis was studied by strongly illuminating one side of the aquarium with a white 100 W lamp positioned next to the wall of the aquarium.

The large aquarium was used to investigate whether there is a preferred depth of swimming. To force the lamprey to swim continuously for longer periods (5–10 min), the animal was detached as soon as it attached itself with its sucker mouth to the wall or bottom of the aquarium. This was achieved by mechanically stimulating the area of the sucker with a metal rod. During analysis of the video recordings, the aquarium was divided into 16 depth zones (each 5 cm deep), four situated above and twelve below the water surface. The number of times the animal entered each depth zone during the swimming session was counted, to reveal any preferred depth of swimming.

## Results

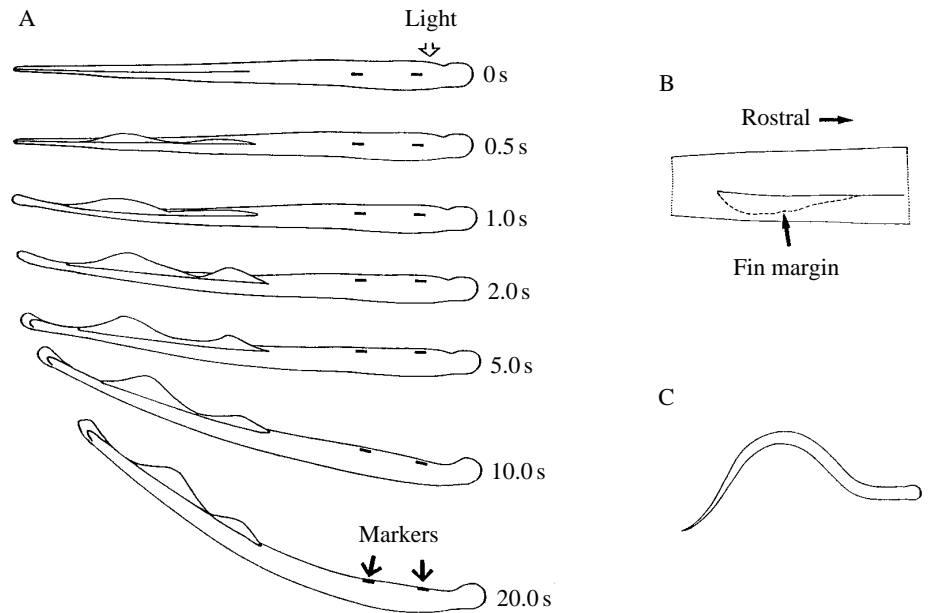
### *Motor responses to eye illumination in the attached state*

In stationary lampreys, attached with their sucker mouth to the bottom of the aquarium, eye illumination evoked five possible stereotyped motor responses, performed while the animal remained in the attached state.

First, movement of the illuminated eye downwards, together with an upward rotation of the contralateral eye, was the most consistent response, occurring in all tests ( $N=62$ , three animals). For technical reasons, it was not possible to record the eye movements while illuminating the eye, so an exact analysis of the time course of this response was precluded. Movement of the eye was, however, almost always the first response to illumination (latency less than 1 s).

Second, rotation of the whole lamprey around its longitudinal axis (Fig. 1A) was observed in 56 of 60 tests (three animals). The illuminated side was, in all cases, rotated downwards. Fig. 1A shows a typical sequence (viewed from above). Initially, the midline, indicated by the markers, was in a symmetrical position, but after 0.5 s a rotation is clearly visible. The major part of the rotation was performed within the first 5 s, but the orientation continued to change slowly until a stable position was reached after about 20 s. In all responding animals, the final angle of roll exceeded 30°, and in 17% of the cases it was 90° or more, so that the animal came to lie on its side or partly on its back, while still attached with the sucker

Fig. 1. Responses of attached lampreys to eye illumination. (A,C, *Lampetra fluviatilis*; B, *Petromyzon marinus*). (A) Dorsal view of a typical response. The animal was marked with ligatures in the dorsal skin of the neck, shown here as short horizontal lines. Time after stimulus onset is given to the right of each projection. Longitudinal rotation (shown by the positions of the markers and dorsal fins) can be seen within 0.5 s. From 1.0 s onwards, there was increasing activation of the ipsilateral neck and body musculature, finally flexing the whole body into an arc. (B) Contralateral flexion of the caudal part of the anterior dorsal fin (dorsal view). The fin assumes a twisted shape (shown by the dashed line). (C) C-shaped lateral flexions on either side of the body were commonly evoked before detachment.



mouth. The latency to the first observable movement varied between 0.5 and 8 s (mean  $\pm$  S.D.,  $1.75 \pm 1.16$  s; median, 1.5 s). It should be taken into account, however, that, owing to this rotation of the whole animal around its longitudinal axis, the position of the stimulus light relative to the eye could not be standardized during the response. This will necessarily affect the amplitude and latency of all motor responses described here. The rotatory movement in the attached state was apparently performed by cranial muscles rotating the head around the sucker.

Third, fin reflexes were studied in the larger species, *Petromyzon marinus*, in which markers could easily be attached to the dorsal fin. Similar responses were occasionally observed in *Lampetra fluviatilis*, but these appeared to be less pronounced (cf. Fig. 1A, where no movement of the fin can be seen). The anterior dorsal fin deviated in the contralateral direction in 72% of the tests ( $N=39$ , four animals). The latency of the response varied between 0.7 and 17.0 s (mean  $3.8 \pm 4.4$  s; median 1.7 s). The deviation was particularly pronounced at the caudal end of the fin ( $16\text{--}59^\circ$ , mean  $38 \pm 14.4^\circ$ ; median  $44^\circ$ ), whereas the rostral end in most cases remained almost in the median plane of the animal (mean movement  $4 \pm 4.6^\circ$ ; median  $0^\circ$ ), so that the fin became twisted (Fig. 1B).

Fourth, activation of the body musculature, giving rise to a C-shaped lateral flexion (Fig. 1C) resembling the mechanical waves seen during locomotion, except that it was non-propagating, was observed in 32% of the tests ( $N=123$ , three animals). In contrast to the ipsilateral neck flexion, C-shaped body flexions appeared on either the contralateral (43%) or the ipsilateral (41%) side. In 15% of cases, two flexions appeared simultaneously, one contralateral and one ipsilateral, giving the body an S-shaped form. The mean latency to the first observable flexion was  $4.6 \pm 1.3$  s (median 2.0 s).

Fifth, ipsilateral flexion of the neck, giving rise to a change of body orientation in the horizontal plane (see Fig. 1A), was

observed in 38% of tests ( $N=62$ , three animals). The first observable change in orientation occurred after  $8.3 \pm 9.5$  s (median 4.0 s). The orientation then continued to change slowly until locomotion started.

#### Activation of locomotion and negative phototaxis

Eye illumination evoked detachment and locomotion in 92% of the tests, with a mean latency of  $16.0 \pm 16.1$  s ( $N=62$ , three animals). In all cases, the locomotor response started with a yaw turn of more than  $15^\circ$ , either away from the source of light or towards it (classified as negative turns and positive turns, respectively). As described previously (Ullén *et al.* 1993b), lampreys displayed a pronounced negative phototaxis: 93% of the responses were negative turns ( $N=57$ , three animals; Fig. 2).

The initial roll movement evoked in the attached state by eye illumination will activate ipsilateral vestibular afferents (Deliagina *et al.* 1992b; Rovainen, 1979), which are known to excite contralateral reticulospinal neurones (Deliagina *et al.* 1992a,b), which in turn excite spinal motor and premotor neurones on the same side (Brodin *et al.* 1988). The possibility that this increased contralateral neuronal activity evoked the negative turn observed during phototaxis was therefore investigated. The relationship between the initial roll response and the subsequent phototaxis was studied by eye illumination of attached intact animals, marked to facilitate analysis of the transverse orientation. In cases where a longitudinal rotation preceded detachment ( $N=36$ , three animals), 100% of the locomotor responses were negative turns (Fig. 2). Of the six responses with no roll, five were negative turns (Fig. 2). Negative phototaxis was thus displayed independently of the roll response in the attached state. The unstable swimming of labyrinthectomized lampreys prevented a direct examination of phototaxis in these animals.

In animals spinalized at the level of spinal segments 1–3

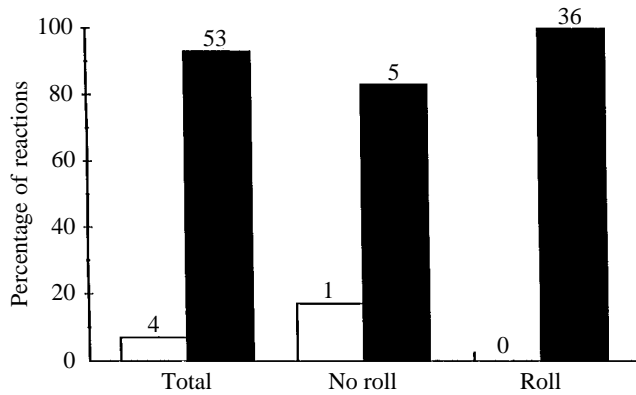


Fig. 2. Negative phototaxis evoked by eye illumination of attached lampreys. All locomotor responses started with a yaw turn, either towards the light source (positive turn) or away from it (negative turn; Ullén *et al.* 1993b). The percentage of positive and negative turns is shown for the whole sample (total;  $N=57$ , three animals), with the number of observations above the bars. In 42 tests, the animals were marked with white ligatures above the bars. The percentages of positive (open bars) and negative (filled bars) turns are shown for the tests in which a roll response was seen before detachment (roll) and for the tests in which no roll response was seen (no roll). In all three groups, the large majority of responses were negative turns. Lampreys thus display a negative phototaxis, which is independent of the roll response in the attached state.

( $N=8$ ), eye illumination still evoked responses mediated by the cranial nerves (eye deviations and rotation around the longitudinal axis), whereas responses mediated by spinal motoneurons (body flexions and fin movements) were abolished (data not shown). Instead of locomotion, detachment was followed by rhythmic lateral movements of the head.

#### Negative phototaxis during locomotion

The effect of illumination on the orientation of lampreys in the horizontal plane during swimming was examined in the large aquarium. A lamprey was induced to swim out of the cage by photostimulation. In normal background illumination, lampreys never made any large changes in swimming direction in the horizontal plane when swimming from the cage (Ullén *et al.* 1995). If a 100 W lamp was positioned so that the half of the aquarium distal to the cage was brightly illuminated from the side, the lampreys in 87% of the cases ( $N=45$ , four animals) turned through  $180^\circ$  in the horizontal plane when entering the illuminated zone, swimming away from the light (data not shown). Negative phototaxis was thus also displayed during locomotion. A detailed characterization of this behaviour and the mechanisms of yaw turns will be presented separately.

#### Visual influence on orientation in the transverse plane

In open water, with symmetrical background illumination, intact lampreys swim with their dorsal side up (Ullén *et al.* 1995). Asymmetrical illumination of the eyes influenced the transverse orientation of the animals during locomotion. When the illumination was stronger from one side, the animals tilted

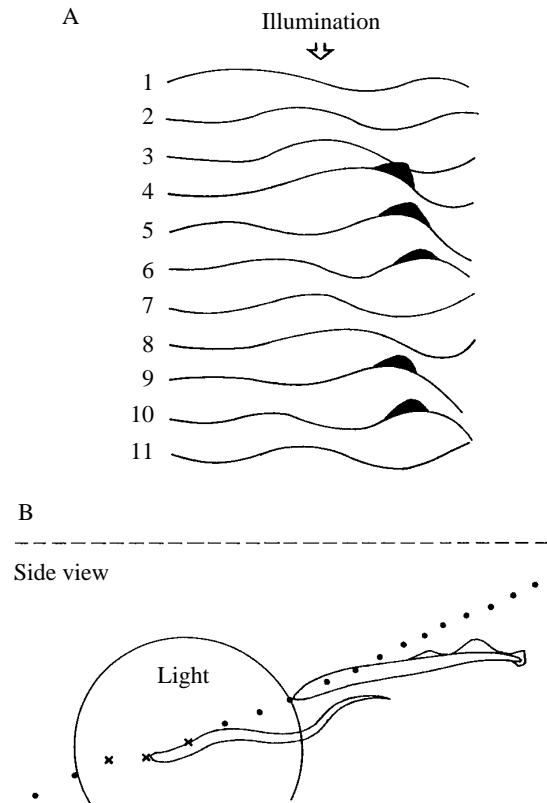


Fig. 3. Roll instability during locomotion evoked by lateral illumination. (A) A lamprey was induced by photostimulation to swim out of the cage in the large aquarium (Ullén *et al.* 1993a). A black screen was put along the left-hand wall to make the illumination stronger from the right. The dorsal view of the body midline and the projection of the posterior dorsal fin are shown in successive frames. In frames 4–6 and 9–10, the lamprey swam tilted around its longitudinal axis, with the illuminated side rolling downwards, as is seen from the position of the fin. There is 40 ms between frames. (B) The same test situation as in A, but a restricted zone of the aquarium was illuminated from the right. Lateral view of the swimming trajectory. Dots indicate the position of the head in each frame. In frames where the lamprey swam tilted with its right side down, the head position is marked with a cross. The dashed line is parallel to the water surface.

towards that side during swimming. Fig. 3A shows the midline of the body and the profile of the posterior dorsal fin (viewed from above) from a typical swimming sequence. In frames 4–6 and 9–10, the animal was tilted towards the illuminated side, as is seen from the position of the fin. Fig. 3B shows the lateral projection of another sequence, in which only a restricted zone (circle) of the aquarium was illuminated from the left side. In symmetrical illumination, the dorsal-side-up orientation was always maintained (Fig. 3B, right). When entering the zone with side illumination, roll tilt movements to the left appear. The lamprey frequently continued to swim with a tilted orientation for a short period (seconds) when the illumination had become symmetrical again, immediately after the photostimulation. This type of disturbance was observed in all animals tested ( $N=10$ ). In lampreys with one eye removed

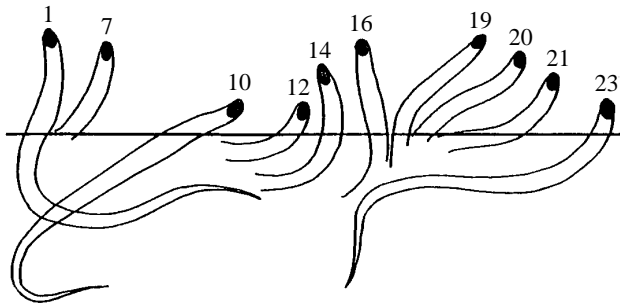


Fig. 4. Continuous upward swimming at the water surface (solid line) in a blinded lamprey. Frame numbers are indicated for each projection (frontal view). Note how, in frames 1 and 16, for example, the head and anterior part of the body are kept almost vertical, high above the water surface. There is 40 ms between frames.

( $N=4$ ), shorter episodes of similar postural instability were often observed in normal illumination. In such cases, the animals swam with the intact side tilted downwards. In animals with both eyes removed ( $N=6$ ), there were no deficits in maintenance of the dorsal-side-up orientation.

#### Orientation of blinded animals in the sagittal plane

With regard to the vertical orientation of the lamprey, no short-latency effects were observed after photostimulation of the eyes during locomotion. Nevertheless, the behaviour and preferred swimming depth during longer periods of free swimming in normal background illumination differed strikingly between intact and blinded animals. Blinded animals ( $N=6$ ) exhibited very frequent episodes of continuous, almost vertical, upward swimming (Fig. 4), during which the animals typically performed jump-like movements at the water surface, often with the head and anterior part of the body above the surface (Fig. 4). Such behaviour can very occasionally be observed in intact animals. Each histogram in Fig. 5 shows the number of times different animals entered different depth zones in the aquarium during a 5 min period. Fig. 5A shows two results for an intact animal. These swam at all depths, but mainly in the deeper half of the aquarium (mean depth zone 7). In contrast, blinded animals, tested 1 day after surgery, spent most of their time near the surface (Fig. 5B), displaying the 'jumping' behaviour shown in Fig. 4, and they only rarely descended to the deeper half of the aquarium (mean depth zone 0). In one-eyed animals (Fig. 5C), the 'jumping' behaviour was less frequent than in blinded animals (mean depth zone 5). The behaviour of the blinded animals in Fig. 5B was re-examined 14 days after surgery (Fig. 5D). Upward swimming at the surface was still more common than in both intact and one-eyed animals, but episodes of normal locomotion at greater depth were more common than immediately after surgery (mean depth zone 3).

## Discussion

### Responses to illumination in the attached state

Rotation of the whole body around its longitudinal axis,

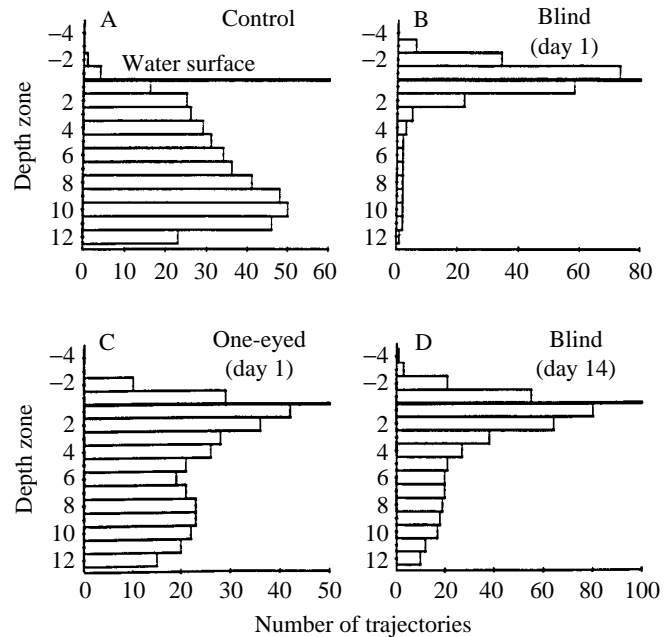


Fig. 5. Preferred depth in intact and blinded lampreys. (A) Histogram showing the number of times a typical intact lamprey entered different depth zones below and above the water surface (the position of the head is considered; each depth zone was 5 cm deep) during a 5 min period of free swimming. Most of the time is spent in the deeper half of the aquarium. Mean depth zone 7. (B) The same diagram for a blinded animal, 1 day after surgery. Most of the time is spent near the water surface, displaying the 'jumping' behaviour shown in Fig. 4. Mean depth zone 0. (C) The same diagram for an animal with one eye removed, 1 day after surgery. This shows a behaviour intermediate to those in A and B. Mean depth zone 5. (D) The same diagram for the blinded animal in B, 14 days after surgery. Upward swimming at the surface still occurred, but was now interspersed with episodes of more normal swimming. Mean depth zone 3.

evoked by illumination of one eye in attached lampreys, may function as a protective reflex, turning the dark dorsal side towards the light and avoiding exposure of the white belly, thereby decreasing the risk of discovery by predators. It is noteworthy that the direction of this rolling movement (ipsilateral side downwards) is the same as that in the dorsal light response of free-swimming fish (von Holst, 1935; Platt, 1983) and lampreys (see below). It has previously been shown that the rolling movements of attached lampreys are performed by specialized trigeminal muscles of the head (Ullén *et al.* 1993a).

The eye and fin responses are similar to those reported in the dorsal light response of teleost fish (von Holst, 1935; Platt, 1983). The direction of the eye movements makes them functionally analogous to the vestibulo-ocular reflexes, assuming that symmetrical illumination of the eyes is used as an indicator of correct eye position. The deviation of the caudal part of the anterior dorsal fin towards the side of illumination would, if it were also to occur during swimming, be expected to evoke a roll movement of the body in the opposite direction and thus to contribute to the dorsal light response (see below).

The ipsilateral flexion of the neck (Fig. 1A) may be a preparation for negative phototaxis, by changing the orientation of the animal in the horizontal plane so that the subsequent swimming is directed away from the light. The C-shaped lateral flexions, which occurred with equal probability on either side of the body, presumably reflect a non-specific activation of the spinal motor circuits before detachment and actual locomotion starts.

#### *Negative phototaxis*

Negative phototaxis, evoked by illumination of one eye in attached lampreys, was displayed independently of the preceding roll response, and it cannot therefore be mediated by vestibular reflexes evoked by the initial roll. A strong negative phototaxis could also be demonstrated during swimming. Negative phototaxis is clearly an effective way of avoiding illuminated areas where the risk of discovery by predators is higher. Similarly, larval lampreys gather in the darker parts of an aquarium if different compartments are illuminated with different intensity (Harden-Jones, 1955; Young, 1935a). Although adult animals are 'directed' by light, larvae lack functional eyes and their light avoidance reaction is due only to their skin photoreceptors. These stimulate movements in more brightly illuminated areas, but the animals appear to stop locomoting in darkness.

#### *Dorsal light response*

Lampreys display a dorsal light response very similar to that described in fish (von Holst, 1935; Platt, 1983): an asymmetrical illumination of the eyes induces a tilt of the body towards the more illuminated side and deviations of the eyes (illuminated eye downwards, contralateral eye upwards). In the absence of any additional influences, vestibular postural reflexes are 'tuned' to stabilize body orientation with the dorsal side up. Illumination of one eye changes the 'set point' of the vestibular roll control system so that the animal maintains a tilted body orientation (Deliagina *et al.* 1993; Orlovsky, 1991; Ullén *et al.* 1995).

As shown in the preceding paper (Ullén *et al.* 1995), an important mechanism for correcting movements in the transverse plane during swimming in lampreys is probably lateral movements of the ventrally flexed tail. The four reticular nuclei constitute the only descending motor system that reaches the caudal parts of the body (Brodin *et al.* 1988). The response characteristics of reticulospinal neurones to vestibular stimulation have been mapped in detail (Deliagina *et al.* 1992a,b; Orlovsky *et al.* 1992). The most likely site for integration of vestibular and visual signals related to postural control appears to be the middle rhombencephalic reticular nucleus (Deliagina *et al.* 1993). Neurones in this nucleus are excited by photostimulation of the ipsilateral eye and have an excitatory influence on ipsilateral spinal motor circuits. They could thus excite tail motoneurones, causing a lateral displacement of the tail and a rotation of the body towards the same side (Ullén *et al.* 1993a).

#### *Orientation of blinded lampreys*

Blinded animals behaved in a dramatically different way from intact animals, in that they swam almost constantly upwards. One-eyed animals displayed a behaviour intermediate between those of intact and blinded animals. This was not a result of postoperative arousal, as only a small compensation was seen 14 days after surgery. A possible interpretation of this finding is that the intensity of light is used to estimate depth. Complete 'darkness' after blinding would then indicate that the lamprey was too deep, and could evoke upward locomotion.

In summary, the present work demonstrates that simple, homogeneous visual stimuli, delivered to the lateral eyes, can evoke a number of stereotyped motor responses in the lamprey, one of the most primitive vertebrates. Information about the general intensity and symmetry of illumination seems to be used in postural control (dorsal light response), to avoid exposure in illuminated areas (negative phototaxis, attached-state roll) and possibly in depth perception. It is particularly interesting that visuo-vestibular interaction in postural control (dorsal light response) may have appeared very early in vertebrate phylogeny, since lampreys diverged from the main vertebrate line around 450 million years ago (Bardack and Zangerl, 1971). The neuronal plasticity involved in this visually induced switch in the 'set-point' of the vestibular roll control system (Ullén *et al.* 1995) is being analyzed in electrophysiological studies (Deliagina *et al.* 1993; Ullén *et al.* 1994).

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