



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

M. Wicklein^{a,*}, T.J. Sejnowski^{a, b}

^aComputational Neurobiology Laboratory, Howard Hughes Medical Institute, Salk Institute, 10010 N. Torrey Pines Rd, La Jolla CA 92037, USA

^bDepartment of Biology, University of California, San Diego, La Jolla, CA 92093, USA

Abstract

Visual perception of depth change can be mediated monocularly by looming the apparent size increase of an approaching object. In *Manduca sexta* we recorded intracellularly from cells that detect both 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 expansion/contraction flowfields. We created a network model incorporating anatomical and physiological properties of class 1 neurons to understand the underlying computational principles for looming detection. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Looming; Monocular depth perception; Visual interneurons; Network model; Intracellular recordings

1. Introduction

Depth perception is a key feature in vision. It is used to detect and avoid objects, and to maintain distance from targets. Animals employ different strategies like stereopsis, vergence, occlusion, motion parallax and looming; [1–6] to compute depth. Most insects, however, have to rely on monocular mechanisms like motion parallax [7–10] and looming [11–13], because their eyes are fixed in the head, have fixed lenses, and are very close together.

* Corresponding author. Computational Neurobiology Laboratory, Howard Hughes Medical Institute, Salk Institute, 10010 N. Torrey Pines Rd, La Jolla CA 92037, USA.

E-mail address: martina@salk.edu (M. Wicklein).

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 sensitive neurons are found throughout the animal kingdom including sphingids [13], grasshoppers [14], pigeons [15], and macaque monkeys [16].

2. Methods

We used standard intracellular recording techniques with subsequent dye filling (Neurobiotin) and processing [13], visual stimuli were generated by a software package (VisionWorks) and presented on a fast computer monitor (refresh rate of 160 Hz). The models were simulated with custom software using MATLAB.

3. Results

3.1. Physiology and anatomy in Sphingids

Visual stimuli representing looming or receding objects can be characterized by four parameters: change in luminance; increase or decrease of area; increase or decrease of object perimeter length; and motion of the object's perimeter or edge. Intracellular recordings reveal visual interneurons in the optic lobes of *M. sexta* that are selectively activated by some of these parameters.

Wicklein and Strausfeld (2000) identified two classes of wide-field neurons that respond selectively to looming and receding stimuli. The two types of looming sensitive neurons in *M. sexta* use different mechanisms to detect the approach or retreat of an object. They proposed that change of perimeter length may be detected by class 1 neurons and expansion or contraction visual flowfields by class 2 neurons. In both cell classes changes in luminance have no role in the detection of looming or anti-looming and both classes are further subdivided into neurons that are excited by image expansion (looming cells) or by image contraction (anti-looming cells).

3.2. Modeling

We created a conceptual model for a “change in edge length” detector and implemented this model of class 1 neurons in MATLAB. To assess the validity of the model we tested both the model and the neurons with the same stimuli; the model should match the output strength of the neuron over a wide range of visual stimuli and be consistent with the known anatomy. The stimuli were presented to the input layer of the model, which projects to edge detectors whose output was summed spatially over the whole or parts of the input field, followed by a time derivative. We

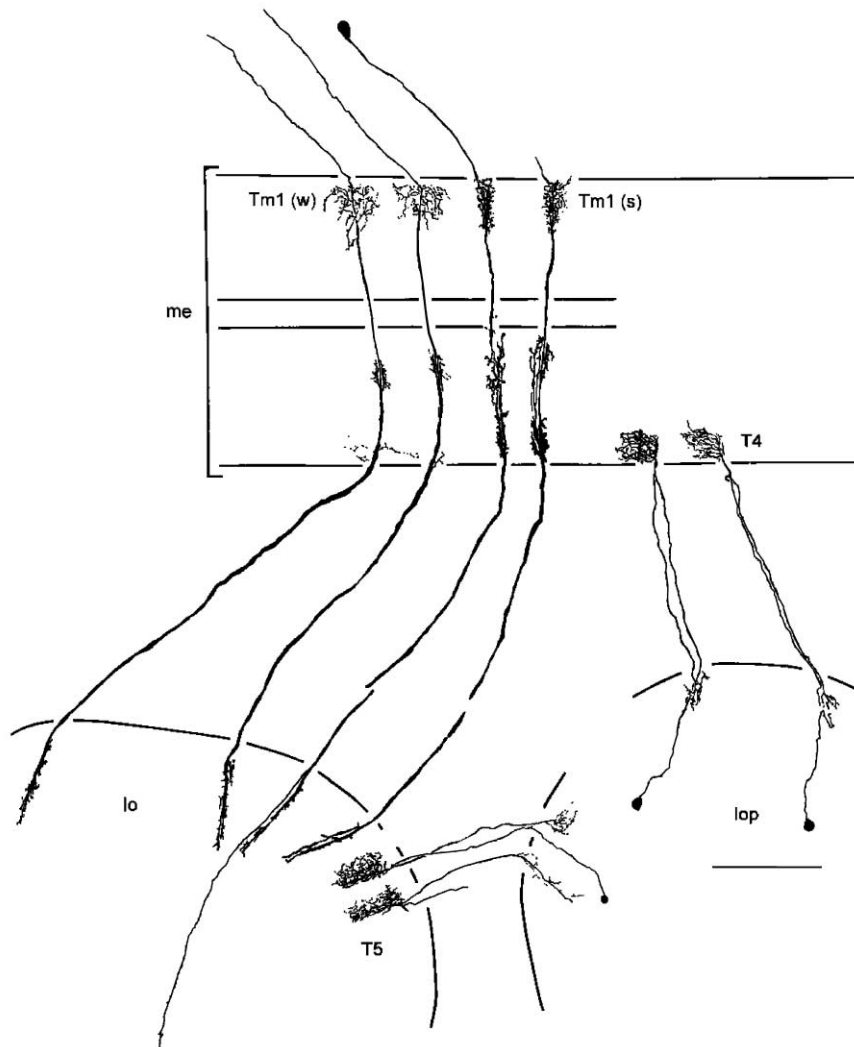


Fig. 1. Reconstructions of Golgi impregnated small-field neurons in the optic lobes of *M. sexta* that are presumed to be in the looming network. lo: lobula, lop: lobula plate, me: medulla, Tm1(w): wide transmedulla cells, Tm1(s): small transmedulla cells, T4, T5: bushy T-cells. The bar indicates 100 μm . Modified after Wicklein and Strausfeld [13].

used available anatomical data, Golgi studies on small field cells and reconstructions of type 1 cells [13], to further constrain the model, so that it includes most of the anatomical properties of the looming-sensitive cell and the network underlying the class 1 neurons. Fig. 1 shows reconstructed small field cells in the visual system of *M. sexta* that are possible inputs to class 1 looming sensitive neurons. In Fig. 2, optical neuropiles are illustrated with their main layers and small field cells with their input

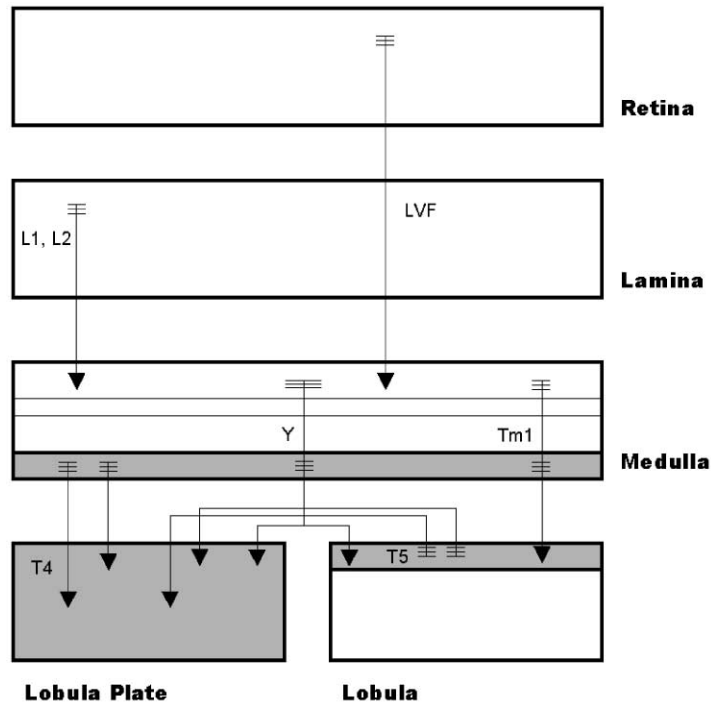


Fig. 2. Schematic diagram of the arrangement of small field elements in relation to the input areas of a type 1 neuron (gray areas). The small field cells proposed as inputs to type 1 cells are: Tm1, T4, T5 and Y cells. Tm1 cells have arborizations in the innermost medulla layer and provide input to T5 neurons, which project to the lobula plate. Y cells have arborizations in the innermost medulla layer and provide inputs to both the lobula and the lobula plate. T4 cells connect the innermost medulla layer with the lobula plate.

and output regions which we relate to input areas of class 1 looming sensitive cells (gray areas) as described in Wicklein and Strausfeld (2000). Class 1 looming sensitive neurons have inputs in the innermost medulla layer, the outermost lobula layer and throughout the lobula plate. There are several small field neuron types that could serve as inputs to these layers. Considering the architecture and known direction of information flow through the visual system of insects [17] we can predict in which order the visual neuropiles receive information. Information is passed from the retina to the lamina and the outermost medulla layers through short and long visual fibers.

Transmedulla cells (Tm-cells) then convey the information from the outer medulla to the inner medulla, from there the information flows into the lobula and the lobula plate via T4, Tm1 or Y cells. Considering the architecture of the type 1 cells it can be deduced that the visual information arrives first in the arborizations that reside in the outermost medulla layer and that there should be a considerable delay before the same information arrives in the arborizations in the lobula and lobula plate. The delay in information flow could be due to additional cable length required to reach the

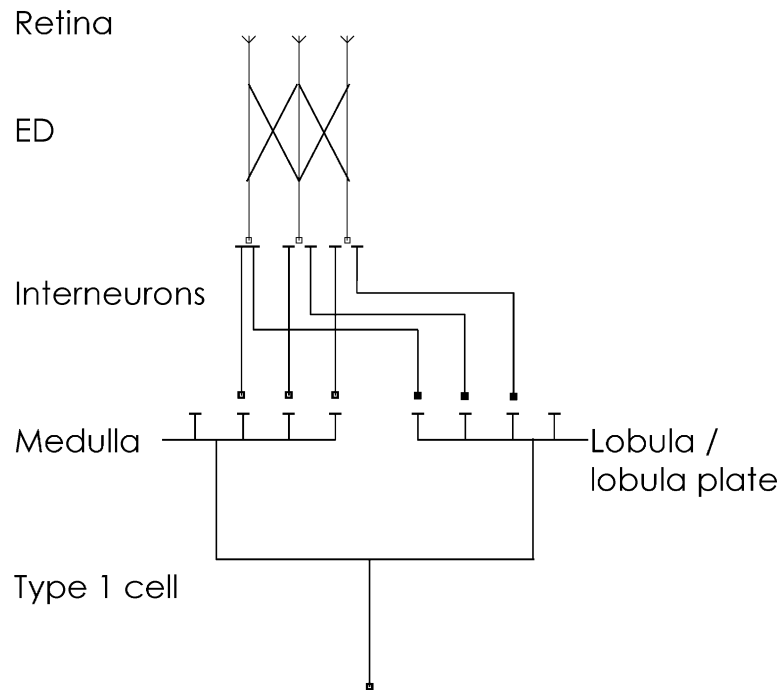


Fig. 3. The model consists of an input layer (retina), with retinotopic projections to a layer of edge detectors. The output of each edge detector (ED) is relayed by interneurons retinotopically to the inputs of the type 1 neurons, where they are spatially summed. Each edge detector connects to two interneurons that relay to the type 1 cell. We propose that the connection to the medulla is direct; the connection to the lobula and lobula plate is delayed by longer cable or an additional synapse. For a looming detector the direct connection to the type 1 neuron would be excitatory, whereas the delayed connection would be inhibitory. An expanding object excites edge detectors and that excitation is transmitted through both 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 $t = 1$ coincides with the excitatory information of time $t = 1 + n$ at the inputs of the type 1 neuron. This results in a sustained increase in excitation in the type 1 neuron for an expanding object. A contracting object on the other hand will lead to a decrease of number of edge detectors and therefore the inhibitory delayed input to the type 1 neuron will always be greater than the direct excitatory input, thus leading to a decrease in excitation in the type 1 cell. The open symbol indicates an excitatory synapse; the full circle indicates an inhibitory synapse.

lobula and lobula plate (Tm1-cells), or an additional synapse that is required (T4, T5 and Y cells) or both. Fig. 3 shows the model for an edge length detector network including these considerations. We assumed an input area with an edge detector layer that is connected to two types of interneurons per column, which in turn project onto the type 1 looming neuron. In the model excitatory connections were made to the arborizations residing in the medulla, and inhibitory connections to the lobula and lobula plate arborizations to looming cells. For an anti-looming cell connections to the medulla should be inhibitory and connections to the lobula and lobula plate

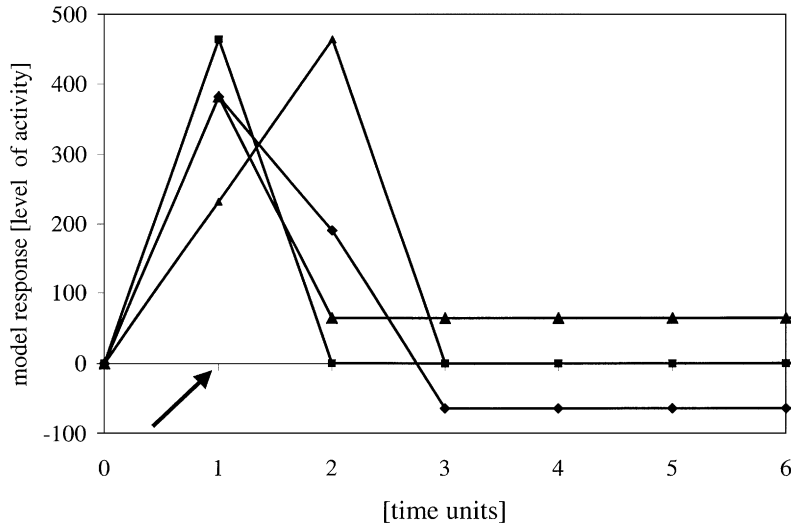


Fig. 4. Results from a model simulation of a “looming neuron” plotted for different stimuli. The responses show an initial response when the stimulus is presented and a steady state response. The initial responses are excitating for all the stimuli, which decline to the sustained levels. The model shows no steady state response to moving edges (squares) or bars (circles). An expanding object (triangles) leads to a positive model response, a contracting object (diamonds) to a negative model response. The arrow indicates the start of the stimulation.

excitatory. The time delay introduced by the architecture of the class 1 neurons itself would provide the time delay necessary for the comparison of edge length over time and therefore the detection of a growing edge (expanding object) versus shrinking edge (receding object).

The numerical output of the model is compared to the instantaneous spike frequency of the neuron under the same stimulus condition corrected by the resting spike frequency. Hence, a zero output represents the resting activity level of the neuron; a positive output an increased firing activity, a negative output a reduced firing activity relative to the resting activity level.

Comparing the output of the model simulation with the recordings from class 1 neurons (Fig. 4), the model captures many of the essential properties of the physiological data. 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. 4). However, the model showed a highly pronounced initial response that is not present or at least is 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. For objects of different size the initial responses scaled with edge length but steady-state responses did not change. The only parameter that influenced the level of steady-state responses was the rate of expansion/contraction: the responses grow with expansion/

contraction speed. No change is observed for edges, bars or gratings moving with different velocities.

4. Discussion

The model predicts that class 1 cells should be insensitive to the size of expanding/contracting objects, the spatial frequency and velocity of moving gratings, but be sensitive to the velocity of expansion or contraction. Invariance of response with respect to object size would allow the cells to detect change of edge length equally well for different object sizes and thus allow the animal to hover in front of and forage on flowers of different corolla sizes. The model predicts that the neuronal response 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, a flower that is moved rapidly toward or away from the moth by a wind gust would elicit a larger response than a slowly moving flower. To avoid collisions with fast approaching flowers the moth would have to change its motor output faster and put more force into the movement. The increased neuronal response might decrease the delay of the motor response and increase its strength. These predictions regarding different object sizes, stimulus velocities and rates of expansion/contraction are being tested in experiments in both cell types by measuring tuning curves for these parameters.

Due to the fixed delays between the medulla input and the lobula/lobula plate inputs the model should be sensitive to the spatio/temporal properties of the stimulus similar to motion detector models like the Reichardt detector (see Ref. [18]). Further experiments will further constrain important model parameters such as the time delay.

Acknowledgements

This work was supported by the NSF and The Howard Hughes Medical Institute.

References

- [1] G.J. Anderson, J. Cisneros, P. Atchley, A. Saidpour, Speed, size and edge-rate information for detection of collision events, *J. Exp. Psychol. Hum. Perform.* 25 (1) (1999) 256–269.
- [2] T.S. Collett, Vision: simple stereopsis, *Curr. Biol.* 6 (11) (1996) 1392–1395.
- [3] G.C. De Angelis, Newsome WT Organisation of disparity-selective neurons in macaque area MT, *J. Neurosci.* 19 (4) (1999) 1398–1415.
- [4] H. Ono, B.J. Rogers, M. Ohmi, M.E. Ono, Dynamic occlusion and motion parallax in depth perception, *Perception* 17 (2) (1988) 255–266.
- [5] J.P. Roy, H. Komatsu, R.H. Wurtz, Disparity sensitivity of neurons in monkey extrastriate area MST, *J. Neurosci.* 12 (7) (1992) 2478–2492.
- [6] H. Sun, B.J. Frost, Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons, *Nature Neurosci.* 1 (4) (1998) 296–303.
- [7] T.S. Collett, Peering—a locust behavior pattern for obtaining motion parallax information, *J. Exp. Biol.* 76 (1978) 237–241.

- [8] E.C. Sobel, Depth perception by motion parallax and paradoxical parallax in the locust, *Naturwissenschaften* 77 (5) (1990a) 241–243.
- [9] E.C. Sobel, The locust's use of motion parallax to measure distance, *J. Comp. Physiol.* 167 (5) (1990b) 579–588.
- [10] M.V. Srinivasan, How insects infer range from visual motion, *Rev. Oculomot. Rev.* 5 (1993) 139–156.
- [11] F.C. Rind, D.I. Bramwell, Neural network based on the input organization of an identified neuron signaling impending collision, *J. Neurophysiol.* 75 (1996) 967–985.
- [12] F. Gabbiani, H.G. Krapp, G. Laurent, Computation of object approach by a widefield, motion-sensitive neuron, *J. Neurosci.* 19 (3) (1999) 1122–1141.
- [13] M. Wicklein, N.J. Strausfeld, The organization and significance of neurons detecting change of depth in the hawk moth *Manduca sexta*, *J. Comp. Neurol.* 424(2) (2000) 356–76.
- [14] F.C. Rind, Identification of directionally selective motion-detecting neurones in the locust lobula and their synaptic connections with an identified descending neuron, *J. Exp. Biol.* 149 (1990) 21–43.
- [15] Y.C. Wang, B.J. Frost, Time to collision is signaled by neurons in the nucleus rotundus of pigeons, *Nature* 356 (6366) (1992) 236–238.
- [16] M.S.A. Graziano, R.A. Andersen, R.J. Snowden, Tuning of MST neurons to spiral motions, *J. Neurosci.* 14 (1) (1994) 54–67.
- [17] N.J. Strausfeld, *Atlas of an Insect Brain*, Springer, Berlin, Heidelberg, New York, 1976.
- [18] M. Egelhaaf, A. Borst, Movement detection in arthropods, in: F.A. Miles, J. Wallman (Eds.), *Visual Motion and its Role in Stabilization of Gaze*, Elsevier, Amsterdam, 1993, pp. 55–77.



Martina Wicklein earned her Ph.D. in neuroscience at the University of Tübingen, Germany, and after a postdoc with Nick Strausfeld at the ARL-DN in Tucson, AZ, she is now a research associate in the CNL at The Salk Institute for Biological Studies in La Jolla, CA. Her main goal is to understand how animals collect and compute visual information that allows them to orient and behave in complex three-dimensional visual environments. Her particular interest lies in features which are extracted by the visual system and how they are used to compute a behavioral response of the animal to stimuli occurring in its natural environment. She is using electrophysiology, computational modeling, behavioral analysis, and histochemistry to analyze her model system, the moth *Manduca sexta*.



Terrence Sejnowski is an Investigator with the Howard Hughes Medical Institute and a Professor at The Salk Institute for Biological Studies where he directs the Computational Neurobiology Laboratory. He is also Professor of Biology at the University of California, San Diego, where he is Director of the Institute for Neural Computation. Dr. Sejnowski received a B.S. in physics from the Case-Western Reserve University, an M.A. in physics from Princeton University, and a Ph.D. in physics from Princeton University in 1978. In 1988, Dr. Sejnowski founded Neural Computation, published by the MIT Press. He is also the President of the Neural Information Processing Systems Foundation. The long-range goal of Dr. Sejnowski's research is to build linking principles from brain to behavior using computational models. This goal is being pursued with a combination of theoretical and experimental approaches at several levels of investigation ranging from the biophysical level to the systems level.