Nonlinear Signal Transmission between Second- and Third-Order Neurons of Cockroach Ocelli

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ABSTRACT   Transfer characteristics of the synapse made from second- to third-order neurons of cockroach ocelli were studied using simultaneous microelectrode penetrations and the application of tetrodotoxin. Potential changes were evoked in second-order neurons by either an extrinsic current or a sinusoidally modulated light. The synapse had a low-pass filter characteristic with a cutoff frequency of 25–30 Hz, which passed most presynaptic signals. The synapse operated at an exponentially rising part of the overall sigmoidal input/output curve relating pre- and postsynaptic voltages. Although the response of the second-order neuron to sinusoidal light was essentially linear, the response of the third-order neuron contained an accelerating nonlinearity: the response amplitude was a positively accelerated function of the stimulus contrast, reflecting nonlinear synaptic transmission. The response of the third-order neuron exhibited a half-wave rectification: the depolarizing response to light decrement was much larger than the hyperpolarizing response to light increment. Nonlinear synaptic transmission also enhanced the transient response to step-like intensity changes. I conclude that (a) the major function of synaptic transmission between second- and third-order neurons of cockroach ocelli is to convert linear presynaptic signals into nonlinear ones and that (b) signal transmission at the synapse between second- and third-order neurons of cockroach ocelli fundamentally differs from that at the synapse between photoreceptors and second-order neurons of visual systems so far studied, where the synapse operates in the midregion of the characteristic curve and the transmission is essentially linear.

INTRODUCTION

Sinusoidally modulated light is useful for examining responses of visual neurons, because the photic input that visual systems receive in a natural environment is such a modulation of light intensity around a mean illuminance. Evidence has accumulated to show that peripheral visual neurons of both vertebrates and invertebrates respond linearly to moderate changes in light intensity. This was first demonstrated for photoreceptors of *Limulus* by Fuortes and Hodgkin (1964), and subsequent

studies on photoreceptors of vertebrate retinas (Baylor and Hodgkin, 1974; Naka et al., 1987) and of insect compound eyes (Pinter, 1972) have confirmed that the responses are essentially linear. Second-order neurons of a variety of visual systems also generate essentially linear responses. This is the case in vertebrate retinas (Naka et al., 1979; Tranchina et al., 1983; Chappell et al., 1985), in *Limulus* lateral eyes (Knight et al., 1970), in insect compound eyes (French and Järvilehto, 1978), and in insect ocelli (Mizunami et al., 1986).

Studies of third-order visual neurons of both vertebrates and invertebrates have shown that their responses contain characteristic nonlinearities. Spekreijse (1969) found that some ganglion cells of the goldfish retina exhibit half-wave rectified responses. The rectified responses have been noted in cat ganglion cells (Hochstein and Shapley, 1976; Victor, 1988), and catfish amacrine and ganglion cells (Sakai and Naka, 1987). The rectifying process in vertebrate retina seems to accompany either a saturating (Hochstein and Shapley, 1976; Victor, 1988) or an accelerating process (Sakai and Naka, 1987; Enroth-Cugell and Freeman, 1987), i.e., the response amplitude becomes either a negatively or a positively accelerated function of the stimulus contrast. In addition to the rectifying nonlinearity, Enroth-Cugell and Freeman (1987) and Victor (1987) suggested that the cat retina contains a nonlinear high-pass process, the time-constant of which is altered with the stimulus contrast, which would account for the enhanced transience of high-contrast responses in ganglion cells. Third-order visual neurons of invertebrates also exhibit more or less rectified and transient responses, compared with those of second-order neurons (insect compound eye: Osorio, 1987; insect ocelli: Simmons, 1982; Mizunami and Tateda, 1988*b*; barnacle ocelli: Stuart and Oertel, 1978). The neural mechanisms underlying the formation of the nonlinearities, however, have not been determined.

Insects have two or three ocelli, in addition to a pair of compound eyes. The insect ocellus is a simple photoreceptive system suitable for examining basic mechanisms of visual processing (Chappell and Dowling, 1972). The insect ocellus does not form images nor does it sense anything other than changes in illumination integrated over the entire visual field (Chappell and Dowling, 1972; Dowling and Chappell, 1972; Wilson, 1978). The cockroach ocellar retina contains ~10,000 photoreceptors, and they converge on four second-order neurons (Weber and Renner, 1976; Toh and Sagara, 1984). The second-order ocellar neurons operate as linear contrast encoders, i.e., they respond linearly to illuminance changes and their contrast sensitivities remain unchanged over a four-log range of mean illuminance levels (Mizunami et al., 1986). Chappell and Dowling (1972) also concluded that incremental responses of dragonfly ocellar second-order neurons follow exactly the Weber-Fechner relationship. The second-order neurons exit the ocellar retina and project into the ocellar tract of the brain where they make excitatory synapses onto a number of third-order neurons (Toh and Hara, 1984; Mizunami and Tateda, 1986; Mizunami and Tateda, 1988*b*).

I examined how and by what mechanisms the linear signals of second-order neurons are further processed when they are passed to third-order neurons. Experiments were done after the application of tetrodotoxin to concentrate on the graded (synaptic) components of the response by blocking action potentials. My major findings are that (*a*) the response of third-order neurons exhibits a half-wave rectifica-

tion: the response to dimming is much larger than that to brightening; (b) the response contains an accelerating nonlinearity: the response amplitude is an accelerating function of the stimulus contrast; (c) the nonlinear response is produced by nonlinear synaptic transmission from second- to third-order neurons: the synapse operates at an exponentially rising part of the overall sigmoidal input/output voltage relationship; (d) the nonlinear synaptic transmission also makes the step-response more transient. The findings are discussed with reference to those in other visual systems, to characterize general and specific aspects of signal processing between second- and third-order visual neurons.

MATERIALS AND METHODS

Preparation

Adult males of the cockroach, *Periplaneta americana,* reared in the laboratory of Kyushu University (Fukuoka, Japan), were studied. The whole animal was mounted, dorsal side up, on a Lucite stage and fixed with bee's wax. The compound eyes and one of two ocelli were shielded from the light with beeswax mixed with carbon black. The dorsal part of the head capsule was removed and the dorsal surface of the brain was exposed. The esophagus was excised and the brain was stabilized by inserting a glass rod into the esophagus foramen. Saline containing a digestive enzyme, 1% Actinase (Type E; Kaken Seiyaku, Tokyo, Japan), was applied to the brain for 1 min to facilitate insertion of the electrode.

Recording

Two microelectrodes were inserted into the ocellar tract of the protocerebrum where the second-order ocellar neurons make synapses onto third-order neurons (Fig. 1; Mizunami and Tateda, 1986). The two electrodes impaled either (a) a pair consisting of a second- and a third-order neurons, (b) a pair consisting of second-order neurons or of third-order neurons, or (c) a single second-order neuron or a single third-order neuron. The first two recordings, (a) and (b), were used to examine synaptic transmission among the recorded neurons, and the third was used to examine the current-voltage relation in the neuron. The electrodes were filled with 5% Lucifer Yellow mixed with 2 M lithium chloride, or with 2 M potassium acetate. The recorded neuron could be identified as a second-order or a third-order neuron from the response. In particular, (a) second-order neurons exhibit hyperpolarizing responses of over 30 mV to a bright step-stimulus given in the dark, whereas the hyperpolarizing response of third-order neurons is <10 mV (Mizunami and Tateda, 1986); (b) membrane hyperpolarization by extrinsic current decreases the light-evoked response of second-order neurons but increases that of third-order neurons (Mizunami and Tateda, 1988b); and (c) second-order neurons produce a nearly sinusoidal response to a sinusoidally modulated stimulus whereas the response of third-order neurons exhibits a characteristic deviation from a sinusoid (see Fig. 2). I stained more than 80 recorded cells and confirmed that these criteria are reliable. Tetrodotoxin (TTX) of 10^{-5} g/ml was added to the saline solution to suppress spike activities for quantitative measurement of the synaptic potentials.

The electrodes were connected to a high impedance, negative capacity, compensated preamplifier (MEZ-8201; Nihon Kohden, Tokyo, Japan) that was equipped so that a constant current could be passed through an active bridge circuit. A small piece of platinum placed in the bathing solution served as an indifferent electrode. The amount of stimulus current was continuously monitored. Measurements indicative of electrical coupling between the two electrodes were not considered for this study.

Stimulus

A light-emitting diode, LED (Sharp Corp., Tokyo, Japan), was used as a light source. The LED has a spectral peak at 560 nm. The LED was driven by a sinusoidal, step or ramp current, provided by a function generator (ET1101; NF Design Block, Tokyo, Japan). The illuminance of the stimulus depended linearly on the magnitude of the driving current. The stimulus light was monitored by a photodiode (TFA1001W; Siemens-Allis, Inc., Cherry Hill, NJ). The light stimulus and cellular response were observed on an oscilloscope and stored on analog tape. For data analysis, the stored signals were digitized and averaged with an averager (DAT 1101; Nihon Kohden, Tokyo, Japan). All experiments were done at room temperature (20–24°C).

Analytical

The sinusoidal light stimulus consisted of two components, a steady mean, I_0, and a dynamic component, $I(f)$, as shown in Fig. 2. I_0 was constant at 20 μW/cm^2 throughout this study. $I(f)$ was defined by modulation frequency (Hertz) and depth of modulation. The depth is defined in the conventional fashion, $(I_{max} - I_{min})/(I_{max} + I_{min})$, where I_{max} is the maximum illuminance and I_{min} is the minimum illuminance. The depth of modulation represents the "contrast" between the stimulus and the adapting light. The resulting response recorded from a second- or a third-order neuron consisted of a steady (DC) potential, V_0, (horizontal lines in records in Fig. 2) and a modulation response, $V(f)$, which were related to I_0 and $I(f)$, respectively. The magnitude of $V(f)$ was defined as $V_{peak} - V_{bottom}$, where V_{peak} is the potential at the peak and V_{bottom} is the potential at the bottom of the voltage modulation.

Two methods were used to characterize the input/output relationship of the synaptic transmission. First, I measured the relationship between pre- and postsynaptic voltages at a fixed modulation frequency, which I refer to as the input/output voltage relationship or characteristic curve of synaptic transmission. In actual experiments, the depolarizing and hyperpolarizing peak potentials of the modulation response were measured from the mean potential, V_0, and the measured V_{dep} and V_{hyp} of the postsynaptic neuron, where $V_{dep} = V_{peak} - V_0$ (always positive) and $V_{hyp} = V_{bottom} - V_0$ (always negative), were plotted against those of the presynaptic neuron. Second, linear system analysis was applied to examine synaptic transmission. I measured the linear transfer function between $V_{pre}(f)$ and $V_{post}(f)$, where $V_{pre}(f)$ and $V_{post}(f)$ are $V(f)$ of pre- and postsynaptic neurons. The transfer gain was defined as peak-to-peak amplitude of $V_{post}(f)$ per unit amplitude of $V_{pre}(f)$. The characteristic curve represents nonlinear aspects of synaptic transmission well (see Results), but is less effective in analyzing the dynamic aspects. By contrast, linear transfer function represents well the dynamic aspects of synaptic transmission, but is less effective in analyzing the nonlinear aspects since it is based on the linear part of the response. Thus, the two analytical methods combined pave the way for better understanding of dynamic and nonlinear aspects of synaptic transmission. The quality of the linear sine-wave analysis of the synaptic transmission depends on the extent to which the response of the presynaptic neuron remains linear. It has been shown that a linear model predicts the actual response of second-order neurons with a fair degree of accuracy (with mean square errors of ~11%: Mizunami et al., 1986).

To examine signal processing between second- and third-order neurons, the transfer function between $I(f)$ and $V_{pre}(f)$ and that between $I(f)$ and $V_{post}(f)$ were compared. Gain of the transfer function was defined by the peak-to-peak amplitude of $V(f)$ per unit of modulation depth. Further insights into nonlinear aspects of signal processing between second- or third-order neurons were obtained by comparing (a) their plots of amplitude vs. modulation depth in response to sinusoidal light and (b) their waveforms of response to square-wave contrast reversal.

RESULTS

Responses of Second- and Third-Order Neurons to a Sinusoidal Stimulus

Intracellular recordings remaining stable for more than 10 min were obtained from more than 50 pairs of second- and third-order neurons. Recordings were made in the ocellar tract, an area where they make synaptic contact (Fig. 1). All recordings were made after the application of TTX. Although third-order neurons can be classified into nine anatomical types (Mizunami and Tateda, 1986; one type is shown in Fig. 1), the synaptic activities recorded from these neurons had much the same properties, as previously noted (Mizunami and Tateda, 1988*b*).

Both second- and third-order neurons respond with hyperpolarizing potentials to a step of light given in the dark (Fig. 2). Because excitatory transmission is maintained at the synapse between these neurons (Mizunami and Tateda, 1988*b*), hyperpolarizations of second-order neurons produce hyperpolarizations in third-order
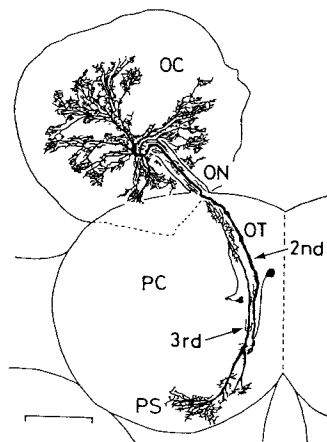

FIGURE 1. Anatomy of a second-order neuron and a type of third-order neuron, PS-I neuron, of the cockroach ocellar system. The neurons stained were from different preparations. Second-order neurons extend their dendritic branches into the ocellar retina. Axons of the second-order neurons pass through the ocellar nerve and project into the ocellar tract of the protocerebrum, where they make synapses onto a number of third-order neurons. The PS-I neuron runs posteriorly and projects into the posterior slope. Details of the anatomy of second- and third-order neurons have been reported (Mizunami et al., 1982; Mizunami and Tateda, 1986). *OC*, ocellus; *ON*, ocellar nerve; *PC*, protocerebrum; *OT*, ocellar tract; *PS*, posterior slope. Scale, 200 μm.

neurons. A prolonged step-stimulus produces an initial rapid hyperpolarization followed by partial recovery in second-order neurons, whereas it produces sustained hyperpolarization in third-order neurons. The difference in the response time-course will be explained later by nonlinear synaptic transfer. From ~30 s after the start of steady illumination, membrane potentials of both second- and third-order neurons reached steady levels. A sinusoidal light modulation was applied after this steady-state light adaptation had been attained.

The response of the second-order neuron to a sinusoidally modulated light is almost sinusoidal (Fig. 2). This observation suggests that the response is practically linear (Mizunami et al., 1986), that is, the magnitude of the response is proportional to the depth of modulation. The response waveform of the third-order neuron, however, deviates from sinusoidal. That is, (*a*) the amplitude of depolarizing

response is much larger than the hyperpolarizing response and (b) the response exhibits a sharp depolarizing peak.

Synaptic Transmission between Second- and Third-Order Neurons

As a first step toward elucidating the mechanisms that underlie the formation of nonlinear responses in third-order neurons, I searched for synaptic connections among second-order neurons, for connections among third-order neurons, and for feedback connections from third- to second-order neurons. Simultaneous intracellular recordings and current injections of ±5 nA were used. The estimated voltage changes during current pulses were ~7–8 mV for second-order neurons, and 8–15 mV for third-order neurons. The estimate was based on data from the current-voltage relationship obtained by impaling the neurons with two electrodes (an example is seen in Fig. 3 A). In all 12 pairs of second-order neurons and seven pairs of third-order neurons, no detectable (>0.1 mV) potential changes were recorded from one neuron when a current was applied to the other neuron. In all 19 pairs of second-
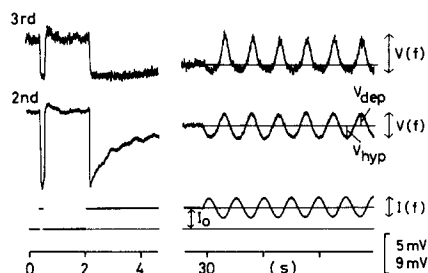

FIGURE 2. Responses of a second- and a third-order neuron evoked either by step-stimuli given in the dark or by a sinusoidally modulated stimulus around a mean illuminance. The sinusoidal stimulus has a modulation depth of 0.7 and a modulation frequency of 2 Hz. Horizontal lines in the records are the steady (DC) potential levels maintained during steady illumination. The lowest trace indicates the stimulus light, monitored by a photodiode. Calibration: 5 mV for the third-order neuron; 9 mV for the second-order neuron.

and third-order neurons, no detectable feedback effects were observed from the second-order neuron when a current was applied to the third-order neuron. Electron-microscopic studies on the cockroach ocellar tract also showed that such connections are rare (Toh and Hara, 1984). Thus, the nonlinear responses of third-order neurons are produced mostly by (feedforward) synaptic transmission from second- to third-order neurons.

In Fig. 3 B, constant current pulses were applied intracellularly to a second-order neuron and the resulting potential changes were measured from a third-order neuron. The measurements were made in the dark. Voltage changes of the second-order neuron during current pulses were estimated from data on the current-voltage relationship obtained by impaling a second-order neuron with two electrodes (Fig. 3 A). The plot in Fig. 3 C shows that the form of the transsynaptic voltage relationship is sigmoidal, typical of chemical synapses (Katz and Miledi, 1967). The semilogarithmic plot (Fig. 3 D) shows that the initial rising part of the curve is an

exponential function of the presynaptic voltage. The line has a form:

$$V_{post} + V_c = V_c \cdot \exp (V_{pre}/k_c) \tag{1}$$

where V_{pre} and V_{post} are the potentials of the second- and third-order neurons, measured from the dark level, respectively. Constant V_c is 1.1 mV, indicating that the third-order neuron receives a steady synaptic input of 1.1 mV from the second-order neuron in the dark. Constant k_c is 2.44 mV, indicating that an e-fold change of the postsynaptic potential is obtained by 2.44 mV changes of the presynaptic potential.

The input/output voltage relationship for synaptic transmission from a second- to
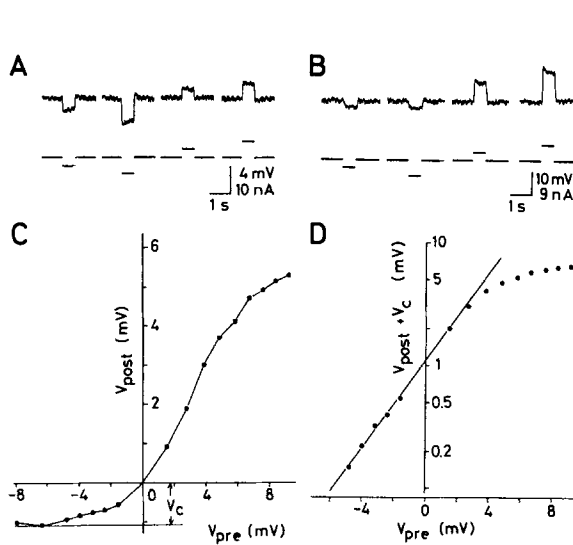

FIGURE 3. (A) Typical records of current/voltage relationship of a second-order neuron, measured by impaling the neuron with two electrodes. (B) Responses of a third-order neuron evoked by current stimuli applied to a second-order neuron. Averaged current-voltage relationships from six second-order neurons were used to estimate presynaptic potential changes during current stimuli for the experiments in B. Actual input resistance of second-order neurons deviates slightly from cell to cell ($\sim \pm 13\%$), thus, the estimated synaptic transfer curve may have slight errors. Lower traces in A and B indicate the magnitude of stimulus current. (C) Input/output voltage relationship of the synaptic transmission. Measurements were made at the steady-state value for 0.5-s current pulses. V_c is the synaptic potential maintained in the dark. V_{pre} and V_{post} are the potentials of the second- and third-order neuron, respectively. The potentials were measured from the dark level, thus, $V_{post} + V_c$ is the actual postsynaptic potential. (D) Semilogarithmic plot of the input/output voltage relationship of the synaptic transmission.

a third-order neuron was further examined using a sinusoidally modulated light (Fig. 4). Data in Fig. 4 are from the same pair of neurons in Figs. 3 B, C, and D (and Figs. 2 and 8 A). When synaptic transmission was evoked by light, voltage changes were elicited in all (four) second-order neurons of an ocellus, and thus, summed synaptic inputs from four second-order neurons were measured from the third-order neuron. In Fig. 4 A, the amplitude of the depolarizing and hyperpolarizing component of the modulatory response of a postsynaptic neuron, measured from the steady (DC) level, was plotted against that of the presynaptic neuron. The data from 0.3 to 10 Hz fit a single positively accelerating curve, thereby indicating that the transmission is time independent (or static) at least over that frequency range. In

Fig. 4 B, the logarithm of the magnitude of the postsynaptic potential is plotted against the presynaptic potential. The postsynaptic potential is represented by $V_{post} + V_l$, where V_l is the synaptic potential maintained during steady illumination, and V_{post} is the potential of the third-order neuron measured from the steady level. As the data show a good fit to a single line, the synaptic transmission has an exponential input/output voltage relationship.

The line has the form:

$$V_{post} + V_l = V_l \cdot \exp (V_{pre}/k_l) \qquad (2)$$

where V_l is 1.3 mV and k_l is 2.54 mV. I conclude that the exponentially rising part of the overall S-shaped input/output voltage relationship is used for transmission of signals for intensity changes around a mean level.
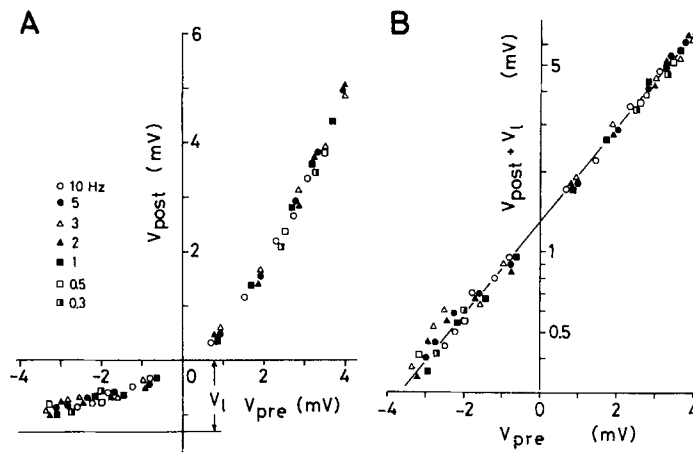

FIGURE 4.   (A) Depolarizing and hyperpolarizing components of responses in a third-order neuron during sinusoidal light modulation, plotted against those of a second-order neuron. The potentials were measured from steady potential levels. V_l is the synaptic potential maintained during steady illumination. Data at a frequency of 0.3–10 Hz are shown. The potentials of second- and third-order neurons were recorded simultaneously. (B) A semilogarithmic plot of the input/output voltage relationship of the synaptic transmission. Data in Figs. 2, 3 B–D, 4, and 8 A are from the same pair of neurons.

Table I summarizes the parameters of (the exponentially rising part of) the synaptic transmission obtained in 19 preparations. In 13 pairs, the synaptic transmission was evoked by light stimulus, and in another six, it was evoked by both current and light stimuli. The light-evoked synaptic transmission, in most cases, fitted well to a single exponential curve over the full range of presynaptic voltage. In six cells, however, light-evoked synaptic transmission exhibited a negative deviation from an exponential curve at the most positive (depolarized) range of presynaptic voltage, where the magnitude of transmission seemed to exceed an initial exponential range of the characteristic curve. V_d in Table I indicates the steady depolarizing potential, maintained in the dark. Other parameters are defined in Eqs. 1 and 2. Table I shows that (a) for both light- and current-evoked synaptic transmission, ~2.5 mV of pre-

TABLE I

Parameters for an Exponential Function Relating Pre- and Postsynaptic Voltages

Stimulus	K_l	K_c	V_l	V_c	V_d	V_d/V_c	N
L and C	2.52 ± 0.14	2.43 ± 0.19	1.31 ± 0.12	0.99 ± 0.08	4.06 ± 0.48	4.10 ± 0.34	6
L	2.48 ± 0.15	—	1.27 ± 0.23	—	3.95 ± 0.47	—	13

Presynaptic voltage changes are evoked either by extrinsic current applied intracellularly to a second-order neuron (C) or by a sinusoidally modulated light applied to the ocellus (L). The parameters are defined in the text (see Eqs. 1 and 2).

synaptic voltage changes produce an e-fold change in the postsynaptic voltage; (b) the sustained synaptic input from a single second-order neuron maintained in the dark, V_c, is roughly one-fourth of that from four second-order neurons, V_d; (c) the postsynaptic membrane potential during steady illumination, V_l, is 1.5–2 mV negative compared with the dark potential, V_d; and (d) the variance of the data among different preparations is minor, thereby suggesting that a number of third-order neurons receive more or less similar synaptic input from second-order neurons. The first two observations, a and b, indicate that light-evoked synaptic transmission can be explained by a simple linear summation of synaptic input from four second-order neurons.

Fig. 5 shows gain (A) and phase (B) portions of the transfer function of the synaptic transmission between second-and third-order neurons. In Fig. 5 A, peak-to-peak amplitude of responses of the postsynaptic neuron, at a fixed amplitude of presynaptic voltage modulation (1, 3, and 5 mV), is plotted against the frequency. In actual
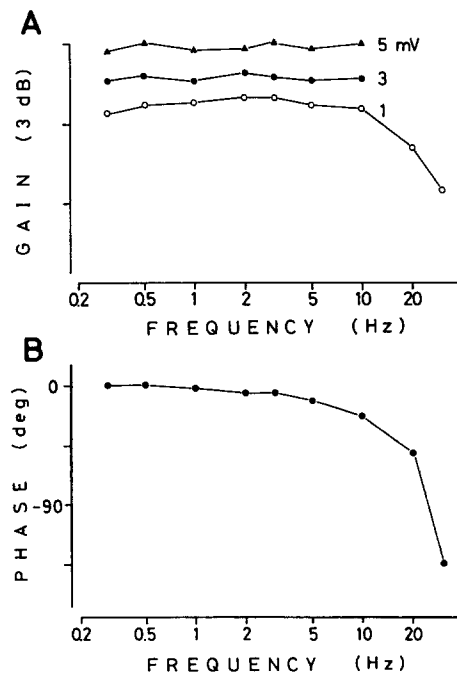

FIGURE 5. Gain (A) and phase (B) portions of transfer function of synaptic transmission between a second- and a third-order neuron. (A) Peak-to-peak amplitudes of postsynaptic voltage modulations at 1, 3, and 5 mV of presynaptic voltage modulation. (B) Phase characteristics of synaptic transmission. Data are at a presynaptic voltage modulation of 1 mV. The phase measured at 3 and 5 mV of presynaptic modulation was identical to that at 1 mV. Responses in the second- and third-order neurons were recorded simultaneously.

experiments, the stimulus frequency was fixed, and the modulation depth of the stimulus was adjusted, for the 1-mV measurement, to produce a 0.5–1 mV and a 1–1.5 mV of peak-to-peak response in a second-order neuron. This sequence was performed over a frequency range of 0.3–30 Hz, and the recorded potentials were averaged for 30–100 cycles. The amplitude of postsynaptic voltage modulation at a 1-mV presynaptic voltage modulation was estimated by linear interpolation between the two measurements. Similar procedures were repeated to obtain a transfer gain at 3 and 5 mV presynaptic voltage modulations, where the gain at frequencies over 10 Hz could not be measured, because of the small presynaptic response at those frequencies. Fig. 5 A shows that synaptic transmission has a low-pass filter characteristic with a cutoff frequency (−3 dB) at 25–30 Hz. Since the graded response of second-order neurons has a low-pass filter property with a cutoff frequency of 12–15 Hz (see Fig. 7 A and Mizunami and Tateda, 1988a), the transmission hardly band-limits the actual presynaptic signals. The gain at 5 mV of presynaptic voltage modulation is ~1 dB larger than that at 3 mV and 2 dB larger than that at 1 mV, i.e., the transfer gain is larger when the presynaptic modulation response is larger. Fig. 5 B shows that there is a phase lag at high frequencies, reflecting the low-pass nature of synaptic transmission.

Observations in Figs. 3–5 show that (a) synapses between second-and third-order neurons operate at an exponentially rising part of the S-shaped characteristic curve; (b) the synapse has low-pass filtering characteristics, which hardly band-limit the presynaptic signal (this will be discussed again in Fig. 7); and (c) the transfer gain is altered depending on the amplitude of responses of the presynaptic neuron. In the next section, responses of second- and third-order neurons to sinusoidally modulated light are compared to discover the manner in which signals of the presynaptic neurons are processed when they are transmitted to the postsynaptic neurons.

Signal Processing between Second- and Third-Order Neurons

The relationship between the amplitude of responses and the depth of sinusoidal light stimulation was examined. The peak-to-peak responses, V_{p-p}, were divided into depolarizing and hyperpolarizing components, V_{dep} and V_{hyp} (see Fig. 2), and V_{dep} and V_{hyp}, were plotted against the depth of modulation (Fig. 6, A and B). Both V_{dep} and V_{hyp} of the second-order neuron exhibit linear increase with an increase in depth of modulation (Fig. 6 A). The depolarizing response of third-order neuron exhibits a positively accelerated increase with the increase in depth of modulation, and the hyperpolarizing response is a saturating function of the depth (Fig. 6 B). This is well explained by the accelerating nonlinearity of the synaptic transmission between second- and third-order neurons (see Fig. 4). As a result, the third-order neuron exhibits rectified responses, i.e., the hyperpolarizing response to light increment is much smaller than the depolarizing response to light decrement, especially when the modulation depth is high. To evaluate the strength of rectification, the ratio of the depolarization to the total peak-to-peak response, V_{dep}/V_{p-p}, was measured. In Fig. 6 C, V_{dep}/V_{p-p} was plotted against the depth of modulation. V_{dep}/V_{p-p} for the second-order neuron is roughly 0.5 (0.5–0.55), thereby confirming that the response is roughly linear. V_{dep}/V_{p-p} for the third-order neuron is relatively small (~0.6) when the depth of modulation is low (0.2) and increases up to 0.8–0.85 with
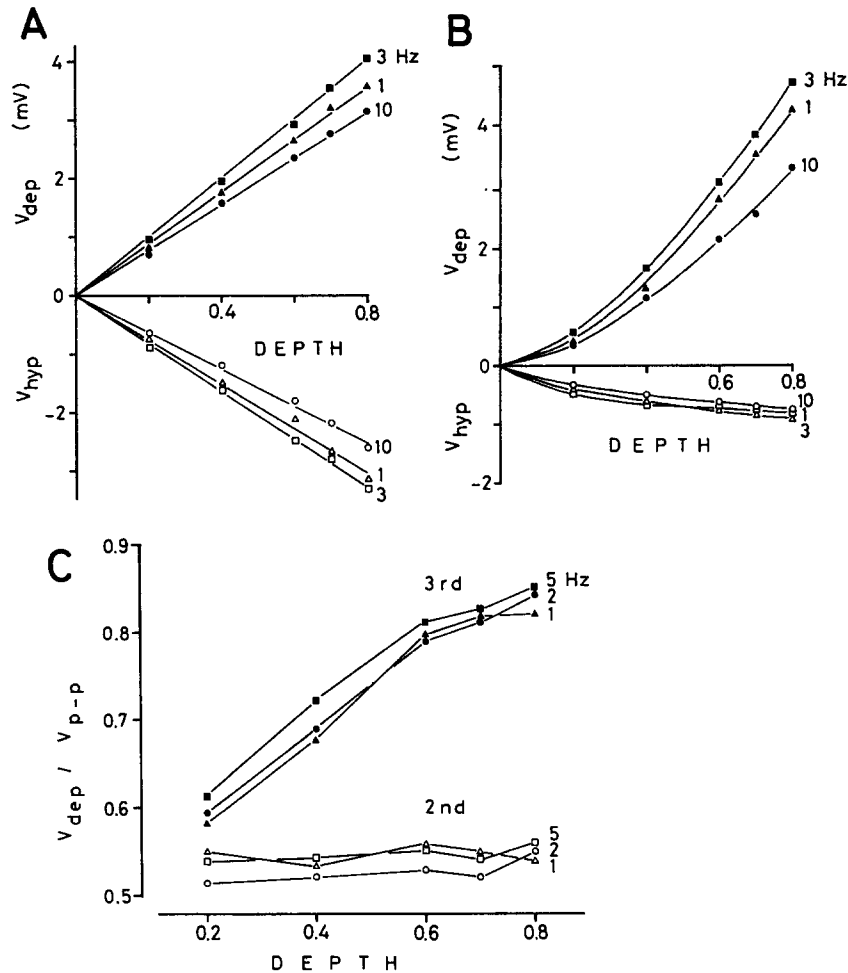
FIGURE 6. (*A* and *B*) Amplitudes of depolarizing, V_{dep}, and hyperpolarizing components, V_{hyp}, of responses of a second- (*A*) and a third-order neuron (*B*) are plotted against the depth of sinusoidally modulated light. $V_{dep} = V_{peak} - V_0$; $V_{hyp} = V_{bottom} - V_0$, where V_0 is the steady (DC) potential levels. V_{hyp} is always negative. $V_{dep} - V_{hyp} = V_{p-p}$, where V_{p-p} is the peak-to-peak response. (*C*) The ratio of the depolarizing component to the total peak-to-peak response, V_{dep}/V_{p-p}, is plotted against the depth of luminance modulation. The ratio, V_{dep}/V_{p-p}, is a measure of the strength of rectification. Data are from a pair of second-and a third-order neurons, recorded simultaneously.

the increase in the depth of modulation; the nonlinearity of the response is larger when the stimulus contrast is higher.

Fig. 6, *A* and *B* also shows that (*a*) the peak-to-peak response of the second-order neuron is a linear function of the stimulus modulation depth, whereas (*b*) the peak-to-peak response of the third-order neuron is a positively accelerated function of the modulation depth.

Fig. 7 shows transfer functions from light input to the resulting response of a

second-order neuron (A and D) and a third-order neuron (B and D). The transfer gains of these neurons are normalized in Fig. 7 C to compare the filtering characteristics. Fig. 7 A shows the peak-to-peak response of a second-order neuron, at a depth of modulation of 0.3 (*open triangles*) and 0.6 (*open circles*). The gain characteristic does not change with the depth. The response of the second-order neuron had a bandpass filter property with optimal frequencies of ~1–5 Hz. The low-pass cutoff frequency was ~12–15 Hz. Fig. 7 B shows the peak-to-peak amplitude of responses of a third-order neuron measured at a depth of 0.3 (*filled triangles*) and 0.6 (*filled*
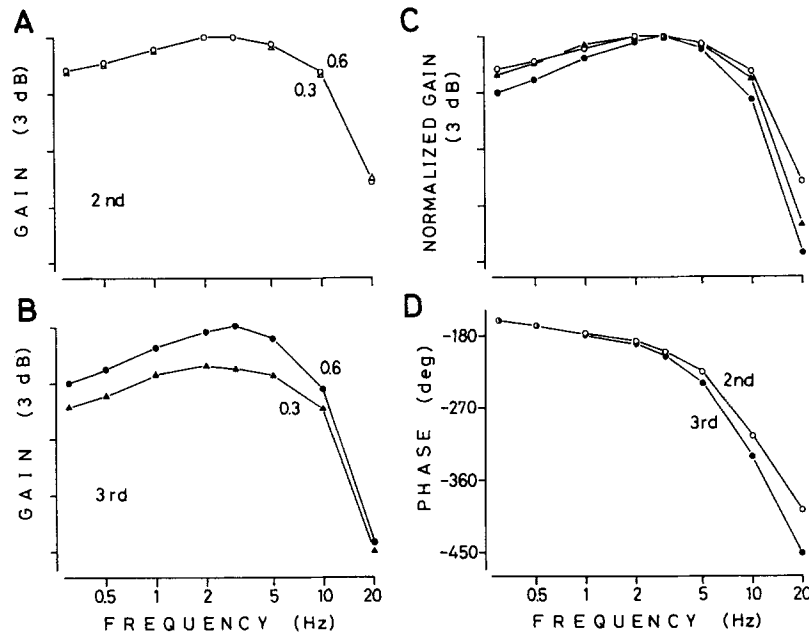

FIGURE 7. The transfer function from light input to the resulting response of a second- and a third-order neuron. Data are from simultaneous recordings of these neurons. (A) Gain characteristics of a second-order neuron. Peak-to-peak amplitudes of responses to a sinusoidal stimulus at a depth of 0.3 (*open triangles*) and 0.6 (*open circles*) are shown. (B) Gain characteristics of a third-order neuron, measured at a depth of 0.3 (*filled triangles*) and 0.6 (*filled circles*). (C) Normalized gain characteristics of a second-order neuron at a depth of 0.6 (*open circles*), and that of a third-order neuron at a depth of 0.3 (*filled triangles*) and 0.6 (*filled circles*). (D) Phase characteristics of a second-(*open circles*) and a third-order neuron (*filled circles*) measured at a depth of 0.6.

circles). When the depth was low (0.3), the filter characteristic of the third-order neuron was similar to that of the second-order neuron (Fig. 7 C), except at 20 Hz where the gain was smaller than that of the second-order neuron due to the low-pass nature of the synaptic transmission (see Fig. 5 A). When the depth was high (0.6), (*a*) the transfer gain for the third-order neuron was larger than that at a depth of 0.3, especially at optimal frequencies (Fig. 7 B), and (*b*) the decay of gain at low and high frequencies was sharper than that at a depth of 0.3 (Fig. 7, B and C). Note that the transfer gain of the synapse between the second- and third-order neurons

was larger when the amplitude of the presynaptic response was larger (see Fig. 5 *A*) and thus the transfer gain of the synapse was largest at optimal frequencies. Fig. 7 *D* shows phase characteristics of a second- and a third-order neuron. Phase characteristics measured at different depths were almost identical. The phase of the response of the third-order neuron lagged compared with that of the second-order neuron at a high frequency range, an event that reflects the low-pass nature of the synaptic transmission (see Fig. 5 *B*).
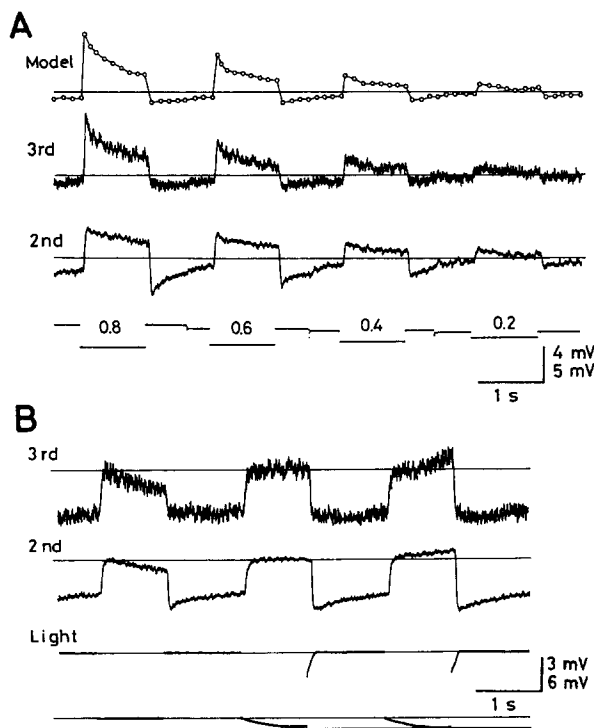

FIGURE 8. (*A*) Responses to square-wave luminance modulation around a mean level in a second-order and a third-order neuron. The stimulus modulation depth was decremented in steps from 0.8 to 0.2. The uppermost trace, marked as *Model*, is made up of the results of predictions of the third-order response, using the static exponential function of Eq. 2. Calibration: 4 mV for the third-order neuron and 5 mV for the second-order neuron. (*B*) At the left, the responses are evoked by a step-stimulus with a depth of 0.7, where an LED was driven by a step-current superimposed on a steady current. At the middle and right traces, a ramp current was superimposed on the step-current, to produce a step-like potential change in the second-order neuron. The lowest trace indicates the stimulus light. Calibration: 3 mV for the third-order neuron and 6 mV for the second-order neuron. *A* and *B* are from different pairs of neurons.

Responses to Step-like Intensity Modulation

The manner in which the nonlinear synaptic transmission affects the response to step-like intensity modulation around a mean illuminance was then investigated. Fig. 8 *A* shows responses elicited by a step-like intensity modulation of a pair of second- and third-order neurons. The response of the second-order neuron to light increment is rougly equal in size and opposite in shape to the response to light decrement, although a small deviation from the symmetry was evident. The depolarizing

(and also hyperpolarizing) response of the second-order neuron exhibited a decay during step stimulus, an event which reflects the high-pass nature of the response to a low-frequency stimulus (see Fig. 7 A). The response of the third-order neuron exhibited an approximate symmetry between depolarizing and hyperpolarizing responses when the depth was low, and where the nonlinearity of the response was small (see Fig. 6 C). With an increase in the depth, (a) the amplitude of the depolarizing response increased over that of the hyperpolarizing response, (b) the waveform of the depolarizing response of the third-order neuron became more transient than that of the second-order neuron, and (c) the waveform of the hyperpolarizing response of the third-order neuron became more sustained than that of the second-order neuron. These observations are essentially similar to those in Fig. 6 B, in which it was concluded that the depolarizing response is an accelerating function of the modulation depth whereas the hyperpolarizing response is a saturating function of the depth. Saturation of hyperpolarizing response of third-order neurons was also prominent for the response to a step of light given in the dark (Fig. 2), where the initial recovery of presynaptic potential accompany little potential changes in the
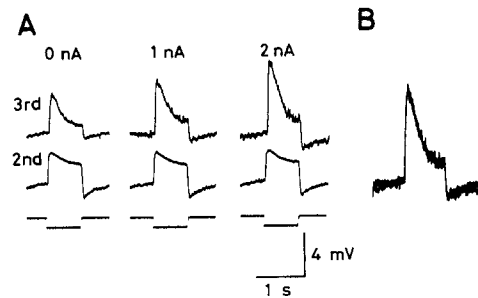

FIGURE 9. The effect of steady (DC) hyperpolarizing current of 1 and 2 nA applied to a third-order neuron A. No potential changes are produced in the second-order neuron during the steady current stimulus. The lowest trace is the stimulus light monitored by a photodiode. In B, the waveforms of responses in A are superimposed. The depth of modulation was 0.6.

postsynaptic neuron, because the transmitter release is almost stopped when presynaptic potential is largely hyperpolarized.

It was rather surprising that the time-course of the step-response appeared transient after synaptic transmission, because the transmission itself was frequency independent, or static (see Fig. 5). To confirm that no high-pass or time-dependent process participated in enhancement of the transient response between second- and third-order neurons, the following measurements were made. First, the voltage response of the second-order neuron in Fig. 8 A was digitized, and the response of the third-order neuron was predicted by a (static) exponential function of Eq. 2. The results of the prediction, marked as *Model* in Fig. 8 A, reproduced fairly well the actual response of the third-order neuron including a rapid decay of depolarizing response during step-stimulus. Second, the time-course of a light stimulus was adjusted to produce a step-like depolarization in the second-order neuron (middle horizontal trace in Fig. 8 B). A step-like depolarization of the second-order neuron produced a nearly step-like depolarization in the third-order neuron, thereby confirming that no high-pass or time-dependent mechanisms participated to sharpen the time-course of the response.

Finally, the possibility that an active membrane property also participated in the observed nonlinear response of third-order neurons was studied. All experiments were done after the application of TTX. There remains, however, the possibility that a TTX-resistant active response participates in the nonlinear response. Note that Fig. 8 *B* (middle horizontal trace) does not fully rule out this possibility, because there might be an active response with a very slow decay time. This possibility was tested with regard to the response to a square-wave intensity modulation, where the nonlinearity of the response is clearly seen as an enhanced transience of the depolarizing response. If voltage-dependent mechanisms did participate in producing the transient depolarizing response, membrane hyperpolarization of a third-order neuron by extrinsic current should decrease the amplitude of the depolarizing response and also decrease the transience of the response. In Fig. 9 *A*, steady hyperpolarizing currents were injected into a third-order neuron during square-wave intensity modulation. With hyperpolarization of the membrane potential, the amplitude of the response increased, because reversal potential of the transmission was found to be positive in relation to the resting potential (Mizunami and Tateda, 1988*b*). In Fig. 9 *B*, waveforms of the responses in Fig. 9 *A* were superimposed. The amplitude-normalized waveforms were practically identical. These observations confirm that nonlinear responses of the third-order neuron mainly reflect nonlinear synaptic inputs, and not active membrane properties.

DISCUSSION

Signal Transmission between Second- and Third-Order Neurons of Cockroach Ocelli

Signal processing at the peripheral level of visual systems is essentially linear for at least a moderate range of change in illumination. The photic signals are, at first, linearly encoded into photoreceptors (*Limulus* lateral eye: Fuortes and Hodgkin, 1964; vertebrate retina: Baylor and Hodgkin, 1974; Chappell et al., 1985; insect compound eye: Pinter, 1972). The linear voltage signals of photoreceptors produce similarly linear responses in second-order neurons (vertebrate retina: Tranchina et al., 1983; Chappell et al., 1985; insect compound eye: French and Järvilehto, 1978; insect ocelli: Mizunami et al., 1986), events that presumably reflect the linear nature of the synaptic transmission between photoreceptors and second-order neurons in a light-adapted state (vertebrate retina: Normann and Perlman, 1979; barnacle ocelli: Hayashi et al., 1985; insect compound eye: Laughlin et al., 1987). The linear signals of second-order neurons are passed to more proximal neurons, where they are processed by nonlinear mechanisms to subtract specific features of photic signals (see below).

I characterized transfer characteristics of the synapse between second- and third-order neurons of cockroach ocelli, and also examined the manner in which presynaptic linear signals are processed during synaptic transmission. In case of the former, I found that (*a*) the synapse operates at an exponentially rising part of an overall sigmoidal characteristic curve, (*b*) the synapse has a low-pass filtering property with a cutoff frequency of 25–30 Hz, which little band-limits the presynaptic signal, and (*c*) summation of the input from four second-order neurons is approximately linear. For the latter, I found that (*a*) the response of the third-order neuron

exhibits half-wave–rectified response: the response to dimming is much larger than that to brightening, (*b*) the amplitude of the response becomes a positively accelerated function of the stimulus contrast, and (*c*) the bandpass filter characteristic of the presynaptic neuron is sharpened, and the transient nature of the step response is enhanced. These signal conversions are well explained by the accelerating nonlinearity of synaptic transmission. I conclude that an essential signal conversion occurs during synaptic transmission from second- to third-order neurons of the cockroach ocelli. This conclusion differs from that obtained in the case of synapses between photoreceptors and second-order neurons so far studied, where the linear signals of presynaptic cells are transmitted to postsynaptic cells without major modification.

Linear and Nonlinear Signal Transmission at First and Second Synapses of Visual Systems

The characteristic curve of synapses between second- and third-order neurons (which I refer to as second synapses) of cockroach ocelli is similar to that at synapses between photoreceptors and second-order neurons (first synapses) reported in other visual systems. These other first synapses have an overall S-shaped characteristic curve (toad retina: Belgum and Copenhagen, 1988; insect compound eye: Laughlin et al., 1987; barnacle ocelli: Hayashi et al., 1985), typical of chemical synapses (Katz and Miledi, 1967), as do second synapses of cockroach ocelli. Sigmoidal characteristics of the chemical synapses have been explained by an exponential relationship between presynaptic voltage and the rate of transmitter release, and a Michaelis-Menten saturation of the effects of transmitters on the postsynaptic membrane (Falk and Fatt, 1972). At the initial rise in the characteristic curve of second synapses of the cockroach ocelli, 2.5 mV of presynaptic potential changes produce *e*-fold changes in postsynaptic potentials. This value is comparable to that measured for first synapses of other visual systems, which are 1.5–1.9 mV for first synapses of fly compound eye (Laughlin et al., 1987), 2 mV for synapses from rod to horizontal cell and those to bipolar cells in toad retina (Belgum and Copenhagen, 1988), and 3.5 mV for synapses from rod to bipolar cells in mudpuppy (Thibos and Werblin, 1978). Other notable similarities in the first and second synapses are that both are graded synapses, i.e., signals are transmitted in the form of graded potentials, and sustained synaptic transmissions are maintained during steady illumination.

Although the input/output relationship of second synapses of cockroach ocelli is similar to that of other first synapses, signal transmission at second synapses of the cockroach ocelli fundamentally differs from that at first synapses: transmission at second synapses is nonlinear and rectifying, whereas it is linear at first synapses. This indicates that first and second synapses operate in different ranges of the characteristic curve, as illustrated in Fig. 10. For linear synaptic transmission, a large amount of transmitter should be tonically released during steady illumination, so that the synapses would operate in the midregion of the S-curve where the transmission is linear. Indeed, Normann and Perlman (1979) concluded that the synapse from cone to horizontal cell of the turtle retina operates in the midregion of the S-curve in a light-adapted condition. A similar conclusion has been obtained for synapses between photoreceptors and second-order neurons of dragonfly ocelli (Simmons, 1982), barnacle ocelli (Hayashi et al., 1985), and fly compound eye (Laughlin et al.,

1987). In the second synapses of cockroach ocelli, the postsynaptic potentials maintained during steady illumination are few, probably because the mean amount of transmitter tonically released during steady illumination is relatively small. Thus, the synapses operate in the positively accelerating part of the S-curve where the transmission is rectifying.

Rectified responses have been noted in some, if not all, third-order neurons of a variety of visual systems. Toyoda (1974) and Miller (1979) proposed that the full-wave–rectified response of ON-OFF amacrine cells of vertebrate retina can be explained if the cells receive half-wave–rectified synaptic input from both ON and OFF bipolar cells. A rectifying process has been proposed to account for responses of ganglion cells of goldfish retina (Spekreijse, 1969) and of cat retina (Hochstein and Shapley, 1976; Enroth-Cugell and Freeman, 1987). Rectified responses have been noted from third-order neurons of locust compound eyes (Osorio, 1987), locust ocelli (Simmons, 1981) and barnacle ocelli (Stuart and Oertel, 1978). It may be that the rectified responses seen in third-order neurons of a variety of visual
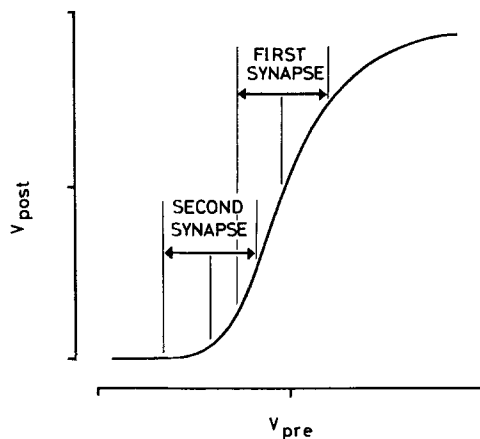

FIGURE 10. Linear and nonlinear signal transmission at graded synapses. The synapse between second- and third-order neurons (second synapse) of cockroach ocelli operates at an initially rising part of S-shaped input/output relationship; thus, the transmission is nonlinear and rectifying. The synapse between photoreceptors and second-order neurons (first synapse) of visual systems presumably operates at a mid-region of the S-curve, since the transmission is essentially linear.

systems are, in general, produced by a nonlinear synaptic transmission. In the catfish retina, Sakai and Naka (1987) concluded that signal transmission from bipolar cells to ganglion cells is linear, whereas transmission from bipolar cells to amacrine cells is nonlinear and full-wave rectifying. This can be explained if bipolar cells tonically release a larger amount of transmitters to ganglion cells than to amacrine cells during steady illumination, as can be deduced from a characteristic curve such as the one in Fig. 10.

Possible Functional Roles of Nonlinearities

The response of third-order ocellar neurons to brightening was much smaller than that to dimming; the response has a rectifying nonlinearity. In barnacle ocelli, Stuart and Oertel (1978) noted that the response to dimming is enhanced as signals are passed from second- to third-order neurons. If the major function of these simple visual systems is to detect dimming rather than brightening, it is reasonable to use a large part of the dynamic range to code signals about dimming. Indeed, the

major role of barnacle ocelli is to respond to dimming, which facilitates a shadow-induced withdrawal of the animal into the shell. In insects, Stange (1981) studied the role of ocelli in visual steering behavior of dragonflies in flight, and concluded that the decrease in illuminance of the ocelli has a strong effect on inducing a steering behavior to avoid nose-diving toward the ground, whereas the increase in illumination is less effective. Furthermore, compression of signals about brightening is economically advantageous. If contrast signals are transmitted by a linear channel, a high level of synaptic activity and neural activity must be maintained during steady illumination.

A similar principle was proposed by Shiller et al. (1986) who studied the monkey visual system. They pointed out that ON and OFF retinal ganglion cells code signals about brightening and dimming, respectively, as an excitatory process. They stated that, by having both ON and OFF channels, signals about both dimming and brightening can be transmitted without maintaining a high rate of spike discharges which require a high rate of metabolic activity. The conversion of linear responses into nonlinear rectified responses (seen between second- and third-order neurons of a variety of visual systems) may reflect a common strategy for an economical contrast coding. This is also a strategy to reduce the response to static (DC) components of the photic input (i.e., to reduce the magnitude of the steady-state response maintained during steady illumination), and to enhance the response to dynamic components: visual systems operate to appreciate changes of illumination, not to appreciate steady levels of illumination.

The time-course of the step response of some, if not all, third-order visual neurons is more transient than that of second-order neurons (barnacle ocelli: Stuart and Oertel, 1978; vertebrate retina: Miller, 1979; insect compound eyes: Osorio, 1987). In cat retina, Victor (1987) showed that the change in response time-course can be modeled by an adaptive high-pass process, i.e., a high-pass filtering process the time-constant of which decreases with an increase in stimulus contrast. In cockroach ocelli, however, changes in the time-course of the step-response are produced simply by a static process, i.e., nonlinear synaptic transmission. Notable differences between an adaptive high-pass process and static nonlinear process are (a) a phase lead is associated with the high-pass process but not with the static nonlinear process and (b) the output of the static nonlinear process depends on the sign of contrast change while that of the adaptive high-pass process does not. Other notable differences between the present observations in cockroach ocelli and the model of Victor (1987) are that second-order neurons of cockroach ocelli have a bandpass filtering property, whereas the distal linear process in the model of Victor (1987) has a low-pass process. The static nonlinear process enhances the transient response only when it follows a high-pass process; the nonlinear synaptic transmission enhances the transient response, because the response of presynaptic neuron has a high-pass filtering property.

A Model for Cockroach Ocellar System

A diagram shown in Fig. 11 summarizes the present results for signal processing in the cockroach ocellar system. Light signals that enter the ocellus are passed through a bandpass linear filter and produce a slow potential response in second-order neu-

rons. The linear filter consists of photoreceptors and synapses between photoreceptors and second-order neurons. Properties of the linear filtering have been discussed in detail (Mizunami et al., 1986). The slow potential signal of the second-order neurons is passed through a static nonlinear filter and produces a graded response in third-order neurons. The static filter has an exponential input/output relationship. A similar linear/nonlinear cascade has been incorporated into models proposed for more advanced visual systems, e.g., catfish retina (Sakai and Naka, 1987) and cat retina (Victor and Shapley, 1979; Enroth-Cugell and Freeman, 1987; Victor, 1987, 1988). This is not surprising since, as has been discussed, signal processing in the cockroach ocellus and that in more advanced visual systems, including the vertebrate retina, share basic and important features.

The model in Fig. 11 does not fully describe the actual signal processing between second- and third-order ocellar neurons, since it is based on observations of graded responses and does not take into account the generation of spike components. The
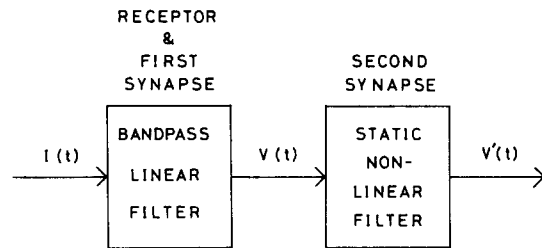

FIGURE 11. (*A*) A model for signal processing in the cockroach ocellar system. Light signals are passed through a bandpass linear filter and then a static nonlinear filter, and produce graded responses in third-order neurons. The linear filter consists of photoreceptors and synapses between photoreceptors and second-order neurons. The nonlinear filter consists of synapses between second- and third-order neurons.

second-order neurons often generate solitary spikes to sudden decrements of illumination (Mizunami et al., 1982). Mizunami and Tateda (1988*a*) observed that some third-order neurons generate solitary spikes to decremental phases of illuminance changes, which correspond to spikes of second-order neurons, whereas other neurons have maintained spike discharges and exhibit a modulation of spike frequency around a mean level, corresponding to graded responses of second-order neurons. A possible interpretation of the system is that the nonlinear transformation combines an urgent event detector (or an alarm system) with an ordinary analogue contrast encoder. To fully understand signal processing in the cockroach ocellar system, further studies on spike discharges of third-order neurons will be necessary.

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