Membrane Conductance Changes Associated with the Response of Motion Sensitive Insect Visual Neurons

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Intracellular recordings and impedance measurements from directionally-selective visual interneurons of the lobula plate of flies show that during motion, transmembrane conductance increases during both depolarizing responses to preferred directions and hyperpolarizing responses to anti-preferred directions. This provides direct evidence that these interneurons are postsynaptic to two separate populations of excitatory and inhibitory input elements.

Non-spiking, directionally-selective, tangential interneurons of the lobula plate in flies (such as HS and VS neurons) respond to visual motion in the preferred direction with graded depolarization of the membrane potential and to visual motion in the anti-preferred direction with graded hyperpolarization of the membrane potential [1]. These neurons have large receptive fields and respond to motion of small objects anywhere in the field [1]. The neurons' dendritic spread in the neuropil corresponds to the retinotopic projection of the physiologically determined receptive field [2, 3], supporting the suggestion [4] that these wide-field cells integrate information from many small-field input neurons. Hausen [5] has suggested that there must be two classes of excitatory and inhibitory inputs because the tangential cells respond with graded potentials of opposite polarity to motion in the preferred and anti-preferred directions.

But suppose that each HS and VS cell merely sums inputs from one type of small-field neuron which also depolarizes in response to motion in the preferred direction and hyperpolarizes in response to motion in the anti-preferred direction. If so, then predictions can be made about changes in membrane conductance of HS and VS cells during their response to different directions of motion. For instance, at rest some transmitter may be continuously released from small-field neurons, corresponding to a certain postsynaptic conductance in HS and VS cells. Depolarization of the presynaptic membrane would cause more transmitter release corresponding to an increased postsynaptic conductance, and hyperpolarization of the presynaptic membrane would reduce transmitter release corresponding to a decreased postsynaptic conductance. According to this prediction, directionally-selective input onto HS and VS cells should be associated with opposite changes in ionic conductance across the cells' membrane when it is depolarized or hyperpolarized. I measured the change in membrane input impedance accompanying the responses of putative HS neurons to motion in opposite directions. Both membrane depolarization and hyperpolarization are each associated with a conductance increase.

The preparation of the lobula plate of the fleshfly *Sarcophaga bullata* is essentially similar to that used for intracellular recording from neurons of the medulla [6, 7]. However, for the experiments reported here the microelectrodes were filled with 3 M potassium acetate to give resistances of 40–200 MΩ before impaling wide-field neurons in the lobula plate. The identity of the recorded cells is inferred from the size and position of the cell's receptive field and from the cell's directional-selectivity compared with recordings associated with dye-filled neurons [1, 3]. The visual stimulus was a square-wave contrast grating (pattern wavelength = 15°) moving at a contrast frequency of 5–7 Hz in a field subtending 50° or more.

The membrane input impedance was measured by injecting positive current pulses (1–4 nA, 250 ms, 2 Hz) through the active bridge of the amplifier, balancing the bridge in the unstimulated cell, and recording the bridge imbalance during visual stimulation (Fig. 1). When the active bridge

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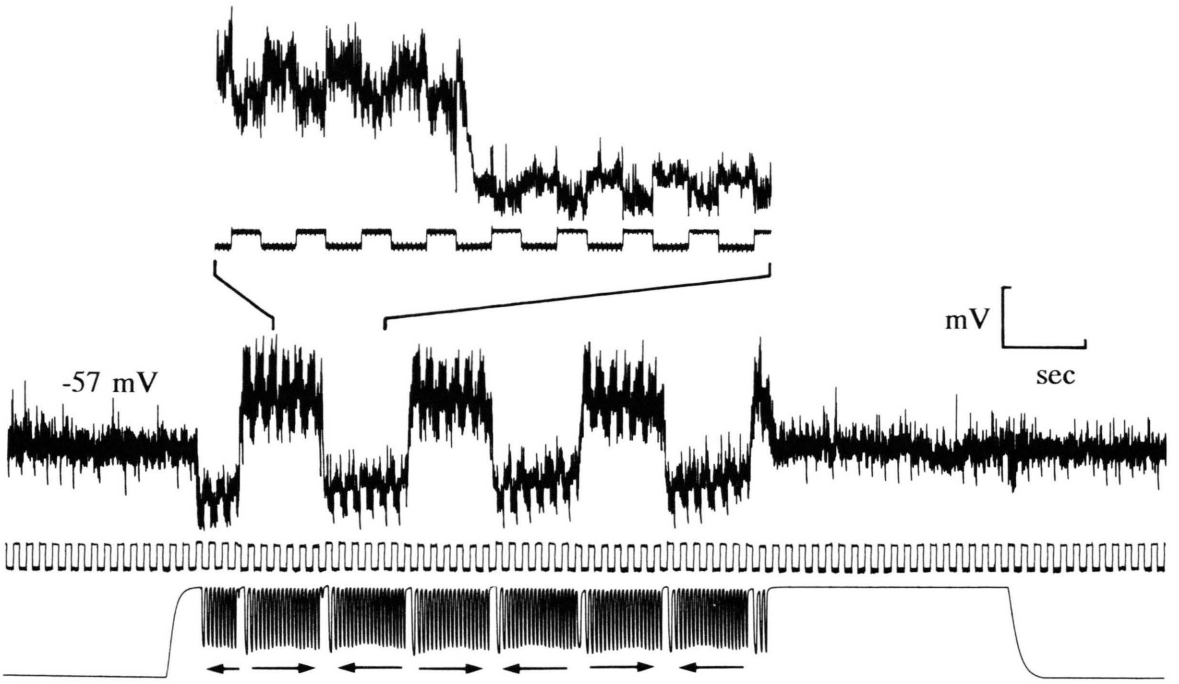

Fig. 1. Intracellular recording from a putative HS(probably E) neuron using the bridge imbalance to determine the change in input impedance during visual stimulation. The traces from bottom to top are: output from a photocell which monitors light ON and grating motion. Arrows indicate the direction of grating motion in front of the right eye: leftward corresponds to back-to-front motion; Output from the current monitor. Upward deflection indicates +4 nA pulses; Recording of the intracellular potential, −57 mV in the dark; and the inset shows the indicated portion of the intracellular recording and current monitor at an expanded time scale. The scale bar is 10 mV for both the figure and inset, and 3 sec or 645 msec for the figure or inset, respectively.

is balanced, it adds a negative voltage which offsets the positive voltage induced by the current pulses. As the membrane conductance increases, the bridge becomes imbalanced, and the current pulses induce a smaller positive voltage which does not offset the negative voltage added by the bridge. Such conductance increases are evident in the expanded record (Fig. 1, inset). At the cessation of stimulation the membrane conductance returns to its previous state and the bridge is again in balance. A decrease in input impedance, the inverse of conductance, was associated with responses to stimulation in both the preferred and anti-preferred directions as measured in a total of 20 separate determinations in 3 putative HS neurons. For the response to motion in the preferred direction the decrease in input impedance was 1.8–2.9 MΩ (mean = 2.1 MΩ) and for motion in the anti-preferred direction the decrease was 0.9–2.4 MΩ (mean = 1.4 MΩ). Experiments with 7 other preparations (5 HS neurons, 1 VS neuron, and injection of negative current into an H-1 neuron) yielded results which could not be quantitatively compared because the magnitude of the current pulses was not recorded. The results, however, were qualitatively similar to those reported above, *i.e.* increase in conductance during responses to motion in both the preferred and anti-preferred directions.

These results are not consistent with the supposition that each wide-field directionally-selective neuron of the lobula plate merely sums small-field directional input from one type of presynaptic neuron. There are two separate, retinotopically arranged ionic mechanisms generating the excitatory response and the GABAergic [8] inhibitory response of the wide-field cells. Two alternative physiological mechanisms have been suggested [9]

which are consistent with the present results. The first is that each point on the wide-field cells may receive inputs from two unidirectional, small-field neurons which have opposite preferred directions. A retinotopic array of small-field columnar neurons, T4 cells, projects from the medulla and single elements have been shown electronmicroscopically to be presynaptic to HS and VS cells [10, 11]. A few directionally-selective responses have been recorded in the medulla electrophysiologically [7, 12, 13] and 2-deoxyglucose activity labelling has revealed motion-sensitivity in the layer of the T4 dendrites [14]. However, T4 cells have not yet been recorded and dye-filled. The second alternative is that directional-selectivity of the postsynaptic cell may arise from the location and timing of non-directional excitatory and inhibitory input signals [15, 16, 17]. Behavioral [18] and electrophysiological [17] experiments with small-field stimuli support a computational model of motion detection in which non-directional small-field channels provide inputs to the wide-field, directional cells. Both alternatives imply that the final sites of bidirectional movement detection [19, 20] must be discrete patches of membrane on the wide-field neurons of the lobula plate, but it remains to be determined whether either of the above alternatives describes the responses of the T4 cells.

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