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SPECTRAL CHARACTERISTIC OF S-POTENTIALS
An Intracellular Horseradish Peroxidase Study in Perch (*Perca fluviatilis*)

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B. Q. Huang and M. B. A. Djamgoz (1988) Spectral Characteristic of S-potentials: An Intracellular Horseradish Peroxidase study in Perch (*Perca fluviatilis*). *Bull. Inst. Zool., Academia Sinica* **27**(3): 183-193. The spectral characteristics of the different S-potentials recorded from the horizontal cells in perch retina have been investigated by the intracellular recording and horseradish peroxidase (HRP) ionophoresis. The results demonstrated that perch horizontal cells has two monophasic luminosity S-potentials: photopic (λ_{max}=620 nm) and scotopic (λ_{max}=580 nm), and one chromaticity type (λ_{max}=580-620 nm). It is suggested that photopic and scotopic horizontal cells are driven by dominant twint cones and rods respectively, and that perch has red- and green-sensitive horizontal cells, but no blue-sensitive one. The spectral characteristics of the S-potentials analyzed by electrophysiological studies, seem to coincide well with the results obtained by behavioural and microspectrophotometric measurent published by Cameron (1982) and Loew and Lythgoe (1978).

Key words: HRP ionophoresis, Perch retina, Spectral characteristic, S-potentials.

Vision under water is significantly different from vision in air and thus studies of fish vision are concerned with many optical properties. Spectral sensitivities are shown to be closely correlated to the natural habitats and determine some behavioural patterns. In addition, Guthrie (1981, 1983) has provided some strong evidence that most teleosts respond to choice tests based on spectral differences and their tectal neurones could resolve chromatic acuity. In retinal level, the light-evoked response of the horizontal cells (the first retinal interneuron between photoreceptors and bipolar cells) are well known as "S-potentials" (Stell and Lightfoot, 1975; Laufer and Negishi, 1978; Shigematsu *et al.*, 1978) in recognition of Svaetichin who first recorded the responses intracellularly in teleosts. S-potentials are driven mainly by photoreceptors and involve signalling chromatic and luminous information during visual processing.

One most common luminosity horizontal cells (L-type) are photopic and sensitive to red spectrum light; green- and blue sensitive cells have also been described (Huang, 1986). The other L-type horizontal cells show a similar spectral sensitivity to rods and belong to scotopic L-type. Both scotopic and photopic L-type horizontal cells hyperpolarizing to all the chromatic lights. In addition, two main chromatic type (C-type) cells have been presented as biphasic and triphasic C-type. Biphasic C-type horizontal cells depolarizes to the longer wavelength, hyperpolarizes to the shorter wavelength. Triphasic

C-type unit depolarizes to middle wavelength, hyperpolarizes to two ends of the spectrum (Kaneko, 1970; Djamgoz *et al.*, 1985).

Cone driving of the different S-potential components has been determined principally by quantum spectral analysis introduced by Naka and Rushton (1966). Although it is a tedious procedure, it has the advantage that values for spectral sensitivity of the horizontal cell can be correlated directly to the spectral absorption curves of photoreceptor measured by microspectrophotometry (MSP).

Perch (*perca fluviatilis*) is representative of the percoid fishes, which are from an evolutionary point of view quite distinct from the other common and well studied freshwater cyprinids. From MSP studies, they have been proved to possess two spectrally distinct cone pigments with $\lambda_{max.}$=535 nm and 615 nm (Loew and Lythgoe, 1978). Perch have no blue sensitive cones and potential of dichromatic vision. It is crucial to know a possible model for the connections between photoreceptors and horizontal cells in a dichromatic retina.

The main aims of the present experiments are:

1) To study the spectral sensitivity of perch retina by S-potential classification and by their relative quantum spectral sensitivity which could correlate with the MSP measurements.

2) To inject HRP into recorded cells in order to trace the morphology of functionally classified horizontal cells.

METHODS AND MATERIALS

The experiments were done on the perch (*Perca fluviatilis*) retinae for intracelluar recording from horizontal cells and marking with horseradish peroxidase (HRP).

Retinal preparation

A fully dark-adapted fish in a well-aerated tank, was killed and a retina was peeled off. The isolated retina with the adhering vitreous body was placed with its receptor side upward in a transparent recording chamber. A piece of nylon net of about 1 mm mesh was carefully covered over the retina to provide a grid system for noting injection details. The nylon net adhered well to the retina and appeared to provide additional mechanical stability. To create a viable environment for the isolated retina, it was surrounded by a ring of moist tissue paper and supplied with moist oxygen. Such a preparation could remain responsive to light for several hours. During the electrophysiological experiments, the retina was maintained in a lab with illumination level at about cone threshold for the experimenters.

Intracelluar recording and HRP ionophoresis

Glass microelectrodes were drawn and filled with 4% HRP (Sigma Type VI) solution and 0.2 M KCl in 0.05 M Tris-HCl buffer, pH 8.6 (Snow *et al.*, 1976). HRP-filled electrodes were tested to ensure reliable operation (no blocking, no undesirable voltage surges) and have tip resistances within the range of 400-600 MΩ. These microelectrodes are most suitable for penetrating into the horizontal cells. A given microelectrode was then connected to the head-stage of a microprobe system (WP1 Model M701), which was, in turn, connected to the main-frame via a break-away box (WP1 Model BB1). For recording or ionophoresis, it was changed to the "normal" or "breakaway" position, respectively. Due to the layered structure of the retinal neurones, it is possible to estimate the type of the recorded neuron by its vertical distance from the photoreceptors. Perch horizontal cells were usually at the depth of 70-130 um after touching photoreceptor side of the retinal surface. Horizontal cells as compared to their neighboring neurones (photoreceptors and bipolar cells) were identified on the basis of their characteristic responses: the larger receptive fields and the weaker center-surround antagonism (Kawasaki *et al.*, 1984;

Lipetz and Kaneko, 1984; Djamgoz *et al.*, 1985). After a stable resting membrane potential, the above two characteristics was obtained to demonstrate the electrode was inside the horizontal cell (Stell and Lightfoot, 1975; Witkovsky *et al.*, 1979; Djamgoz *et al.*, 1985). HRP was injected into a suitable neurone by passing 10 nA positive current for about 30-40 seconds. During ionophoresis it was safer to return to recording mode to check if the electrode was still under working conditions.

The stimulus light used to identify and classify horizontal cell responses were derived from an optical system served by a 250 W tungsten-halogen lamp connected to a d. c power supply. A light spot of about 0.5mm dia. was focused on the retina from underneath and, during recording it was flashed with an "on" duration of 200 ms. The intensity and wavelength could be changed by inserting different interference filters. The amplitude of light-evoked S-potentials (V) and the stimulus intensity (logI) were related to establish the V-logI curve and calibrated by radiance energy to obtain the quantum spectral sensitivity (Djamgoz *et al.*, 1985).

HRP histochemical reaction

After completing a recording and ionophoresis session, the recording chamber containing the retina with the nylon net attached was flooded with fixative (2.5% glutaraldehyde, 1% paraformaldehyde, 3% sucrose in 0.06 M sodium phosphate buffer). After two hours fixation, the retina was rinsed and then washed thoroughly overnight in phosphate buffer. The wash solution was then replaced by a mixture of 0.2% diaminobenzidine tetrahydrochloride (DAB) and 0.01% hydrogen peroxide in phosphate buffer for a 1 hour incubation. Following incubation, the retina was returned to the buffer for examination of the HRP reaction product.

For light microscopical examination, marked neurones were localized in the squares of the grid system by viewing the retina with the nylon net. Well-injected, isolated cells were photographed or drawn with camera lucida in the wholemount.

RESULTS

S-potentials from horizontal cells

From 160 intracellular recording, the perch S-potentials could be classified into the luminosity S-potential (L-type) and the chromaticity S-potentials (C-type) (Fig. 1). L-type S-potentials could be further grouped

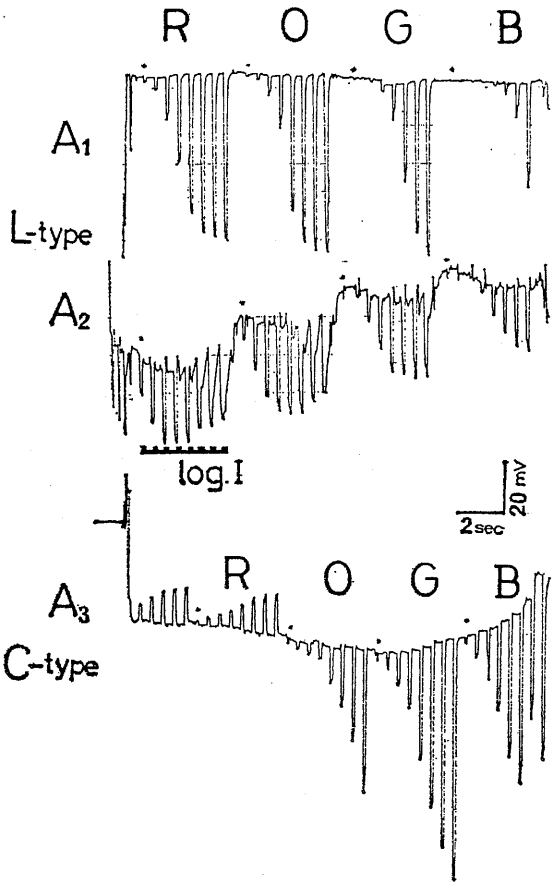

Fig. 1. Luminosity S-potentials (A1, A2) and chromaticity S-potential (A3) obtained from perch horizontal cells. At each wavelengths (R: 674 nm, O: 617 nm, G: 534 nm, B: 454 nm) responses are evoked to eight different intensities (log I=−2.8 with a solid circle, to 0.0, 0.4 log unit step, from left to right increasing intensity).

into two subtypes, L-type 1 and L-type 2 (Fig. 1 A1, A2 respectively). Both luminosity S-potentials had hyperpolarizing responses to all the wavelength flashes, but the saturation response of L-type 2 occurred at lower intensity. Therefore L-type 2 were possibly driven by rods which were sensitive to the lower illumination and defined as scotopic L-type horizontal cells. In addition, Table 1 summaries two distinctive characteristics between them. Compared to L-type 2 horizontal cells, L-type 1 cells were demonstrated to adapt brighter illumination with rapid repolarization to off of the stimulus light and only saturation at the higher intensity light.

Perch has typical biphasic chromaticity S-potentials (Fig. 1 A3). These horizontal cells showed depolarization to longer wavelength flashes, but hyperpolarization at shorter wavelengths. 12 of the recorded cells were showed the chromaticity S-potential. All of these were biphasic C-type S-potentials, no triphasic S-potentials have been recorded.

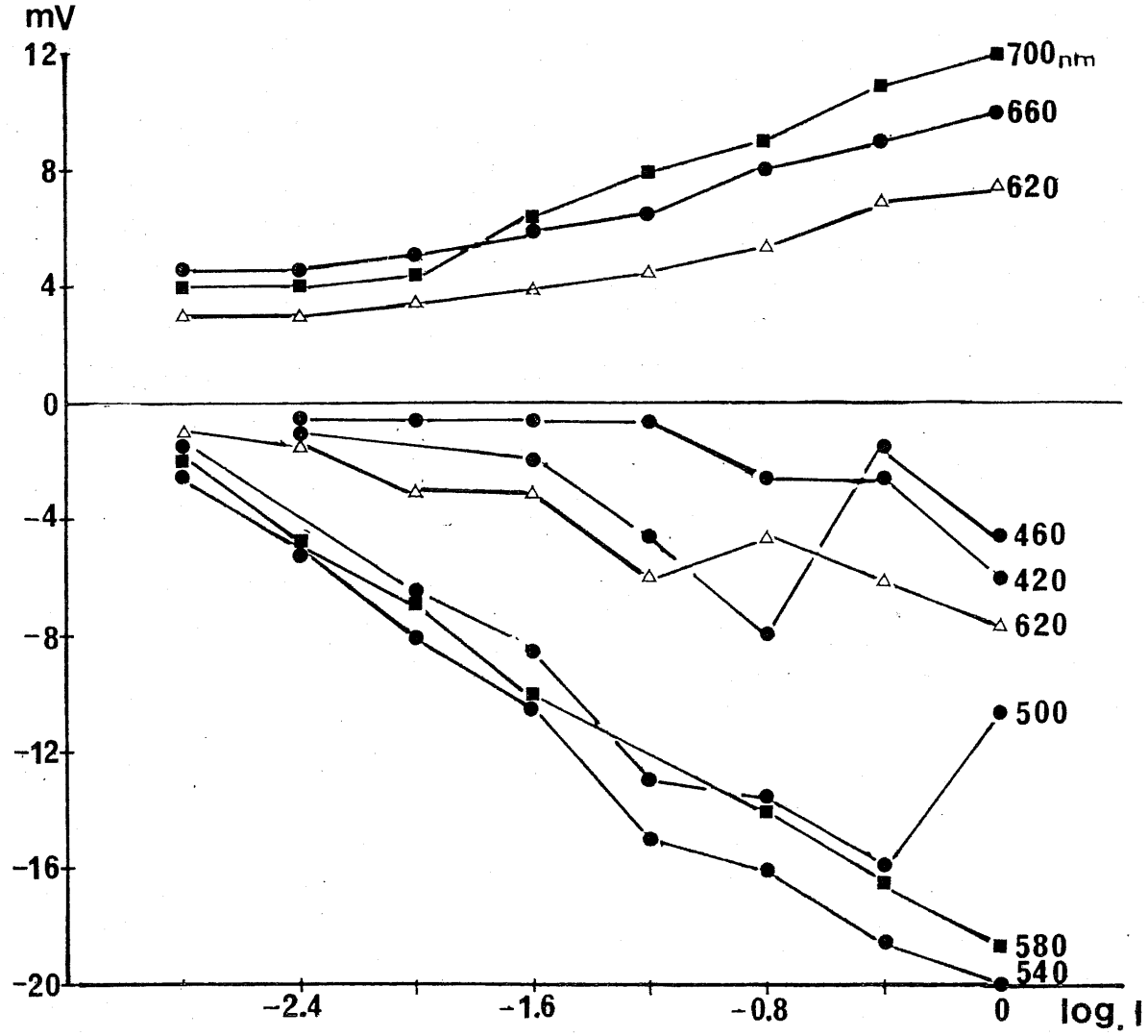

Fig. 2. One representative example of a V-log I curve showing the chromaticity S-potential in perch and the relationship between the amplitudes (V) of the responses and the intensities (log I) of the stimuli.

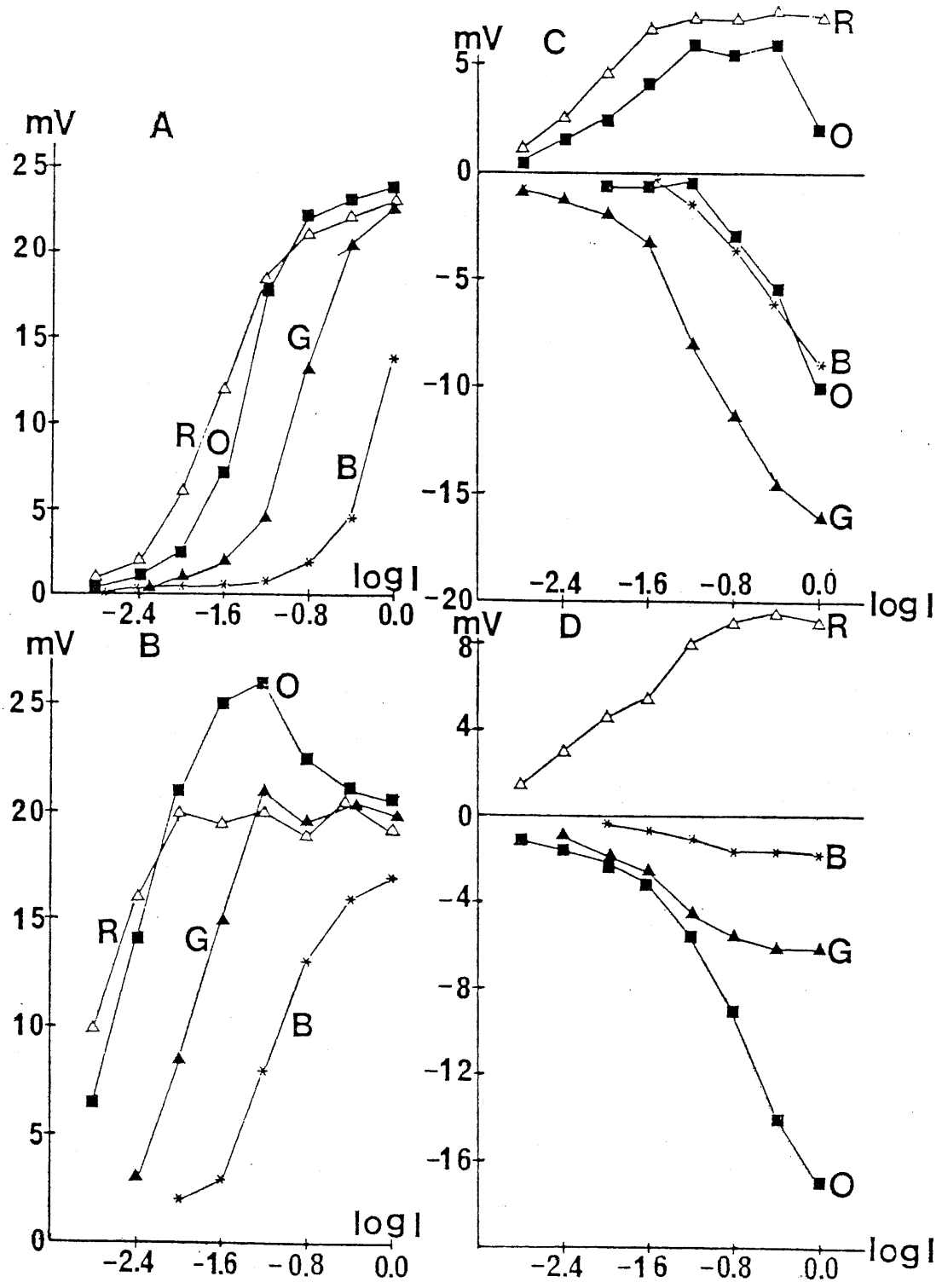

Fig. 3. The V-log I curves from two L-type (A, B) and two C-type (C, D) S-potentials of perch horizontal cells. A: L-type 1; B: L-type 2; C & D: C-type.

Recordings from perch C-type horizontal cells were invariably obtained after the L-type cells, which was suggestive that in perch retina, C-type cells comprised the more proximal layer. It would have to be confirmed by HRP injection but, in general, C-type horizontal cells are thought to be more difficult to penetrate than the L-type neurones, and also might be less numerous.

In Fig. 2, one representative C-type horizontal cell was responded to a series of wavelengths and intensities. The V-logI curve was demonstrated a maximal hyperpolarization at about 540 nm light and maximal depolarization at 660-700 nm stimulus lights. Therefore, it was a typically biphasic C-type S-potential similar to those of other teleosts (Witkovsky *et al.*, 1979; Djamgoz *et al.*, 1985), and its "null point" (the borderline wavelength between hyperpolarization and depolarization wavelength) was at 580-620 nm (Djamgoz and Downing, 1983).

Spectral analysis of S-potential

(1) *V-log I*

Fig. 3 was showed four representative V-log I curves of perch S-potentials. L-type 2 cells (Fig. 3B) started the saturated response at the low intensity (log. I=-2.0) of red flash. Both L-type 1 and 2 (Fig. 3A and 3B) horizontal cells were more sensitive to the longer wavelengths. 10 of the recorded biphasic, chromaticity S-potentials were depolarized to 674 nm light and hyperpolarized to 617, 534 and 454 nm light stimulus (as show in Fig. 3D), also 2 cells showed both hyperpolarization and depolarization to 617 nm light (Fig. 3C). Therefore it is likely the "null point" of these C-type S-potentials is at about 617 nm.

(2) *Quantum Spectral Sensitivities*

The quantum spectral sensitivity curves (Q_λ) obtained from L-type 1 horizontal cells was demonstrated a better agreement (Note the spectral sensitivity curve Q_λ and red-sensitive cones had the same peak at 620 nm, but S_λ at 660 nm) with the absorption peak of red-sensitive cone photopigment measured by MSP (Fig. 4). An obvious conclusion can be made that the predominant photoreceptor inputs to these units should be from the red-sensitive cone population.

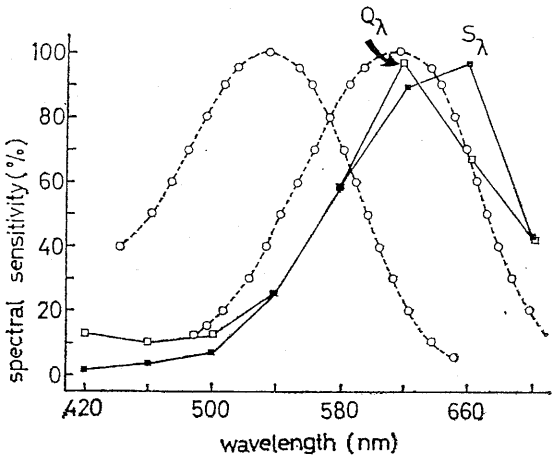

Fig. 4. The spectral sensitivity (S_λ) and relative quantum spectral sensitivity curves (Q_λ) derived from 12 units of L-type S-potential of perch horizontal cells are shown. The mean values are used in this graph. The standard deviations are omitted for clarity. Note the peak at 620 nm and the absorbance peaks of two types of cones (535 and 615 nm). The spectral absorbance curves of the two cone types are from Lythgoe, 1979.

Identification of the Recording Site by HRP Labelling

12 of the ionophoretically injected HRP neurones were successfully stained by histochemical procedures. Since retinal tissue is comparatively thin, HRP labelled neurones could be localized from the unsectioned or even uncleared retinae. Injection sites could be identified easily by using the grid system of the nylon net. The labelled neurones were rendered conspicuous by the brown diaminobenzidine tetrachloride (DAB) reaction deposit (Fig. 5A). It was likely that perch retina contained some unknown chromagenic substances. From the wholemount observations, the labelled neurones did not stand out from their cone mosaic as clearly

as in the case of cod (Huang, 1986).

Morphologically, there appeared to be two types of L-response horizontal cells (Fig. 5B). One type had a large soma (diameter about 30 um) with some short (less than 30 um long) but thick dendritic processes. This type of horizontal cell had a single long axon which could be traced for more than 300 um. The other type of horizontal cell had a smaller soma (average diameter less than 20 um), but was more stellate with many thinner processes surrounding the perikayon area. The latter did not have any distinguishable axon and the ratio of soma diameter to dendritic diameter was notably smaller than that of the former type of horizontal cells (the former and the latter were shown in marked with 1, 2, 3 and 4, 5 of Fig. 5B respectively).

The former group of the traceable cells (with distinctive axon, also shown in the top Fig. 5A) was likely to be classified as a cone horizontal cell (photopic, i. e. L-type 1) and the latter possibly as rod horizontal cells (scotopic, i. e. L-type 2) defined as morphologically identified in catfish (Lam

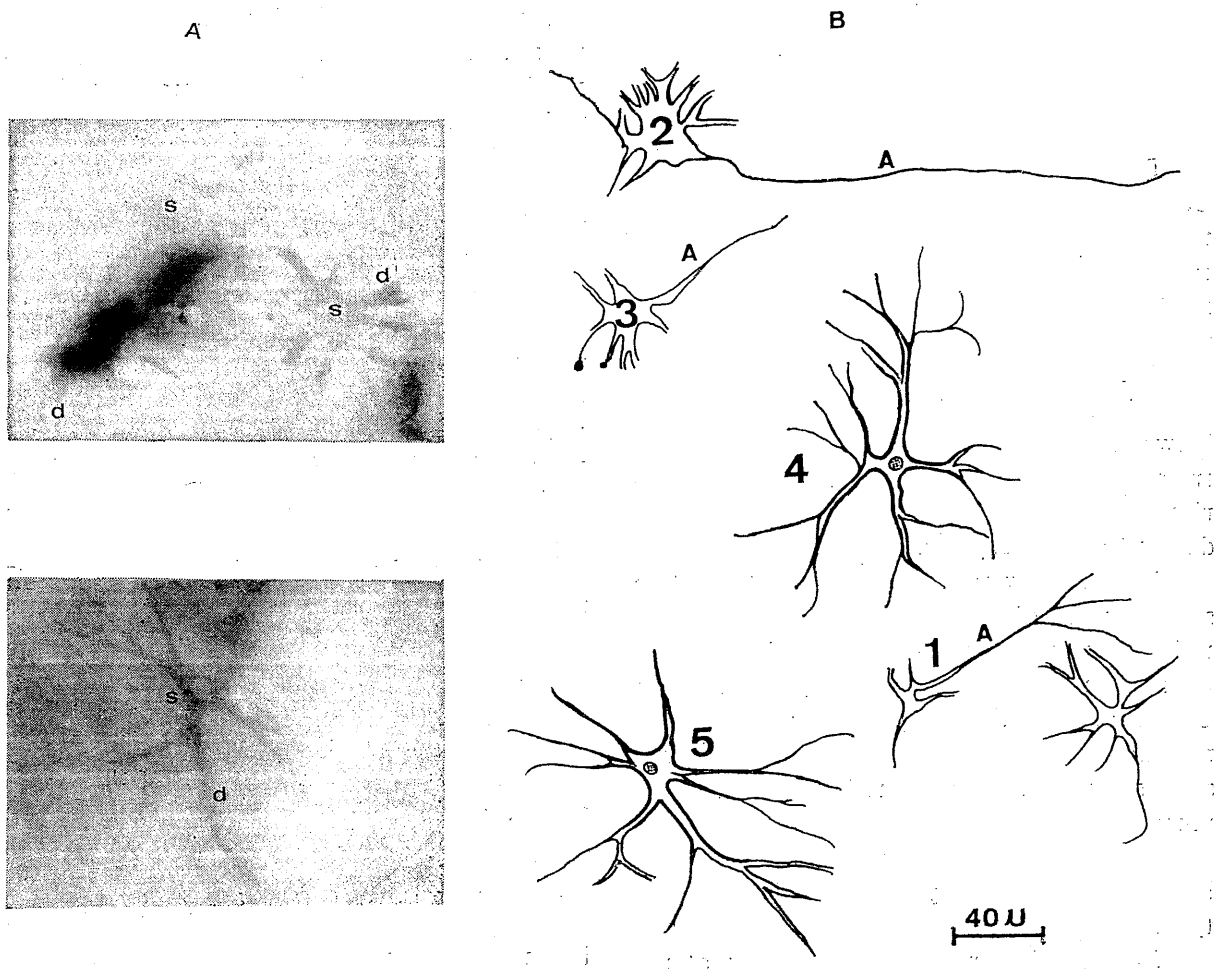

Fig. 5. Some representatives of HRP intracellular ionophoretically stained retinal neurones of perch. Flat wholemount views are shown. Microphotographs (A) and camera lucida drawings (B) demonstrate the cell types. d: dendrite; S: soma; A: axon. Note in (B), those cells marked 1-3 have a larger ratio of soma diameter and dendrite field diameter, and cells marked 4, 5 have not been found any axon.

and Ayoub, 1983) and in goldfish and carp (Stell, 1975; Stell and Lightfoot, 1975; reviewed in Piccolino and Witkovsky, 1984). The morphological characteristics of the well-injected horizontal cells were carefully traced. Two of the twelve studied cells had no discernable axon, whereas the other ten cells had obvious axonal extensions (Fig. 5). The corresponding electrical recordings from these two neurones did not show as strongly as a rod-driven horizontal cell, but the morphological characteristics of them did demonstrate as a rod-driven cell (reviewed in Piccolino and Witkovsky, 1984). These experiments in HRP ionophoresis failed to trace any C-type horizontal cells.

DISCUSSION

Because of the phylogenetic relationship, Cameron (1982) compared the spectral sensitivity from perch behavioural studies with the action spectra from pikeperch S-potentials and suggested physiological measurements might offer more compelling evidence for a direct comparison in perch due to the differences in habitat and/or behavioural patterns between them. The present results derived from S-potential also allow a direct comparison of the spectral sensitivity to MSP data of photoreceptors.

MSP data were demonstrated these two species were dichromatic with red-sensitive twin cones and green-sensitive single cones in their retina (Loew and Lythgoe, 1978; Cameron, 1982). The present physiological measurements from S-potentials of perch also showed two similarities to those of pikeperch:

1) Both had two types of S-potentials, i.e. monophasic L-type and biphasic C-type.

2) Both had maximal sensitivity at red for monophasic S-potential and red-depolarization, green-hyperpolarization for biphasic one.

The present studies on the spectral sensitivity of perch L- and C-type S-potentials showed one peak at 620 nm and two peaks at 540 and 700 nm, respectively. These results were coincide well with the behavioural measurements at peaks 550 and 640 nm (Cameron, 1982) and also agreed with the presence of tectal cells at 650 and 700 nm (Guthrie, 1983). In addition, both cone MSP measurements obtained by Loew and Lythgoe (1978) and present experiments on horizontal cells could not find any evidence of the peak around 480–550 nm which was also obtained by the behavioural studies (Cameron, 1982). By contrast, cardiac reflex studied by Cameron himself (1982) could not show any sensitivity in the blue band at all. In addition, Cameron (1982) also obtained the absorption spectra for lense and cornea which acts as a cut-off filter and cuts off at wavelength less than 500 nm. It is likely that perch has no blue cones or S-potentials and the disagreement is probably caused by the interaction between red and green cones (Djamgoz and Downing, 1983).

There was one difference between these two species. The present physiologic data were shown perch had rod-driven horizontal cells (L-type 2). By contrast, on the basis of physiological evidence, no rod-driven horizontal cells were detected in pikeperch. On the other hand, electron microscopic observations of rod spherules clearly indicate the presence of horizontal cell dendrite terminals in pikeperch retina (Witkovsky *et al.*, 1979). Several investigations were done to distinguish the different types S-potential (Toyoda *et al.*, 1978; Copenhagen *et al.*, 1983) by horizontal cells responses. At present report, a convenient criteria to distinguish the photopic and scotopic (L-type 1 and L-type 2) horizontal cells were summarized in the results (Table 1) of this study and applied successfully on both perch and cod S-potentials (Huang, 1986). Therefore it is likely that perch has scotopic (rod-driven) horizontal cells.

From HRP labelling neurones, it was also reasonable to classify two morphological

TABLE 1

	L-type 1	L-type 2
response to "off" of the longer wavelength stimulus light (fig. 2A1, A2)	rapid repolarization	slow repolarization
amplitude of response to the longer wavelength light (fig. 4A, B)	saturation at the higher intensities	saturation at the lower intensities

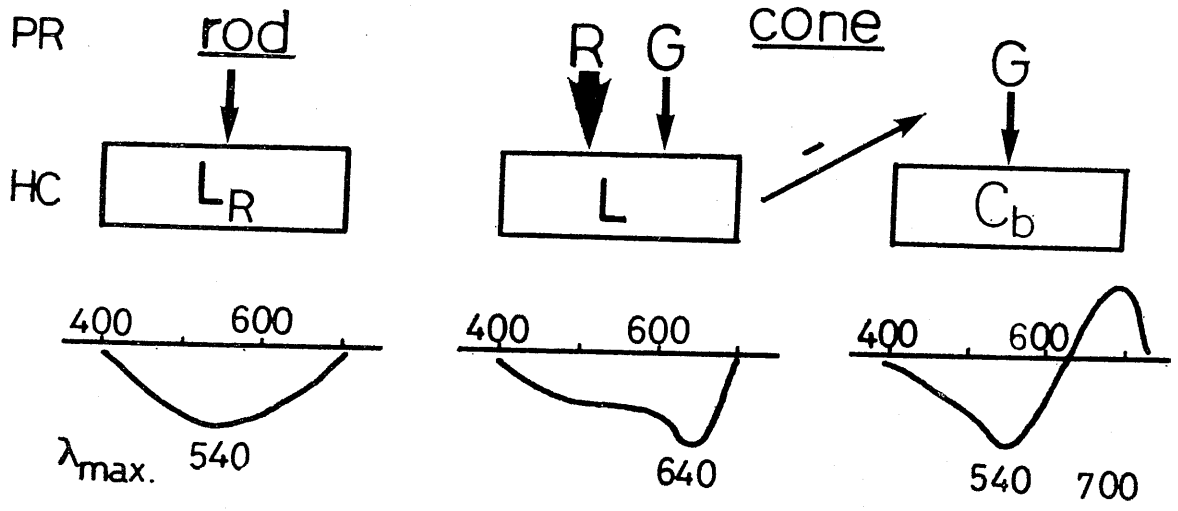

Fig. 6. A possible organization of the photoreceptors (PR) and their connections to horizontal cells (HC) in order to relate the spectral sensitivities to the S-potentials in perch. twin cone ↓ (R: red) single cone ↓ (G: green), — inverting pathway.

types of L-type horizontal cells. The horizontal cells with distinguishable axons were likely to be classified as the cone horizontal cells and the others possibly as rod-driven ones as identified in catfish (Lam and Ayoub, 1983) and in goldfish and carp (Stell, 1975; Stell and Lightfoot, 1975; reviewed in Piccolino and Witkovsky, 1984). The corresponding electrical recordings from these two neurones were not demonstrated conspicuously as a rod-driven horizontal cells (Witkovsky *et al.*, 1979). However, further evidence by the electron microscope investigations are needed in order to prove if the presence of horizontal cells dendritic terminals connecting with rod spherules.

Many investigations have been performed on the connections between photoreceptors and horizontal cells in order to establish a possible model to evaluate the mechanisms of chromaticity and luminosity. Stell and Lightfoot (1975), with their morphological observations on the goldfish retina, presented a "synaptic model" to explain the cone-horizontal cell connectivity. This model has been widely applied in teleost S-potentials. In order to relate the spectral sensitivity of the photoreceptors and the horizontal cells in the perch retina, a possible connections between them was shown in Fig. 6. It is known that horizontal cells could mediate initial function of visual cells by two-way synaptic transmission. One is sign-preserving pathway from visual cells to horizontal cells, the other is sign-inverting via the feed back pathway from the interaction of its neighboring horizontal cells (Stell and Lightfoot, 1975). Since perch has red and green-sensitive cone inputs only (no blue-sensitive cones), photopic L-type cells have red-sensitive

response (which is more predominate). Because of the inputs from green-sensitive cones (sign-preserving, i. e. hyperpolarization to green light) and from L-type cells (sign-inverting, i. e. change hyperpolarization to depolarization), C-type horizontal cells have the resultant responses with depolarization at red-band and hyperpolarization at green-band. The scotopic L-type cells are driven by rods with hyperpolarization at the same spectral sensitivity. The results obtained from the present experiments were successfully applied on the model for proposed the connection between visual cells and horizontal cells.

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淡水鱸S電位之光譜特性

胞內記錄與HRP研究

黃寶貴 詹果士

利用細胞內記錄與 HRP 胞內注射 (ionophoresis) 以探討淡水鱸視網膜內之水平細胞 (horizontal cells) 受光刺激產生S電位；並分析其特性。實驗結果顯示淡水鱸有兩種單相式 (monophasic) 之明暗性 (luminosity) S電位：(1)光適性 (photopic)，(2)暗適性 (scotopic)，敏感波長分別爲 620 nm 和 580 nm。淡水鱸另有雙相式 (biphasic) 之色覺性 (chromaticity) S電位，敏感波長在 580-620 nm間。由此敏感波長與感光細胞經由顯微光譜分析儀 (MSP) 測定之 λ_{max} 比較，可推斷光、暗適性之水平細胞可能分別受制於其突觸前 (presynaptic) 之雙生錐細胞 (twin cones) 與柱細胞 (rods)。本實驗利用電生理學與 HRP 作形態分析淡水鱸之S電位之光譜特徵，與 Cameron (1982) 和 Loew, Lythgoe (1978) 等分別利用行爲學研究與 MSP 分析所得淡水鱸之色覺特徵極爲吻合。