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BEHAVIORAL AND NEUROPHYSIOLOGICAL DEMONSTRATION OF A LATERALIS SKIN PHOTOSENSITIVITY IN LARVAL SEA LAMPREYS

BY MARK RONAN* AND DAVID BODZNICK
Department of Biology, Wesleyan University, Middletown, CT 06457, USA

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Summary

Larval lampreys respond to skin illumination with a delayed burst of swimming in an attempt to escape the light. The photoresponse, which is independent of the lateral eyes and pineal organs, is most readily elicited by light shone on the tail. Behavioral studies in larval lampreys demonstrate that photosensory afferents innervating the tail are carried by a trunk lateral line nerve supplying regions caudal to the head. The present results confirm that bilateral transection of this nerve in larval sea lampreys markedly diminishes the photoresponse. The trunk lateral line nerve consists of the recurrent ramus of the anterior lateral line nerve and a ramus of the posterior lateral line nerve. Bilateral transection of the recurrent ramus does not affect the photoresponse, indicating that lateralis photosensory afferents enter the brain *via* the posterior lateral line nerve and terminate in the medial octavolateralis nucleus. Photosensory units were subsequently recorded in the trunk lateral line nerve, posterior lateral line nerve and the lateral line area of the medulla. Medullary photosensory units were localized to the medial nucleus, previously regarded as the primary mechanosensory nucleus. Photosensory units in lateral line nerves and the brain exhibited low, irregular spontaneous activity and, after latencies of 1–4 s, responded to tail illumination with repeated impulse bursts. Response thresholds were 0.1–0.9 mW cm^{-2}. Responses to sustained illumination were slowly adapting. A skin photosense is thus an additional lateralis modality in lampreys.

Introduction

Behavioral studies dating from the turn of the century indicate that several anamniotic vertebrates respond to illumination of the skin (reviewed by Steven, 1963). In the typical photoresponse, skin illumination is followed by locomotor activity after a latency of several seconds. These photoresponses do not depend on visual or pineal organs and cannot be attributed to thermal effects of the light. The

*Present address: Medical Sciences Program, 256D Myers Hall, Indiana University, Bloomington, IN 47405, USA.

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responses are thought to be mediated by unknown photosensitive elements in the skin. The photoresponses of some species are apparently oriented to the direction of illumination (i.e. a phototaxis); in other species, the direction of light-induced locomotion is independent of the light's location (photokinesis), with only the speed and frequency of movement influenced by the light intensity (Fraenkel and Gunn, 1940; Harden-Jones, 1955). Many species appear to be negatively photokinetic and, when illuminated, their non-directed locomotion ultimately displaces them to regions of lower light intensity.

Among anamniotes sensitive to skin illumination, behavioral studies have focused on the skin photosensory systems of lampreys and hagfishes, the two groups of extant agnathans. Parker (1905) first observed that larval lampreys (ammocoetes) at rest on the bottom of a darkened aquarium begin to swim after several seconds of general illumination. Following partial illumination of the tank over several minutes, ammocoetes moved preferentially to the darker areas even after transection of the optic nerves. Subsequently, Young (1935*a*) and Steven (1950) confirmed the negative photokinetic response of larval lampreys and, using discrete spots of light, found the tip of the tail to be the most sensitive region. Light shone on the tail elicited movement after 2–3 s, whereas light of equal intensity directed on the skin overlying the pineal organs or the immature lateral eyes evoked a response only after a minimum of 30–50 s. Illumination of the pineal complex and/or the lateral eyes did not affect the response to tail illumination (Young, 1935*b*). In addition to its long latency, the ammocoete photoresponse also showed a slow adaptation rate and limited dynamic range (Francis and Horton, 1936; Steven, 1950). Finally, Young (1935*a*) made the unexpected discovery that the skin photosense on the tail of ammocoetes is abolished by bilateral transection of the trunk lateral line nerve innervating the trunk and tail.

The trunk lateral line nerve in lampreys contains afferents originating in both the posterior lateral line nerve and the recurrent ramus of the anterior lateral line nerve (Fig. 1) (Johnston, 1905; Lindström, 1949). The recurrent ramus contains chiefly, if not exclusively, electrosensory afferents (Bodznick and Preston, 1983), which enter the brain in the dorsal root of the anterior lateral line nerve and terminate in the ipsilateral dorsal octavolateralis nucleus (Ronan and Northcutt, 1987), the medullary electrosensory nucleus (Bodznick and Northcutt, 1981). Posterior lateral line nerve fibers, long thought to be exclusively mechanosensory, project bilaterally to the medial octavolateralis nucleus. Thus, photoreceptive fibers in the trunk lateral line nerve must project to the brain by one or both of these paths.

In the present experiments, the skin photosense of larval sea lampreys was examined using behavioral and neurophysiological methods. The response of ammocoetes to tail illumination was tested following transection of separate lateralis rami to determine by which of the two possible pathways photosensitive afferents reach the brain. Extracellular recordings in the lateral line nerves and the octavolateralis area of the medulla were undertaken to confirm the presence of lateralis photosensitive afferents, to determine the termination of primary

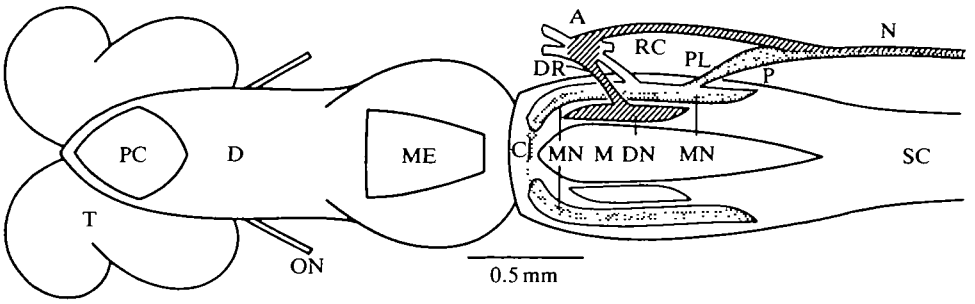

Fig. 1. Schematic representation of the brain of a larval sea lamprey in dorsal view showing the primary projections of the lateral line nerves to the medullary lateralis nuclei. The recurrent ramus (RC) of the anterior lateral line nerve (hatched) projects *via* the dorsal nerve root (DR) to the ipsilateral dorsal octavolateralis nucleus (DN). The posterior lateral line nerve (PL) (stippled) projects bilaterally to the medial octavolateralis nucleus (MN). The primary afferents of the recurrent ramus and the posterior lateral line nerve join caudal to the posterior lateral line nerve ganglion (P) to form a trunk lateral line nerve (N), which innervates the trunk and tail. A, anterior lateral line nerve ganglion; C, cerebellar region; D, diencephalon; M, medulla; ME, mesencephalon; ON, optic nerve; PC, pineal complex; SC, rostral spinal cord; T, telencephalon.

photosensory units in the brain and to initiate physiological characterization of skin photosensory units in a vertebrate.

Materials and methods

Larval sea lampreys (*Petromyzon marinus*) were collected by electroshock in streams of central Connecticut from March to November with permission of the Connecticut Department of Environmental Protection. The lampreys were kept in glass aquaria containing aerated fresh water (11–13 °C) and lined on the bottom with mud and sand. Fresh pond or stream water containing algae and detritus was added periodically. The animals were 11–15 cm in total length, indicating that they were in the final year or two of the larval stage, a period lasting 5–7 years in sea lampreys (Hardisty and Potter, 1971).

Behavioral studies

Ammocoetes were removed from their dimly lit aquaria and rapidly transported to the testing site. Behavioral experiments were conducted in a Faraday cage draped with opaque black plastic. Fig. 2 illustrates the holding apparatus used for behavioral tests. In the faint light of the cage, the lamprey was funnelled headfirst into a translucent plastic tube slightly wider (8–10 mm) and longer (12–16 cm) than the animal. These dimensions provided the animals, which are positively thigmotactic, with sufficient surface contact to favor lengthy periods of inactivity while still allowing energetic tail movements. The open ends of the tube were secured by a large-mesh plastic screen. Holes drilled through the 1 mm thick wall of the tube

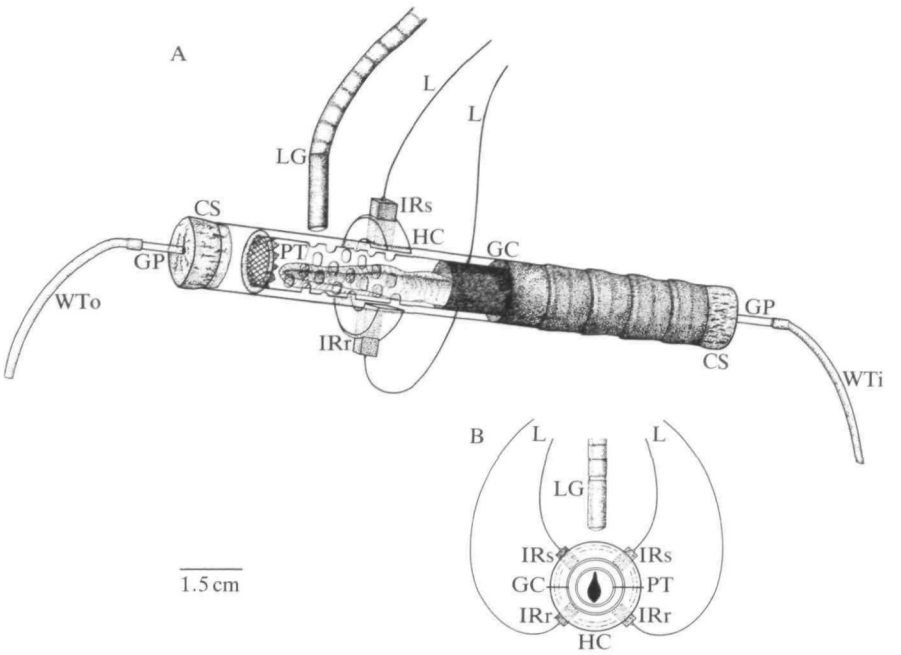

Fig. 2. (A) Drawing of the test apparatus used in the behavioral analysis of the lateralis photosensory response in larval lampreys. (B) Diagramatic cross section through the apparatus. Movements of lamprey's tail (black silhouette) were monitored by two sets of infrared sensors positioned orthogonally on the glass cylinder. CS, cork stopper; GC, outer glass cylinder; GP, narrow glass pipe; HC, holding collar for infrared sensors; IRr, infrared receiver; IRs, infrared sender; L, electric leads to power supply and amplifier; LG, quartz-fiber light guide; PT, inner plastic tube; WTi, water inflow tube, WTo, water outflow tube.

at the level of the head and tail promoted water flow through the tube and around the animal. Holes in the tail end additionally provided more direct access of the stimulus light to the animal's tail.

When sealed, the plastic tube containing the ammocoete was placed in a larger (11 mm diameter) borosilicate glass tube. Aerated water at 10–12 °C was continuously pumped through the tube. A plastic collar containing two infrared monitors was secured on the clear end of the glass tube at the level of the animal's tail. The infrared monitors, which consisted of separate sender and receiver units on opposite sides of the tube, detected movements of the tail in the dark. Partial or complete interruptions of the infrared beams by tail movements were registered as voltage transients on an oscilloscope and chart recorder. The skin photosensory system of lampreys is insensitive to infrared radiation (Steven, 1950).

Stimulus illumination was white light supplied by a Dolan–Jenner quartz–halogen source and focused by a biconvex quartz lens on the proximal end of a quartz-fiber optic guide (61 cm long, 3.5 mm diameter). The distal end of the light guide was positioned slightly above the glass tube at the level of the animal's tail. Neutral density filters (Tiffen, Kodak) could be introduced into the light path. The

duration of illumination was controlled by a leaf shutter (Uniblitz). The outer wall of the front (head) end of the plastic tube was blackened and the front two-thirds of the glass tube was wrapped in opaque black tape to diminish, if not eliminate, spread of light from the tail to the head region.

The full intensity of the light source was measured using a silicon photodiode (S1226–5BQ, Hamamatsu) placed in a position comparable to that occupied by the lamprey's tail but without water inside the inner plastic tube. Transmittance of visible light (400–700 nm) by the neutral density filters, alone or in series, was measured with a Hewlett-Packard spectrophotometer (HP 8451A). Light intensity attenuated by the neutral density filters was calculated as a fraction of the full intensity equal to the percentage transmission of each filter alone or in combination. No correction was made for the sensitivity of the photodiode in the near infrared (700–950 nm); consequently, the estimated light intensity for visible wavelengths is somewhat greater than the actual value.

Behavioral tests were initiated after the ammocoete had been in the dark for 45–120 min. This period permitted the animals to recover from the initial handling and allowed sufficient time for full dark adaptation of the skin photosense (Steven, 1950). The first trial began after the animal had rested quietly for a minimum of 5 min. Control tests consisted of 4–6 trials at each of five different light intensities: 0.4, 0.6, 1.5, 6.1 and 14.6 mW cm^{-2}, presented in random order. At the beginning of each trial, the tail was illuminated for 10 s, and the animal was monitored for movement over a total period of 25 s (10 s with illumination, 15 s in dark). Movements made within this period were counted as photoresponses. A minimum of 5 min of darkness separated successive trials, and animals were required to exhibit no movements in the 2.5 min directly preceding the next trial. Random tests for spontaneous or vibration-induced activity were identical to experimental tests except for the absence of light. Experimental animals were selected to meet two conditions: prolonged inactivity in the dark and consistent responses to the two most intense photic stimuli. Lampreys not satisfying both criteria were eliminated at an early stage of testing. Completion of a full series of tests required approximately 2.5 h.

Following control trials, ammocoetes were anesthetized by immersion in 0.1 % MS222 (tricaine methanesulfonate), wrapped in a moist towel, and placed on ice. Under a stereomicroscope, the trunk lateral line nerve innervating the trunk and tail in four animals was exposed and transected bilaterally at a point approximately 1 cm behind the gills. In four other lampreys, the recurrent branch of the anterior lateral line nerve was exposed and transected bilaterally at the point where it crossed the otic capsule. Sham transections of the trunk lateral line nerve and the recurrent ramus were made in two separate ammocoetes. Two additional ammocoetes received forebrain transections after the control tests. Wounds were sutured closed and sealed with Histoacryl tissue cement (Braun-Melsungen). Following recovery from anesthesia, lampreys were returned to the home aquaria for 4–12 days before retesting. Postsurgical tests were conducted in an identical manner to the control series. At the conclusion of the tests, the animals were re-

anesthetized, fixed in 10 % formalin, and the heads were dissected to verify nerve transections and to determine the extent of the forebrain lesions. Data were tested for statistical significance using either the *G*-test with Yates' correction or the *t*-test for paired comparisons (Sokal and Rohlf, 1981).

Physiological studies

The brain, the trunk lateral line nerve and the posterior lateral line nerve of ammocoetes were examined for evidence of photosensory units. Larval lampreys were collected from their aquaria and placed in the darkened cage where they were anesthetized in MS222. A cuff of black plastic was slipped over the tail during surgery. Anesthetized lampreys intended for recordings from the brain or intracranial portion of the posterior lateral line nerve were secured by pins to the floor of a shallow glass dish lined with Sylgard (Dow Corning). The animal was submerged in cold physiological saline (Matthews and Wickelgren, 1978), and the dish was placed on ice under a stereomicroscope. The cartilaginous cranium over the brain was removed, and the animal was decerebrated at the junction of the midbrain and diencephalon. Extirpation of the forebrain eliminated the optic tracts and pineal complex. The cranium was resected to expose the medulla and one or both posterior lateral line nerves fully. Animals were immobilized by combined intramuscular and intraperitoneal injections of Pavulon (pancuronium bromide, Organon), 0.2–0.5 ml at 0.1 mg ml^{-1}. Alternative routes of administration were direct injection into the pericardium or into a subpharyngeal sinus.

After surgery, the dish was removed to the darkened cage and placed on a metal block in an insulated plastic tank filled with ice. A glass-fiber light guide, 91 cm long and 7 mm in diameter, was positioned a set distance above the tail. Light was provided by a quartz–halogen illuminator and neutral density filters were introduced into the light path in some cases. As in behavioral studies, the full intensity of the light source was measured with a silicon photodiode, while the reduced intensity of light passing through neutral density filters was calculated according to the measured transmission of the filters alone or in series. One series of experiments conducted at the Marine Biological Laboratory, Woods Hole, employed a xenon arc lamp equipped with a monochrometer and neutral density filters.

Recordings from the trunk lateral line nerve were made in animals positioned on a plastic platform suspended in a small tank of water. Water (8–12 °C) was continually passed across the animal's gills. The lateral line nerve was exposed halfway between the head and tail in a part of the trunk elevated above the water level. Prior to recording, the sheath surrounding the nerve was treated with 1 % trypsin in lamprey Ringer for 10–40 s. Animals were immobilized with 0.3–0.9 mg kg^{-1} Tubocurare (introperitoneally, intramuscularly or intrasinus).

Extracellular recordings from the brain or posterior lateral line nerve were made with indium-filled, platinum-black-tipped glass electrodes or glass micropipettes (tip diameter 5–25 μm) filled with 2 mol l^{-1} NaCl. Glass micropipettes of large tip diameter (20–35 μm) were used for the extracellular recordings in the

trunk lateral line nerve. Amplified multi- and single-unit activity was examined on a storage oscilloscope and dot display raster. A window discriminator permitted isolation of single-unit responses from some multiple-unit records. The locations of photosensitive units recorded in the brain with indium electrodes were marked by electrolytic lesions (1–20 μA for 5–10 s). These brains were then fixed, embedded in paraffin, sectioned at 12 μm, and histologically examined for lesions marking the recording sites. In addition to light stimulation, weakly electric fields and mechanical stimuli were delivered to experimental animals. Weakly electric stimuli were d.c. step fields produced by a stimulator and delivered through an isolation unit and two salt bridge electrodes, one each at the head and tail ends of the recording dish. Mechanical stimuli were soft water jets, water drops and light touches to the body.

Results

The larval sea lampreys tested for their photoresponses remained largely immobile in the dark. In all control and postsurgical trials, spontaneous movements in the absence of light were rare (2 of 48 trials). As noted, preliminary screening favored selection of animals showing minimal dark activity and maximal responsiveness. Approximately 5–10 animals were rejected on these grounds. Twelve animals were tested further. That some animals were excluded because of their poor response rate to the brightest lights in control tests implies that the sensitivity of the photoresponse varied considerably among animals in this paradigm.

Normal photoresponse

When the tail of a quiet animal was illuminated in a control test, the lamprey began to move after a latency of several seconds (Fig. 3A). Most movements in response to light were vigorous deflections and torsions of the trunk and tail, which usually persisted for 10 s or longer in the dark before subsiding. However, a few photoresponses, particularly those elicited by dimmer stimuli late in a test series, involved only brief or minor tail deflections. The tendency of individual animals to respond to tail illumination was dependent on light intensity and was consistent with a narrow dynamic range for the photoresponse (Fig. 4B,D). The mean response frequency in control tests with all 12 animals increased from 41.0 % (S.D. 35.7 %) at 0.4 mW cm^{-2} to a maximum of 93.8 % (S.D. 15.5 %) at an intensity 1.2 log units higher (6.1 mW cm^{-2}) ($P<0.01$; t-test). There was no significant difference in response frequency among the three highest intensities tested (1.5–14.6 mW cm^{-2}). Photoresponses had latencies of 1.5–13 s and exhibited considerable variability; no consistent difference in latency was apparent across the five light intensities.

Transection of the trunk lateral line nerve

All four *Petromyzon* ammocoetes that had undergone bilateral section of the

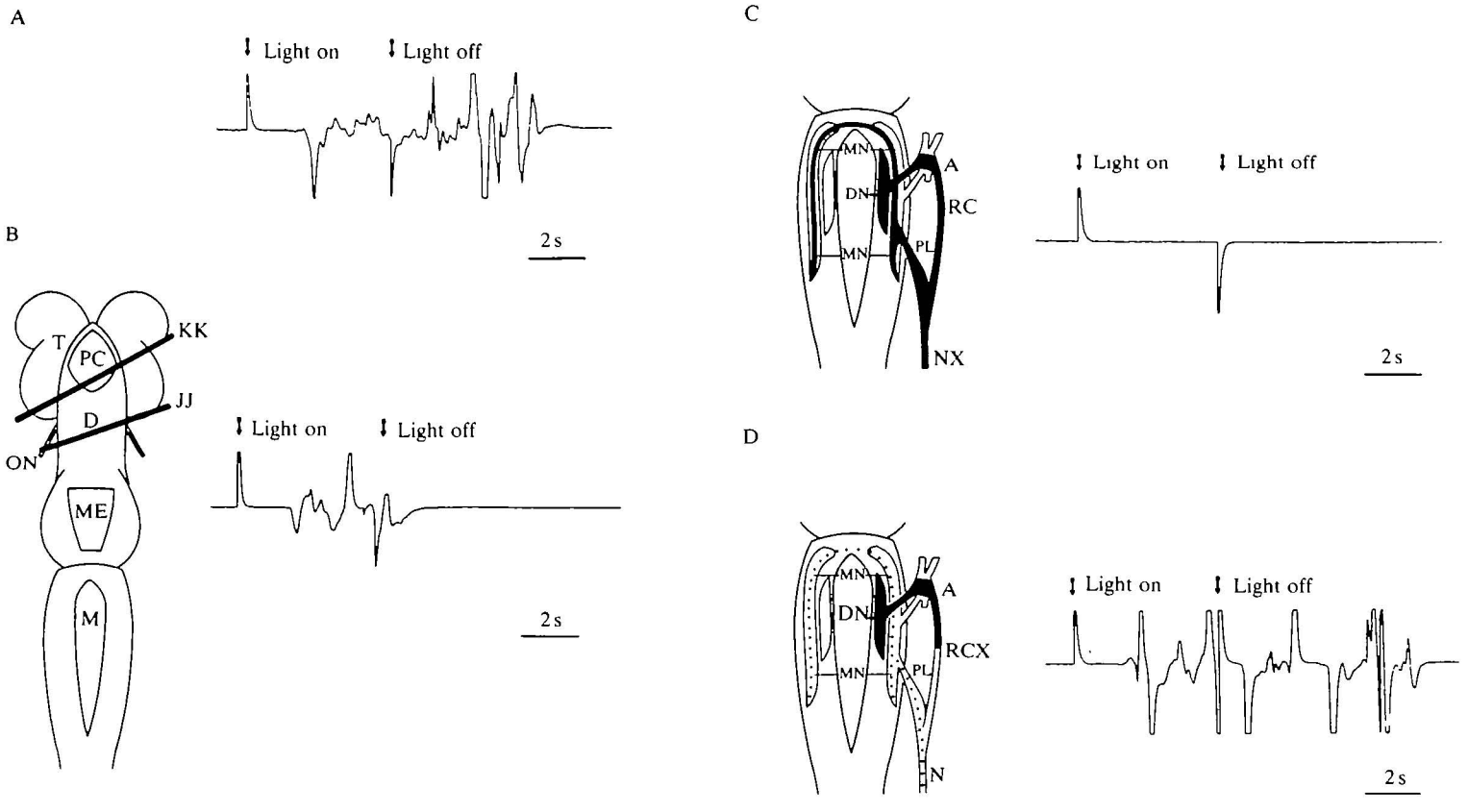

Fig. 3. Behavioral responses of larval sea lampreys to illumination of the tail with white light for 10 s at an intensity of 1.5 mW cm^{-2}. A deflection of the trace from the baseline indicates movements detected by the infrared monitors. Stimulus artifacts are seen at light onset and offset if not obscured by the response. (A) Normal response of an intact animal. (B) Response observed following transection of the forebrain. Black bars indicate level of transection for the two lampreys tested (JJ and KK; see Fig. 5). (C) Response following transection of the lateral line nerve supplying the trunk and tail (NX). Blackened areas indicate that the lesion severs the projection of the recurrent ramus to the ipsilateral dorsal nucleus and the bilateral projection of the posterior lateral line nerve to the medial nucleus. (D) Response following transection of the recurrent ramus of the anterior lateral line nerve (RCX). Blackened areas indicate that the lesion severs the projection to the dorsal octavolateralis nucleus. Bilateral projection of the posterior lateral line nerve (dotted) to the medial octavolateralis nucleus is still present. Abbreviations as in Fig. 1.

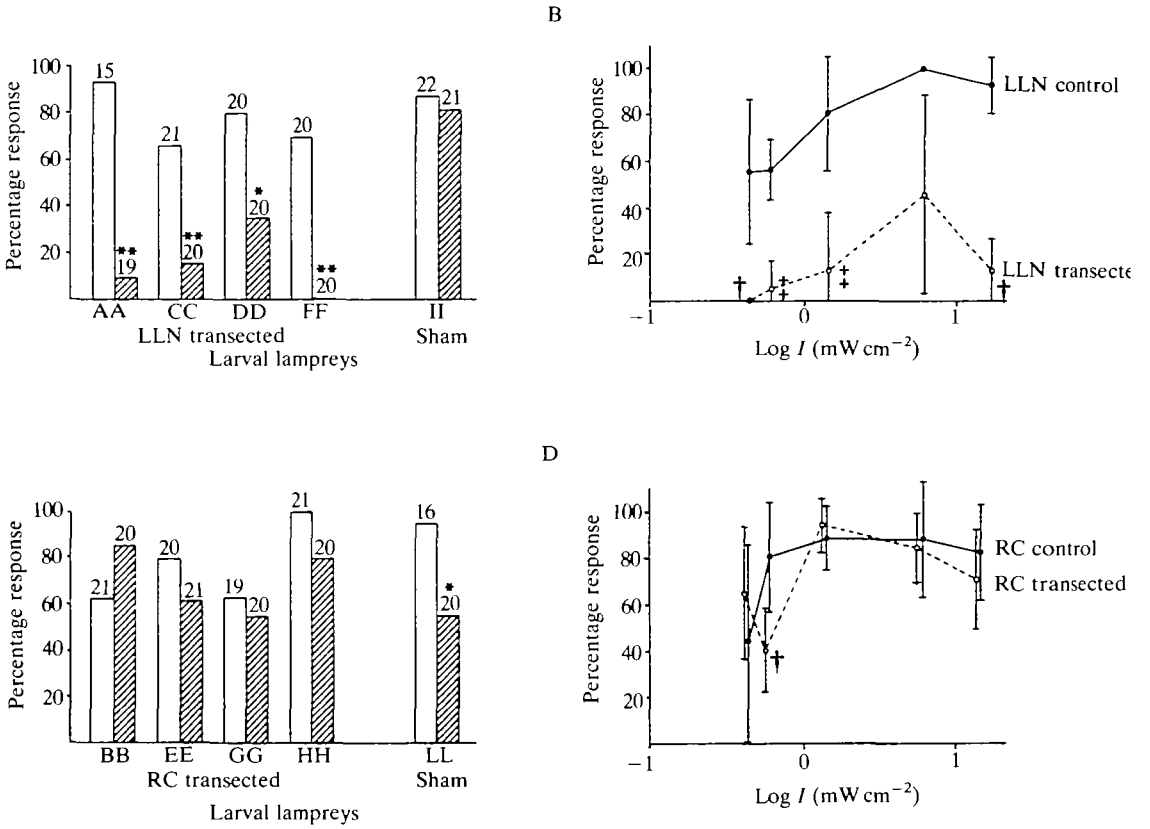

Fig. 4. Responses of larval sea lampreys to tail illumination. (A) Response frequencies of four larval lampreys (AA, CC, DD, FF) before (open bars) and after (hatched bars) bilateral transection of the trunk lateral line nerve (LLN). Each animal was tested 3–6 times at each of five light intensities. The responses of the control lamprey (II) before and after sham transection of the nerve are shown on the right. The number of trials is indicated above the bars. Statistical significance is indicated by * ($P<0.025$) or ** ($P<0.005$) (G-test with Yates' correction). (B) Mean response frequencies (±S.D.) at each of five light intensities exhibited by the four larval lampreys in A before (filled circles) and after (open circles) bilateral transection of the trunk lateral line nerve. Statistically significant differences between control and operated lampreys are indicated by † ($P<0.05$) or ‡ ($P<0.02$) (t-test for paired comparisons). (C) Response frequencies of four larval lampreys (BB, EE, GG, HH) tested as in A before (open bars) and after (hatched bars) bilateral transection of the recurrent ramus (RC) of the anterior lateral line nerve. The responses of the control lamprey (LL) before and after sham transection of the nerve are shown on the right. Statistical significance is indicated as in A. (D) Mean response frequencies (±S.D.) at each of five light intensities exhibited by the four larval lampreys in C before (filled circles) and after (open circles) bilateral transection of the recurrent ramus of the anterior lateral line nerve. Statistical significance indicated as in B. Light intensity (I) is measured in $mW\,cm^{-2}$.

trunk lateral line nerve showed a greatly diminished photoresponse (Figs 3C; 4A,B) when retested 4 (animals DD, FF), 6 (animal CC) and 12 days (animal AA) after surgery. One animal (FF) showed no response to tail illumination; the three remaining animals responded in only 9 % (AA), 20 % (CC) and 35 % (DD) of the trials (Fig. 4A). The decrease in each case was highly significant (G-test with Yates' correction). Most postsurgical photoresponses were evoked by higher light intensities (Fig. 4B). However, at each level of illumination but one, the combined photoresponses of the operated lampreys were significantly diminished (t-test for paired comparisons) compared to their control responses. An apparent decrease at 6.1 mW cm^{-2} did not reach statistical significance ($0.05<P<0.1$). Despite the diminished photosensitivity after surgery, the four experimental lampreys were, nonetheless, capable of vigorous and sustained swimming movements when disturbed mechanically. Subsequent dissection confirmed that the trunk lateral line nerve had been sectioned bilaterally in each of the four animals. Bilateral sham transection of the trunk lateral line nerve did not significantly diminish the photoresponse (animal II, Fig. 4A).

Transection of the recurrent ramus of the anterior lateral line nerve

As stated above, the trunk lateral line nerve contains both anterior and posterior lateral line nerve afferents, which project to the dorsal and medial octavolateralis nuclei, respectively (Fig. 1). Although the inaccessibility of the intracranial portion of the posterior lateral line nerve makes its bilateral transection difficult in an animal that must survive for postsurgical testing, the recurrent ramus of the anterior lateral line nerve is readily approached.

After bilateral transection of the recurrent ramus, larval sea lampreys still responded to illumination of the tail (Fig. 3D). Behavioral testing of four lampreys 5 (animal GG), 6 (animal EE), 7 (animal HH) and 8 days (animal BB) after surgery revealed no significant differences between postsurgical photoresponses and control responses (Fig. 4C,D). A significant decrease in response frequency was observed in one animal (LL), which underwent sham transection of the recurrent nerve ($P<0.025$; G-test), suggesting that surgical trauma or the retesting process may diminish responsiveness. Examination of the fixed heads revealed that the recurrent ramus had been transected bilaterally in all experimental animals.

Brain transections

Two larval lampreys were retested 4 (KK) and 5 (JJ) days after forebrain transections. Both animals appeared to swim normally. Postsurgical responses to tail illumination did not differ significantly (G-test) from the control responses (Figs 3B, 5). There was no obvious difference in response magnitude between pre- and postsurgical trials.

Examination of the brains of these lampreys revealed that the lesion in animal JJ passed right through the diencephalon caudal to the optic chiasm and pineal complex (Fig. 3B). The transection in animal KK cut diagonally through the

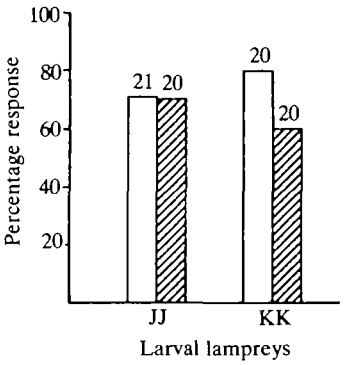

Fig. 5. Response frequencies of two larval lampreys (JJ, KK) to tail illumination before (open bars) and after (hatched bars) transection of the forebrain. Numbers of trials are indicated above the bars. Differences were not statistically significant (*G*-test).

telencephalon medium, sparing the right side of the optic chiasm and possibly the caudal end of the pineal body.

Physiology

Physiological recordings of single- or few-unit photic responses confirm behavioral tests, indicating that photic receptors in the tail skin are innervated by posterior lateral line nerve fibers that course in the trunk lateral line nerve and terminate in the medial octavolateralis nucleus of the medulla. Unit responses to light on the tail were recorded from primary afferents in the trunk lateral line nerve (N=4) and in the posterior lateral line nerve within the cranium (N=5). Photic primary afferents showed low, irregular spontaneous activity, though the exact rate of spontaneous firing was difficult to determine in many cells because of incomplete unit isolation. All photic afferents responded to tail illumination with repeated bursts of impulses 0.5–2 s in duration with 2–5 s interburst intervals. Minimum response latencies with the most intense stimuli ranged from 1.1 to 2.2 s and the bursting responses were sustained throughout the stimulus duration. Unit responses to mechanical stimuli were found at the same recording sites as photic responses and photic units were never isolated well enough to rule out the possibility that they were also responsive to the mechanical stimulation. Electrosensory responses were found at some recording sites in the trunk lateral line nerve but not in the posterior lateral line nerve in the cranium.

Unit responses to tail illumination were also recorded from 40 sites within the medulla. Responses to mechanosensory but not electrosensory stimuli could be recorded from all the recording sites responsive to photic stimuli, and all 15 recording sites localized by lesions were within the medial nucleus (Fig. 6). Two units were recorded from the medial nucleus contralateral to the intact nerve in an animal that had undergone unilateral transection of the trunk lateral line nerve.

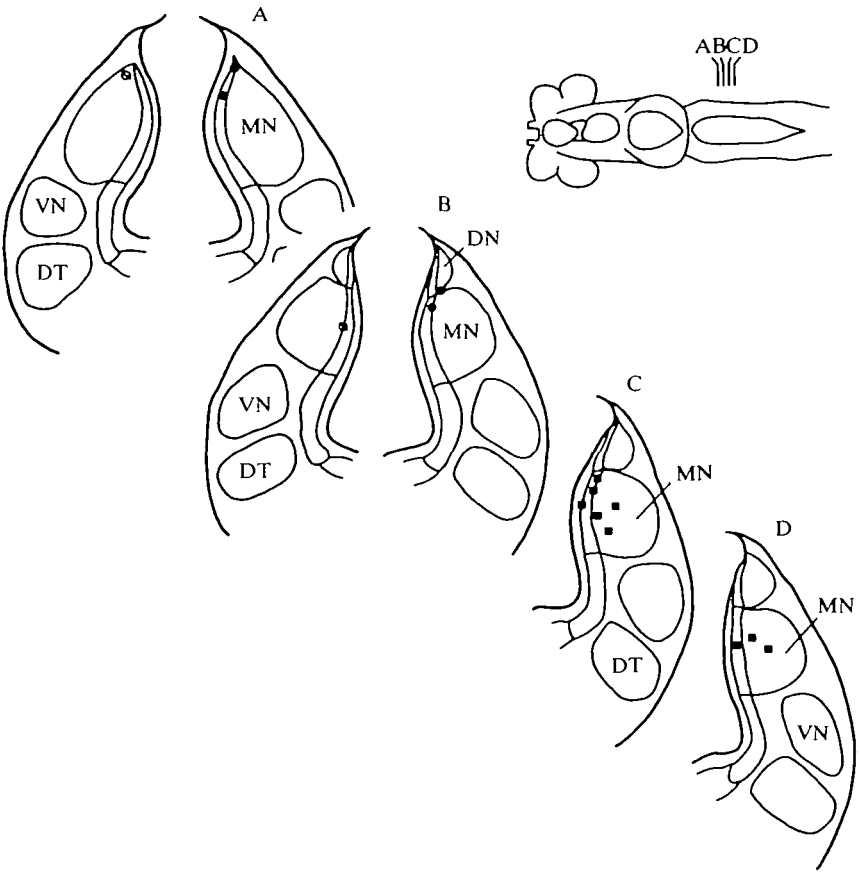

Fig. 6. Transverse sections through the alar medulla of a larval sea lamprey showing where the photosensitive units were recorded. Levels of sections shown at upper right. DN, dorsal octavolateralis nucleus; DT, descending trigeminal tract; MN, medial octavolateralis nucleus; PLLN, posterior lateral line nerve; VN, ventral octavolateralis nucleus. ●, sites ipsilateral to the intact PLLN; ⌀, sites contralateral to the intact PLLN; ■, undetermined laterality (PLLNs intact).

Finally, two additional photic units were recorded in the cerebellar region at the rostral end of the medulla.

Photic units recorded within the brain had physiological properties like those of the primary afferents, and some or all of these units may have been primary afferents. Spontaneous activity rates were very low and irregular, 0–3.7 s^{-1}, and gave way to sustained bursting responses to tail illumination (Fig. 7). Response latencies were 1–4 s with a mean of 1.3 s (S.D. 0.3 s) for the most intense stimuli and, for the six units where it was measured, the threshold for a just-detectable response ranged from 0.1 to 0.9 mW cm^{-2}. Although units were tested with only a limited intensity range up to 1.5–2 log units over threshold, the responses of at least some cells appeared to saturate within this range. All medullary units responded with impulse bursting indistinguishable from that observed in the

Fig. 7. Two units in the brain of a larval sea lamprey fire in a bursting pattern in response to illumination of the tail. The duration of illumination is indicated by the lower trace.

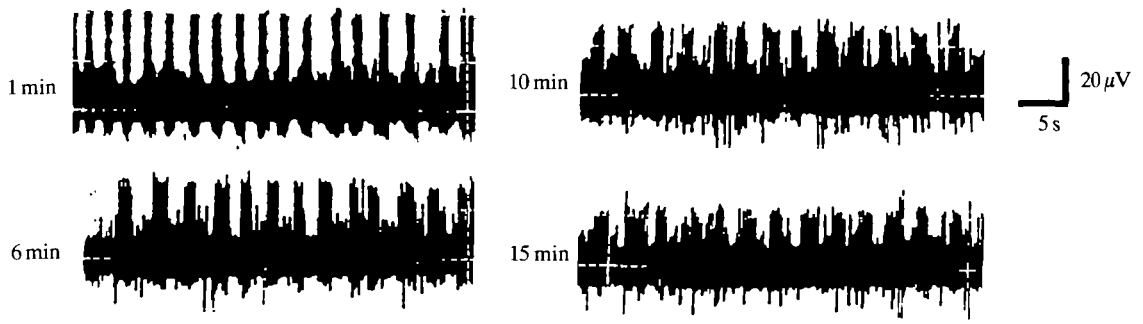

Fig. 8. Response of a single photosensitive unit in the brain of a larval sea lamprey to continuous illumination of the tail with a small spot of blue light (480 nm). The duration of illumination is indicated.

photic units recorded in the nerve. Responses to sustained illumination were extremely slowly adapting. In the single longest-held unit a strong response persisted for more than 15 min of continuous light, although the bursts were more loosely organized at the end of this period (Fig. 8). Medullary photic units failed to respond to electric fields sufficient to activate lamprey electroreceptors, but, as in the lateral line nerves, incomplete isolation made it impossible to exclude photic unit sensitivity to mechanosensory stimuli.

Discussion

Distinct mechano- and electrosensory modalities have been recognized within the lateral line system of larval lampreys. The present behavioral and neurophysiological findings, combined with previous behavioral results, clearly establish the existence of a third lateralis modality – a skin photosensory system. In the following section, the photoresponse behavior of ammocoetes and the basic physiological characteristics of their photosensory units are first discussed. The identity of the skin photoreceptors is subsequently considered. Lastly, the

photosensory systems of lampreys and hagfishes, the other type of extant agnathan, are compared.

Skin photoresponse: behavior and physiology

Larval lampreys at rest in the dark respond to illumination of the tail by swimming (Parker, 1905; Young, 1935*a*; Francis and Horton, 1936; Steven, 1950). Ammocoetes normally bury themselves in the substratum of stream beds during the day, and, given the chance, larval lampreys induced to swim by skin illumination soon burrow head first into the substratum. The tail's sensitivity to light may ensure that the entire animal disappears underground (Young, 1935*a*). The low sensitivity and long latency of the photoresponse may have marginal significance, the response simply serving to move visually deficient animals to cover when ambient illumination attains sufficient intensity. However, free-swimming adult lampreys with well-developed eyes also exhibit a skin photoresponse (Young, 1935*a*), so the behavioral significance of the skin photosensitivity in petromyzontids remains unclear.

Two observations indicate that the photoresponse is initiated by light rather than merely by heat. The response persists despite the passage of circulating water, which acts as a heat filter. Moreover, the spectral sensitivity of the behavioral photoresponse peaks in the green (530 nm), and wavelengths longer than 600 nm elicit no response (Steven, 1950). Incomplete spectral sensitivity functions obtained for two central photic units in the present study showed that sensitivity was reduced at 550 nm and absent at wavelengths of 600 nm or greater.

The robust response of larval lampreys to tail illumination served as a behavioral assay in the present study to examine further the participation of the lateral line in the photoresponse. Bilateral transection of the trunk lateral line nerve in larval *Petromyzon* largely eliminates the response, particularly at lower light intensities. Sham transections of the nerve caused no significant decrease in photoresponsiveness. These results substantiate Young's (1935*a*) and Steven's (1950) conclusion that lateral line nerves innervate photoreceptors on the tail of larval lampreys. In contrast, bilateral transections of the recurrent ramus did not significantly reduce the photoresponse.

Our behavioral and physiological results indicate that photosensory afferents enter the brain in the posterior lateral line nerve and terminate in the medial octavolateralis nucleus, which thus receives photic as well as mechanosensory input. It is not known if photosensory units recorded in the medulla are primary afferents; however, their presence in the medial nucleus ipsilateral to an intact posterior lateral line nerve, in the contralateral medial nucleus and in the intervening cerebellar region corresponds to the known projections of the posterior lateral line nerve (Ronan and Northcutt, 1987; Ronan, 1988).

The course of photosensory information beyond the medial nucleus is not known. Efferents of the medial nucleus consist of commissural and ascending lemniscal projections to the midbrain (M. C. Ronan, unpublished observations). Commissural fibers pass through the basal medulla, where they may contact

neurons mediating swimming behavior. Several neuronal populations in the medullary reticular formation are implicated in the initiation of swimming in larval lampreys (McClellan, 1984; McClellan and Getting, 1986; Ayers and Rovainen, 1987).

Although earlier behavioral studies indicate that the lamprey skin photoresponse has a high threshold (Parker, 1905; Francis and Horton, 1936; Steven, 1950; Harden-Jones, 1955), our behavioral response paradigm did not permit an accurate assessment of the threshold of the photoresponse. The tests were performed with only a limited range of light intensities and preselection ensured that only the most responsive animals were tested. Finally, the use of infrared units to monitor the animals' activity necessitated their confinement, a condition in accord with their strong thigmotaxis (Francis and Horton, 1936). The ammocoete preference for surface contact, which helped keep the animals reasonably quiet, would probably elevate the photoresponse threshold.

Following bilateral transection of the trunk lateral line nerve, the occurrence of photoresponses was greatly diminished: two animals consistently did not respond to any level of illumination, two other lampreys did respond to the most intense light ($\geq 6.1\,mW\,cm^{-2}$). The persistent photoresponse to intense illumination may be due to rostral spread of light striking the tail. Larval lampreys respond to illumination of the head, albeit with far longer latencies than is seen following tail illumination (Young, 1935*a*). Alternatively, there may be additional photosensitive tissue in the tails of ammocoetes. Young (1935*a*) attributed light-induced movements observed in a few ammocoetes that had undergone bilateral transection of the trunk lateral line nerve to illumination of photosensitive units present in the spinal cord.

Skin photoreceptors have not previously been recorded electrophysiologically in any vertebrate. Recordings of central and peripheral photic units indicated several physiological correlates of photoresponse behavior. Like the behavioral response, the responses of photosensory units, including primary afferents in the lateral line nerves, had very long latencies. Even with intense light stimuli ($6.1\,mW\,cm^{-2}$), the shortest latency observed was more than 1 s, and the mean for a small sample of primary afferents was 1.7 s (S.D. 0.4 s; $N=6$) compared with 4.2 s (S.D. 2.3 s; $N=11$) for behavioral responses at similar intensities. Although the nervous system of lampreys lacks myelin, it is unlikely that conduction time can account for such long latencies, since primary electrosensory afferents in the lateral line nerves have latencies of 0.1–0.3 s (Bodznick and Preston, 1983). Rather, it appears that the long latencies of the photoreceptors and the photoresponse are due to slow phototransduction in the peripheral receptors.

Both the photoresponse and the photoreceptive units appear to have relatively high thresholds. Unit thresholds of $0.1–0.9\,mW\,cm^{-2}$ for a just detectable response are comparable to intensities required to elicit a behavioral response in about 50 % of trials (approx. $0.5\,mW\,cm^{-2}$) in the present study. While the range of intensities used in our tests was too limited to give complete intensity–response functions for photoreceptor units, the data suggest that, like the behavioral

response, at least some receptors have limited dynamic ranges extending over only 1–2 log units. Finally, photosensory units are very slowly adapting, showing little dimunition over 15 min of continuous tail illumination in one case. Similarly, the behavioral photoresponse persists despite continuous illumination (Francis and Horton, 1936). It is noteworthy that all skin photosensory units recorded, both in the lateral line nerves and in the brain, responded to continuous illumination with regular, repeated bursts of impulses throughout the stimulus period. Such bursting responses are not found in other lateralis modalities. This property along with the very long latency, high threshold, and slow adaptation rate are not, to our knowledge, found in pineal or retinal photoreceptors and may be unique to the skin photosense. It may be noted here that skin photoreceptors must also differ from other vertebrate photoreceptors in their embryonic origins. Photoreceptors of the lateral eyes and pineal complex are central nervous system structures derived from neural plate ectoderm. In contrast, skin photoreceptors in lampreys may develop from lateral line epidermal placodes.

It is not known if the photosensory units in the posterior lateral line nerve and in the brain are unimodal. Spikes of photic units recorded in the nerves and brain were generally of low amplitude and were seldom completely isolated from mechanosensory units. Mechanosensory capability cannot be ruled out in photosensitive units. Nevertheless, well-isolated mechanosensory units recorded in the medial nucleus did not respond to tail illumination. Photic units do not appear to be electroreceptive. Those in the brain showed no response to electric fields of a polarity and intensity to which lamprey electroreceptors readily respond (Ronan, 1988). No photosensory responses were recorded from end bud electroreceptors on the head of a dark-adapted adult lamprey. Lastly, lateralis afferents labelled by horseradish peroxidase injections of end buds terminated in the electroreceptive dorsal nucleus rather than in the mechanosensory medial nucleus (Ronan and Bodznick, 1986).

Dermal photoreceptors have not been identified in any agnathan or gnathostome. Initially, free nerve endings in tail skin – presumably light-sensitive terminals of the posterior lateral line nerve in the case of lampreys – were assumed to act as photoreceptors (Eigenmann, 1900; Parker, 1905). Subsequent elucidation of such photoresponse characteristics as spectral sensitivity and dark adaptation suggested the presence of a photopigment, possibly porphyropsin, sequestered within receptor cells (Steven, 1950). Notable in this regard is the presence of an opsin-based photopigment in photosensitive skin irridocytes of a teleost, *Cheirodon innesi* (Lythgoe *et al.* 1984).

Cells in the skin of larval brook lampreys have been proposed as possible photoreceptors on the basis of their distribution, internal structure and innervation. Some epidermal cells near neuromasts exhibit a yellow coloration (Young, 1935*a*). Similar to these are round cells, approximately 10 μm in diameter and commonly found in small clusters in tail skin (Steven, 1951). These cells also contained a faint yellow pigment which faded under continuous illumination. Skin samples treated with Methylene Blue revealed clusters of stained cells similar to

the yellow-pigmented cells; each cluster was innervated by branches of a single nerve fiber, which terminated as boutons on individual cells but also gave off free endings to the epidermis (Steven, 1950). The origins of the innervating fibers could not be ascertained.

Multivillous cells, skin cells in larval and adult *Lampetra fluviatilis* bearing numerous apical microvilli, may be comparable to the pigmented epidermal cells (Whitear and Lane, 1983). Multivillous cells have so far been found on the skin of the branchial region and tail, where they occur as isolated groups of 2–4 cells without surrounding support cells. An electron-dense synaptic bar, a basal membrane specialization characteristic of lateralis receptors in vertebrates, is seen in multivillous cells at the point of contact with innervating neurites (Flock, 1965; Yamada, 1973; Bullock, 1982; Whitear and Lane, 1983). Sinnets, a unique cytoplasmic feature of multivillous cells, appear as braided tangles of clear-cored cylinders grouped in tetrads and may conceivably serve as sites of pigment deposition (Whitear and Lane, 1983).

Identification of the lateralis photoreceptors in lampreys is complicated by the existence of lateralis electroreceptors. Electroreceptors, like the dermal photoreceptors, are known from physiological studies to be present on ammocoete tails, but their specific morphology is yet to be identified (Ronan, 1988). Apart from the sinnets, multivillous cells resemble the electroreceptor cells of end buds (Whitear and Lane, 1981, 1983; Ronan and Bodznick, 1986). The presence of synaptic bars suggests only that multivillous cells are some type of lateralis receptor, possibly either a photoreceptor or an electroreceptor. As noted, it is unlikely that a single lateralis receptor is sensitive to both light and electric fields. Sinnets may store photopigment, but their function is not known. If multivillous cells are non-photosensitive, epidermal light receptors may, nonetheless, resemble them in being individual sensory cells distributed in small clusters through the skin of the tail.

Phylogeny of skin photoreception

A skin photosensory system is present in hagfishes. When illuminated, hagfishes at rest in the dark begin to swim after a latency of several seconds (Newth and Ross, 1955; Steven, 1955; Patzner, 1978). Hagfishes possess poorly developed eyes and no pineal organ. They are benthic marine organisms that lie buried in the mud of the continental shelf during the day (Adam and Strahan, 1963; Patzner, 1978). In hagfishes as well as lampreys, the dermal photoresponse may serve to move animals with little visual capability out of the light into darker and less dangerous surroundings. Behavioral tests in Atlantic hagfish (*Myxine glutinosa*) implicate the skin on the head and on the tail near the cloaca rather than the underlying muscle or spinal cord as the most photosensitive tissue (Newth and Ross, 1955). Skin on the tail of Pacific hagfishes (*Eptatretus burgeri* and *Paramyxine atami*) is also sensitive to light (Patzner, 1978). Behavioral results indicate that the photosensory systems of lampreys and hagfishes are similar in latency, adaptation rate and spectral frequency sensitivity (Newth and Ross, 1955; Steven, 1955). However,

hagfishes possess only a rudimentary lateral line system at best. Shallow grooves in the head skin of Pacific hagfish, the only potential lateralis end organ apparent in myxinoids, lack sensory cells (Fernholm, 1986). Lateral line nerves to the trunk and tail are absent. Photoreceptors on the tail of hagfishes appear to be innervated by spinal nerves, and the spinal cord rather than primary lateralis afferents carries photic information from receptors to other levels of the neuraxis. Spinal cord transection in *Myxine glutinosa* eliminates responses to illumination from body regions distal to the lesion (Newth and Ross, 1955).

The distinct photosensory systems of lampreys and hagfishes are probably not homologous (Newth and Ross, 1955). This interpretation is in keeping with the probable embryonic origins of the two systems. In amphibian embryos, lateralis ganglia, nerves and receptors are derived from epidermal placodes, with no contribution from the neural crest (Landacre, 1910; Stone, 1922; Knouff, 1927; Holmgren, 1940). Rostral spinal ganglia in lampreys develop from head neural crest (Knouff, 1927; Newth, 1956). The skin photosensory system found in lampreys thus probably originates in lateralis placodes, whereas the spinally innervated photosensory system of hagfishes must be derived, in part, from neural crest.

A skin photoresponse has been observed in teleosts, including catfish, grouper and blind cavefish (Eigenmann, 1900; Payne, 1907; Jordan, 1917; Van Heusen, 1917; Breder and Rasquin, 1950), larval and adult salamanders (Reese, 1906; Eycleshymer, 1908; Pearse, 1910; Laurens, 1914; Cole, 1922; Hawes, 1945) and ranid tadpoles above 4–5 cm in length (Cole and Dean, 1917; Obreshkove, 1921). All of these vertebrates possess a lateral line system, consisting in part of a posterior lateral line nerve and medial octavolateralis nucleus. With the possible exception of *Necturus maculosus*, innervation of skin photoreceptors in these gnathostomes is unknown. The aquatic urodele *Necturus maculosus* possesses a functional lateral line system, but transection of the spinal cord abolishes the photoresponse following illumination of the skin distal to the spinal lesion (Pearse, 1910). Skin photoresponses are also reported in adult *Rana clamata*, *sylvatica* and *pipiens* and *Bufo americanus*, *fowleri* (Parker, 1903; Pearse, 1910) and an apodan, *Ichthyophis glutinosa* (Ross, 1959). Lateral line systems are absent in adult terrestrial anurans, having degenerated during metamorphosis (Larsell, 1925; Brown, 1946). Larval *Ichthyophis glutinosa* possess both mechanoreceptive and electroreceptive lateral line systems (Hetherington and Wake, 1979; Wahnschaffe *et al.* 1985), but neuromasts and the posterior lateral line nerve may be absent in postmetamorphic *Ichthyophis*, as is the case in the adults of some other fossorial apodans (McCormick and Braford, 1988; and personal communication). Skin photosensitivity in adult anurans, and possibly in *Necturus* and *Icthyophis*, functions without lateral line participation. As in hagfishes, photic information from the tail may be carried to other levels of the neuraxis by the spinal cord. At present, two seemingly distinct dermal photosensory systems (lateralis *versus* spinally innervated) are recognized in agnathans, and there is insufficient information to consider one or the other as the ancestral condition. Insights into

the evolution of skin photoreception in vertebrates require information concerning whether the photoresponse in each gnathostome is mediated by a lateral line system, a spinal system or even a combination of the two.

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