Photo-Reception and Contact Chemo-Reception in Silkworm Larva

By SHIGEO ISHIKAWA

Chief, 1ts Laboratory of Silkworm Rearing Method,
Sericulture Division, Sericultural Experiment Station (Maebashi)

The accomplishment of locomotive and feeding activities of silkworm larvae depends to a great extent upon the detection and assessment of light and chemical aspects of the environment.

These environmental factors affect first to trigger excitation in the receptors of the corresponding sensory organs. Then, for a fuller understanding of the behavioral responses to environmental factors we must know more about the functions of the receptors concerned by application of electrophysiological methods.

Sensitivities of photoreceptors in the stemmata

The stemmata (or the lateral ocelli) are the sole visual organs possessed by silkworm larvae. The six pairs of stemmata are so arranged on the head that little or no overlapping of the visual field exists. Each stemma possesses, a corneal lens, a crystalline lens and three pigments cells.

The receptive layer, possessing a structure like that of the ommatidium, consists of three retinula cells which send their axons to the brain in the ocellar nerve.

The larva, cut between thorax and abdomen, was secured on to a silver plate which served as an indifferent electrode, where the head was rigidly fixed with plasticine. The head being cut open, all the surrounding tissues were removed so as to expose the ocellar nerve.

The electroretinograms (ERGs) of stemmata were recorded with the silver hock electrode hanging the proximally blocked ocellar nerve.

The ERGs consist of the retinular potentials, which were originated in the receptive layers and were spread on the ocellar nerve electrotonically. For illustrating the characteristics of the sensitivity of the photoreceptors in the stemmata the ERGs were analyzed.

The height of ERG increased in roughly parallel with the increase of logarithm of light intensity between 0.5 and 5,000 lux. The stemmata become completely dark-adapted in about one hour and completely light-adapted in about 10 minutes. They follow flicker up to 25–30 per second.

ERGs of the white-eye and red-eye mutants were compared with those of normal black-eye. The white-eye was more sensitive to light stimulation than the normal eye. The red-eye was in-between.

From the responses to various intensities of monochromatic lights of wavelength 340 to 638 mμ, response–log relative intensity curves were obtained. These curves are not parallel among different wavelengths (Fig. 1).

These curves were used to construct the spectral sensitivity curve by deducing the relative number of quanta required to evoke a constant response.

The spectral sensitivity curves showed one peak in the near ultraviolet and another hump or peak in the blue-green or green region of the spectrum. The latter peak was more prominent at lower intensities than at

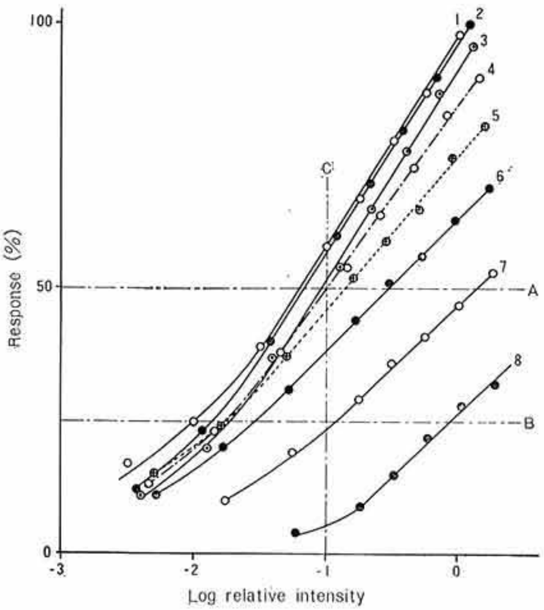

Fig. 1. Height of response as a function of log relative energy (quantized) for several wavelengths: at 340 mμ (Curve 1), 400 mμ (2), 433 mμ (3), 484 mμ (4), 537 mμ (5), 562 mμ (6), 598 mμ (7), and 638 mμ (8)

higher ones (Fig. 2).

Monochromatic light adaptation selectively influenced the relative spectral sensitivity (Fig. 3) and the form of the ERGs, suggesting that two receptor systems (UV and G) which differ in spectral sensitivity exist in the silkworm stemmata. The peak of the sensitivity of the G receptor system seems to be at about 540 mμ.

However, no exact position of the maximum sensitivity of the UV-receptor system could be illustrated. The existence of the two receptors provides good reason to assume that the silkworm stemmata are able to detect colors.

Sensitivities of contact chemoreceptors in the maxilla

The maxilla of silkworm larva consists of maxillary lobe (or headpiece), maxillary palpus, and other parts (palpifer and stipes).

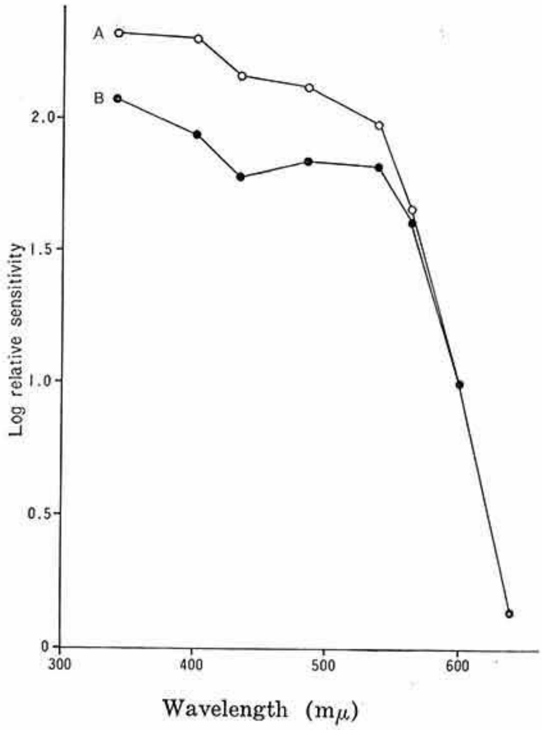

Fig. 2. Spectral sensitivity curves calculated for two constant responses (A and B in Fig. 1) from the response-log relative intensity curves shown in Fig. 1

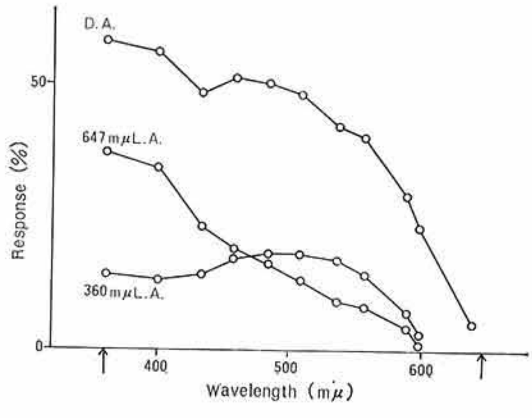

Fig. 3. Spectral efficiency curves at relatively low stimulus intensity in dark-adapted state (D. A.) and light-adapted state (L. A.) at 647 and 360 mμ, respectively

Fig. 4. Schematic representation of the maxilla of silkworm larva
Ss: Sensilla styloconica
Sb: Sensilla basiconica

The maxillary lobe bears two large sensilla styloconica, two sensilla trichodea, and one sensilla chaeticum. The third segment of the palpus bears at its apex a group of six to eight small sensilla basiconica (Fig. 4).

The sensilla trichodea on the head of the silkworm have been identified as mechanoreceptors electrophysiologically. A chemoreceptive function of the maxillae of lepidopterous larvae has been assigned to the styloconic and basiconic sensilla.

A fluid-filled micropipette was placed over the tip of one of the styloconic sensilla. It is employed both as a recording electrode and as a source of chemical stimulation. The signal was amplified, displayed on a cathode ray oscilloscope, and photographed.

By the technique these two sensilla styloconica (Ss-I and II) were identified as taste organs containing certain chemoreceptors. Each receptor is specifically different with regard to the chemicals to which it is sensitive.

The lateral sensillum styloconicum (Ss-I) contains receptors which are specifically sensitive to sugars, inositol, glucose, salts and some hitherto unidentified substance, and the medial sensillum (Ss-II) has specific receptors for salts (two receptors), bitter substances and water. The sensitivities of these receptors are summarized in Table 1.

The synergistic or inhibitory effect on the activities of various receptors was observed at the peripheral level. For instance, the frequency of the impulses of the bitter substance receptor evoked by strychnine nitrate (3.3×10^{-7} M) increased according to the increase in the concentration of mixed sodium chloride ranging from 10^{-2} M to 4×10^{-2} M.

On the contrary, the concentration of mixed sodium chloride being increased above 10^{-1} M, the bitter substance receptor activity was completely abolished and salt receptor impulses appeared instead of the impulses of the bitter substance receptor.

A similar excitatory and inhibitory effects of mixed bitter substance on the salt receptor activity were also observed according to its relative concentration.

The specific inhibitor on the sugar receptor was found in the leaves of *Artemisia vulgaris*. The receptor activity was completely depressed at low concentration of sucrose, whereas a partial recovery occurred at high concentrations, the concentration of the leaf extract being constant. This inhibitor seems to have no influence on the responses of the other receptors.

With regard to hostplant selection, the activities of the sugar and inositol receptors in the lateral hair and of the bitter-substance receptor in the medial hair seems to play relatively important roles in the responses to various plant juices.

To test this, each response pattern evoked by a plant juice was compared with the feeding response to the agar-diet containing about 60 per cent of its leaf-powder, using many host and non-host plant leaves.

Table 1. Classification of the taste qualities in silkworm larva on the basis of maxillary chemoreceptor activities

Taste quality	Stimulative substance		Receptor
Sugar	Some carbohydrates:		Sugar receptor (Ls) in I
	Sucrose	++++	
	Maltose	+++	
	Methyl-α-D-glucoside, D-Arabinose, L-Rahmnose, D-Glucose, L-Sorbose	++	
	L-Arabinose, D-Fructose, D-Galactose Trehalose, Raffinose, Melezitose and some others	+	
Inositol	Inositol:		Inositol receptor (Li) in I
	myo–isomer	+++	
	epi–isomer	+++	
	neo–isomer	±	
	rac–isomer	–	
	Mannitol, Dulcitol, Sorbitol	–	
Glucose	Typically sensitive to glucose		Glucose receptor (G) in I
Electrolyte	Some inorganic salts Some organic salts Some organic acids Some amino acids Especially sensitive to monovalent cations		Salt receptor (N_1, N_2, N_2') in I and II
Bitter substance (or Deterrent)	Feeding deterrent substances:		Bitter substance (or Feeding deterrent) receptor (R) in II
	Some alkaloids:		
	Strychnine	++++	
	Brucine, Pilocarpine, Berberine	+++	
	Nicotine	++	
	Quinine, Hyoscine and others	+	
	Some glycosides:		
	Salicin	+++	
	Rutin, Quercitrin and others	+	
	Choline chloride	+	
Water	Pure water		Water receptor (W) in II
Not identified	Unknown substances containing some plant leaves of Cruciferae		Receptor in I

I: lateral hair (Ss-I), II: medial hair (Ss-II)

Consequently, it was demonstrated that the response pattern correlates roughly with the feeding response: activation of both sugar and inositol receptors considerably stimulates feeding, whereas activation of the bitter-substance receptor plays a crucial role in the inhibition of feeding.

As far as the activities of these three

receptors are concerned, the presence of adequate amounts of sucrose and inositol and the deficiency of the substances stimulating the bitter-substance receptor seems to be necessary for increasing the feeding response.

Addition of sucrose and inositol to the diets and, at the same time, inactivation of the bitter-substance receptor by HCl treatment of the maxillary medial hair stimulated the feeding responses to many diets with non-hostplant leaf-powders. This result confirms the significance of these receptors in the hostplant selection.

Compared with some polyphagous, lepidopterous larvae, the feeding behavior of *Bombyx* is characterized especially by the high sensitivities of the bitter-substance receptor (feeding-deterrent receptor) for many kinds of feeding deterrents associated with various non-hostplants.

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