

Perception of change in depth in the hummingbird hawkmoth *Manduca sexta* (Sphingidae, Lepidoptera)

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Abstract Visual perception of depth change can be mediated monocularly by the apparent size increase of an approaching object, looming. In *Manduca sexta* we recorded intracellularly from cells that detect looming and report both the approach and retreat of an object. The cells compute looming in two fundamentally different ways: class 1 neurons measure the change of perimeter/edge length of the object; class 2 neurons respond to the expansion/contraction flowfield. We created a network model incorporating the anatomical and physiological properties of the class 1 neurons to help us understand the underlying computational principals leading to looming detection.

Introduction

Perception of depth is a key feature in vision. It is used to detect and avoid objects, to pursue and maintain distance from targets. Animals employ different strategies like stereopsis, vergence, occlusion, motion parallax and looming to compute depth (Anderson et al., 1999; Collett 1996; DeAngelis and Newsome, 1999; Ono et al., 1988; Roy et al., 1992; Sun et al. 1998). Most insects, however, have to rely on monocular mechanisms like motion parallax, because their eyes are fixed in the head, have fixed lenses, and are very close together (locust: Collett, 1978; Sobel, 1990a,b; bees: Srinivasan 1993) and looming (locust: Rind and Bramwell. 1996; Gabbiani et al. 1999; sphingids: Wicklein and Strausfeld in press).

Looming, the detection of an apparent size increase in an approaching object is a simple and reliable strategy to measure the change of distance between an observer and an object. On its own it cannot define a 3-D map of a scene, but it can reliably detect changes in depth. In contrast to occlusion and motion parallax, looming does not involve background features or self-motion of the observer, but only requires that the object is different from the background to be detectable. Looming is used by many vertebrates and insects and looming sensitive neurons are found throughout the animal kingdom including sphingids (Wicklein subm.; Wicklein and Strausfeld in press), grasshoppers (Rind, 1990), pigeons (Wang and Frost, 1992), and macaque monkeys (Graziano et al., 1994).

Foraging hawkmoths (*M. sexta*) approach flowers at high velocities, then decelerate to arrive at a distance from the flower that permits insertion of the proboscis. The moth hovers in front of the flower during feeding and maintains its position even while the flower moves, irrespective of movement direction. This is controlled by the visual system, which is superbly adjusted to the nocturnal lifestyle of the moth.

Methods

We utilize standard intracellular recording techniques with subsequent dye filling (Neurobiotin) and processing. Visual stimuli are presented with a software package (VisionWorks) on a fast computer monitor (refresh rate of 160 Hz). The computer models are programmed in MATLAB.

Results

Physiology. Intracellular recordings have identified two classes of wide-field neurons (class 1 and class 2 cells) that respond to looming or receding stimuli. These stimuli can be decomposed into three parameters: change in overall brightness, by virtue of change in area; increase or decrease of object perimeter length; and motion of the object's edge. Expanding or contracting light and dark discs in front of contrasting backgrounds provide a change in object area and change of object perimeter (edge) length and edge motion. Inward and outward rotation of spirals isolates edge motion since this stimulus neither changes its area or its perimeter length. With movement of horizontal and vertical gratings we tested the cells for directionally selective motion sensitivity.

Class 1 cells respond only to an approaching or retreating disc but not to rotating spirals or moving gratings, whereas Class 2 cells respond to all the stimuli. The present results suggest that class 1 and 2 neurons use different mechanisms to detect the approach or retreat of an object. The cardinal parameters are change of perimeter length for class 1 neurons and expansion or contraction visual flowfield for class 2 neurons. We will concentrate on the anatomical and physiological characteristics of the class 1 neurons and use them as background and constraints for a model of detection of changing depth. The cells sustain excitation or inhibition during object expansion/contraction but show no response to spirals (fig 1 B, C and E, F). Stimulation with white discs against dark background results in the same activation as stimulation with dark discs against a light background, demonstrating that changes in overall brightness play no role in the detection of looming or anti-looming. Class 1 cells consist of two cell types, looming neurons (fig. 1 D, E, F) and anti-looming neurons (fig. 1 A, B, C). Looming neurons respond to looming stimuli with an increase in firing rate and to contracting stimuli with a decrease in firing rate (fig. 1 E). Anti-looming neurons respond with an increase in firing rate to contracting stimuli and with a decrease in firing rate to expanding stimuli (fig. 1 B).

Class 1 neurons have wide dendritic arborizations in the innermost stratum of the medulla, the outer stratum of the lobula, and all layers of the lobula plate and terminals in the ipsilateral optic foci of the posterior slope (fig 1 A, D).

Modeling. We created a conceptual model for a "change in edge length" detector (fig. 2). We assume an input layer (retina) that is connected to a retinotopically-organized layer of edge detectors (ED). These in turn give rise to two populations of interneurons that connect to the input regions of the class 1 neuron. As shown in figure 1 class 1 neurons have inputs in the medulla and in the lobula complex (lobula and lobula plate). In our model we assume that for a looming detector, excitatory interneurons connect the edge detector layer with the medulla whereas inhibitory interneurons connect the edge detectors with the lobula complex. To create an anti-looming neuron the polarity of the connections would have to be changed, so that the edge detector layer would have inhibitory connections to the medulla but excitatory connections to the lobula complex. Visual information has to travel through the medulla to arrive in the lobula or lobula plate therefore the connection to the lobula complex is delayed either by cable length or by additional synapses or both and constitutes a delay line. This delay line allows comparisons over time between the level of excitation in the edge detector layer, which corresponds to a change in edge length due to approach or retreat of the object.

We implemented the conceptual model that is based on the class 1 neurons in MATLAB. To assess the validity of the models we test the model and the neurons with

the same stimuli. A valid model has to match the output strength of the neuron over a wide range of visual stimuli and has to be consistent with the known anatomy. The stimuli in the input layer of the model projected to edge detectors whose output is summed spatially over the whole or parts of the input field followed by a time derivative. The output of the model is compared with the instantaneous spike rate of the neuron under the same stimulus condition; zero output of the model represents the resting activity level of the neuron, a positive output an increased firing activity and a negative output an inhibition (reduced firing activity) relative to the ongoing or resting activity level. The model showed strong transient initial responses and sustained steady state responses that were positive to looming and negative to anti-looming stimuli, no responses were elicited by moving single bars, edges or gratings (fig 3). When stimulated with objects of different sizes the initial response scales with the edge length but the steady state response is not changed. The only parameter tested so far that has an influence on the level of the steady state response is the rate of expansion/contraction: the response level is higher for faster expansion/contraction. No change is observed for edges, bars or stripe patterns that move with different velocities.

Discussion

Comparing the output of the model simulation with the recordings from the class 1 neurons, we conclude that the model captures many of the essential properties of the physiological data gathered from class 1 neurons. Both the cells and the model show sustained responses that are ongoing as long as the stimulus is presented. Neither the cells nor the model respond to moving gratings and the response to expanding and contracting objects are at least qualitatively the same. But the model shows a very pronounced phasic initial response that is not present or at least very much reduced in the neurons. This could be due to either temporal or/and spatial averaging in the network preceding the neuron or the neuron itself. The model predicts that the class 1 cells should be insensitive to the size of an expanding/contracting object, the spatial frequency and velocity of movement of stripe patterns, but be sensitive to the velocity of expansion or contraction. Invariance of response in respect to object size would allow these cells to detect change of edge length equally well for different object sizes and in turn allow the animal to hover in front of and forage on flowers of different corolla sizes. The model predicts that the response of the neuron would code for the rate of expansion/contraction, which in turn would translate into the approach or retreat speed of the flower. In a behavioral context this means that a flower that is moved rapidly toward or away from the moth by a wind gust would elicit a larger response by the cell than a slow moving flower. To avoid collision with a fast approaching flower the moth will have to change its motor output faster and will have to put more force into the movement. The increased neuronal response might decrease the delay of the motor response and increase its strength.

The model predictions regarding different object sizes and rates of expansion/contraction are being tested in electrophysiology experiments in the class 1 cells by measuring tuning curves for these parameters.

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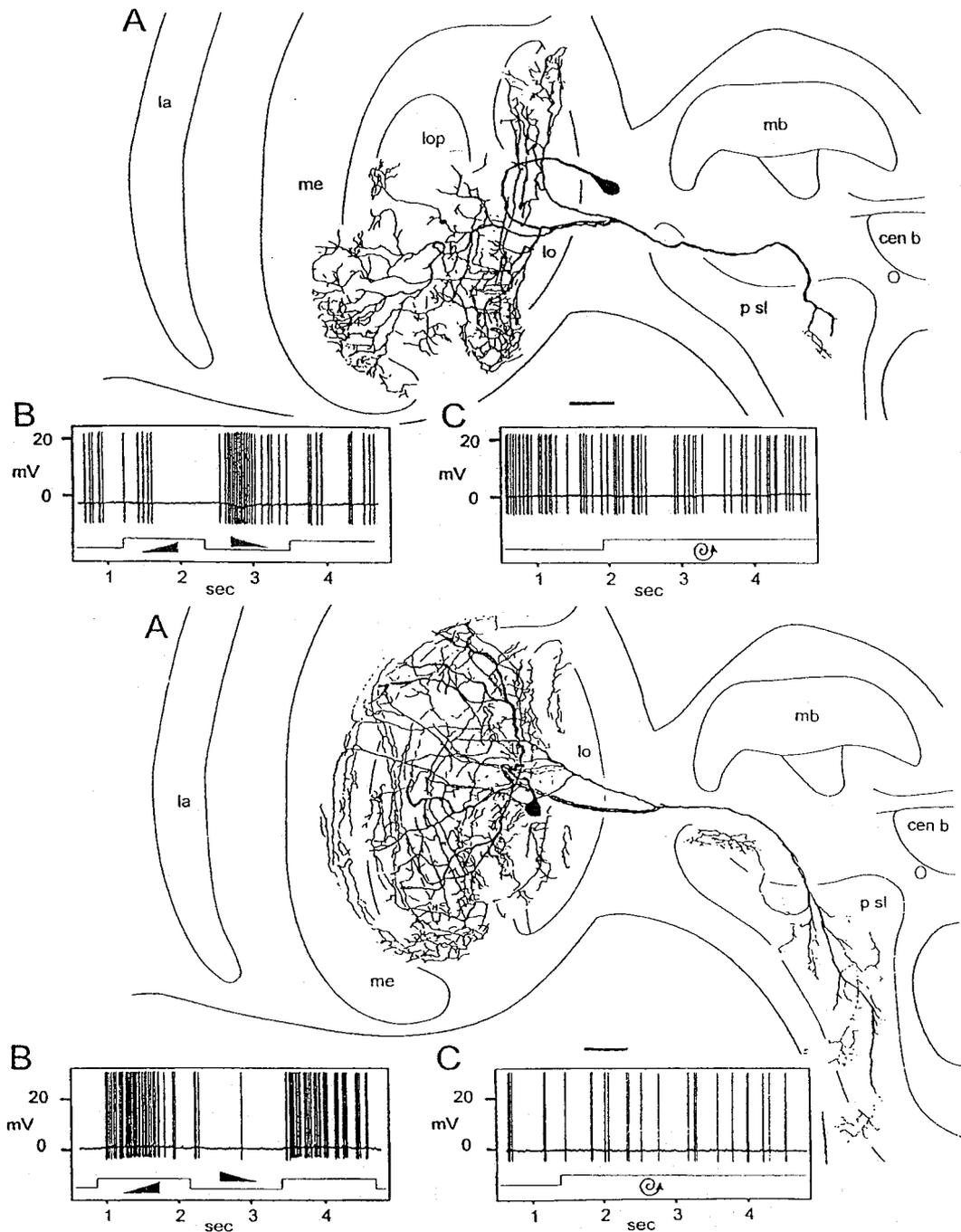


Fig. 1 Responses and reconstruction of a class 1 anti-looming cell (A, B, C) and a class 1 looming cell (D, E, F). Class 1 looming cells show strict tuning to disc expansion, inhibition to disc contraction, and no responses to spiral rotation as shown in the spike trains. The symbols used are: a wedge pointing to the left indicates expansion; a wedge pointing to the right indicates contraction; a spiral with an outward pointing arrow head indicates an outward rotating spiral; a spiral with an inward pointing arrowhead indicates an inwardly rotating spiral. Two examples for the anatomical structure of class 1 cells are shown. The processes are arranged across parts of the medulla's retinotopic mosaic (the lower part of the medulla in the cell in fig. 1 A and the central part in the cell in fig. 1B). Processes are distributed across the whole lobula and lobula plate, which is apparent in both cells. The terminals arborize in neuropils connecting the brain with the subesophageal ganglion. A small collateral from the axon provides a field of blebbed processes within the optic peduncle (fig. 1 B), suggesting their relationship with axons of other visual interneurons. Scale bar = 100 μ m.

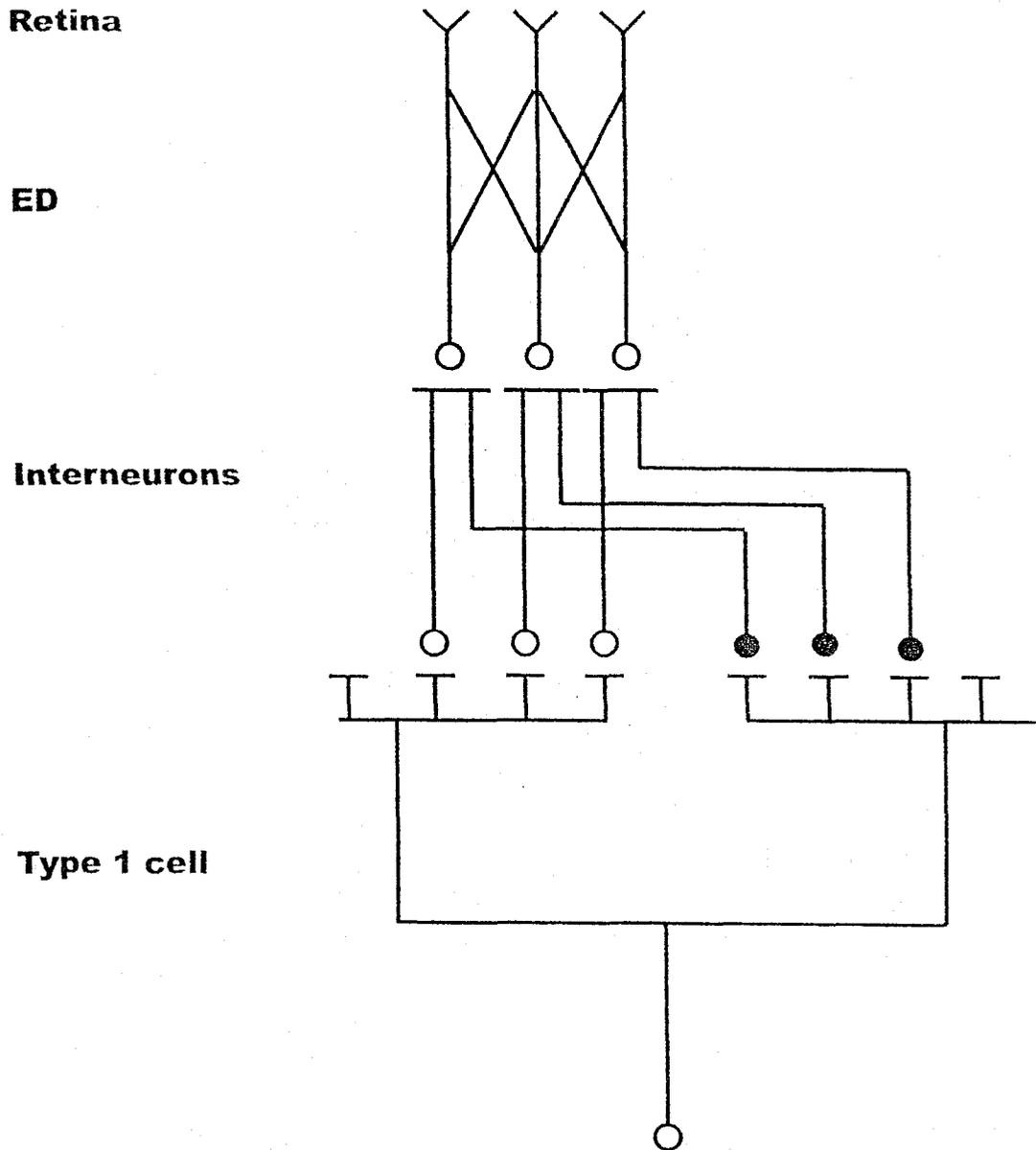


Fig 2 The model consists of an input layer (retina) with retinotopic projections to a layer of edge detectors(ED). The output of each edge detector is relayed by interneurons to the inputs of the type 1 neuron and are spatially summed. Each edge detector connects to two interneurons one connects directly to the type 1 cell, the other has a delay. In the case of a type 1 cell we propose a direct connection to the medulla (left input area), and a delayed connection to the lobula and lobula plate (right input area), which would involve longer cable, an additional synapse or both. For a looming detector the direct connection to the type 1 neuron would be excitatory (open circles), whereas the delayed connection would be inhibitory (filled circles). An expanding object is going to excite an increasing amount of edge detectors over time and that excitation is going to be transmitted through the excitatory and inhibitory interneurons to the type 1 cell. Due to the different delays in the excitatory and inhibitory pathway, the information in the inhibitory pathway at time $t(1)$ will coincide with the excitatory information of time $t(1+n)$ at the inputs of the type 1 neuron. This will result in a sustained increase in excitation in the type 1 neuron for an expanding object. A contracting object will lead to a decrease of the number of edge detectors that are excited and therefore the inhibitory delayed input to the type 1 neuron will always be bigger than the direct excitatory input, thus leading to a decrease in excitation in the type 1 cell. The open circles indicate an excitatory synapse; the full circles indicate an inhibitory synapse.

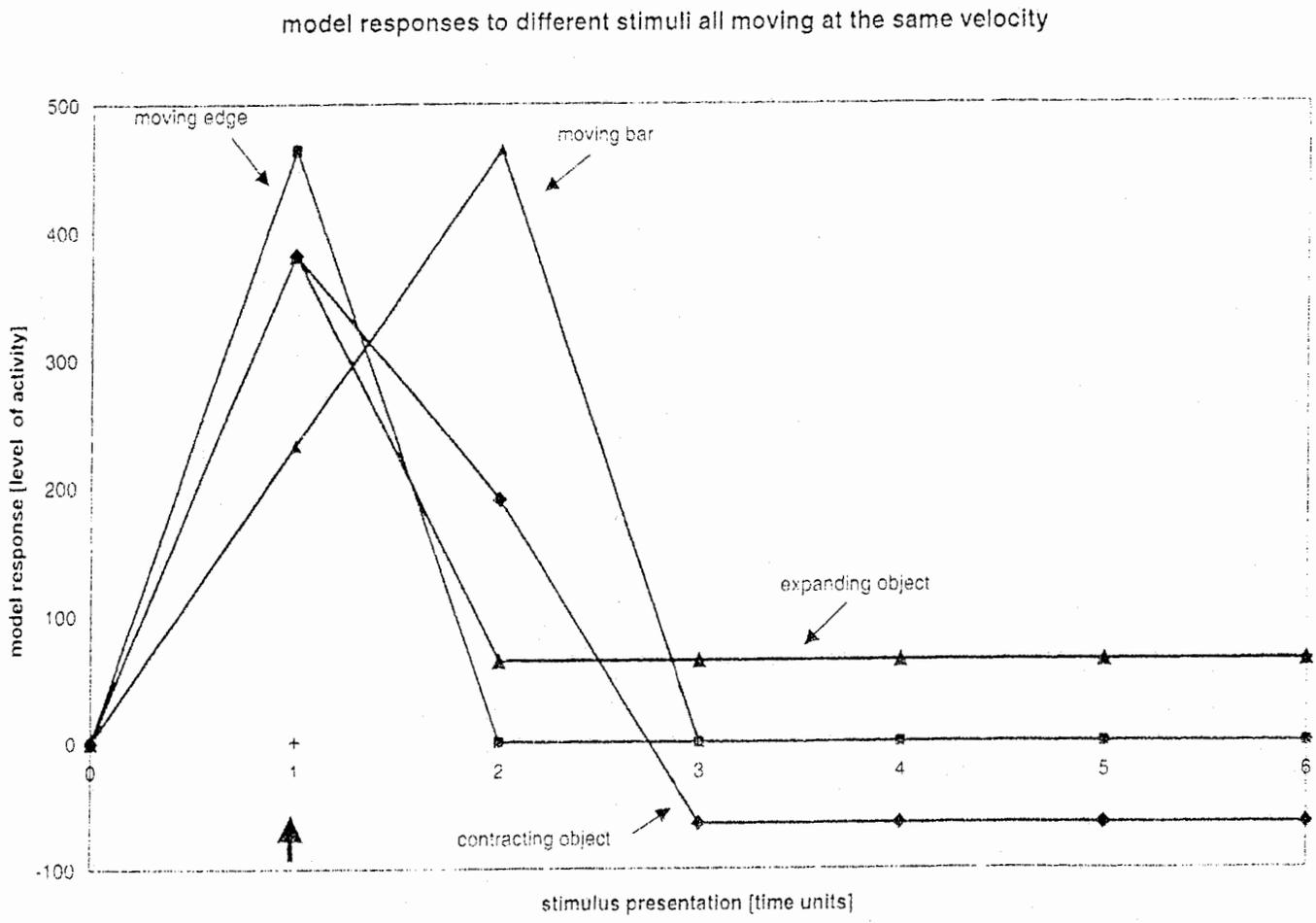


Fig 3 Simulation results for a “looming neuron” for different stimuli. The responses can be separated into an initial response when the stimulus is presented and a steady state response. The initial responses are excitations for all the stimuli that decline to the sustained levels. A positive model output corresponds to an excitation of the neuron a negative model output corresponds to an inhibition; zero model output corresponds to resting frequency. The model shows no steady state response to moving edges (dashed line circles) or bars (dotted line squares). An expanding object (solid line triangles) leads to a positive model response, a contracting object (solid line crosses) to a negative model response.

