The optic lobe of the fly is one of the prominent model systems for the neural mechanism of the motion detection. How a fly who lives under various visual situations of the nature processes the information from at most a few thousands of ommatidia in their neural circuit for the detection of moving objects is not exactly clear though many computational models of the fly optic lobe as a moving objects detector were suggested. Here we attempted to elucidate the mechanisms of ON-edge motion detection by a simulation approach based on the TEM connectome of Drosophila. Our simulation model of the optic lobe with the NEURON simulator that covers the full scale of ommatidia, reproduced the characteristics of the receptor neurons, lamina monopolar neurons, and T4 cells in the lobula. The contribution of each neuron can be estimated by changing synaptic connection strengths in the simulation and measuring the response to the motion stimulus. Those show the paradelle pathway provide motion detection in the fly optic lobe has more robustness and is more sophisticated than a simple combination of HR and BL systems.

Keywords: neural circuit, vision, fly, motion detector, biophysical modeling

1. Introduction

Living animals have many superior adaptive abilities that have been shaped by millions of years of evolution in complex natural environments changing at different timescales. A major portion of adaptability is implemented in the brain, the highest-level sensory information processing and behavior control center. However, it is quite difficult to investigate whole functional circuits of neurons in large brains like those of humans that have billions of neurons. Here we focus on the superior visual information processing ability of small insect brains to detect moving objects, especially making use of the genetically accessible model system Drosophila melanogaster, a fruit fly. Drosophila has a small, submillimeter scale brain that consists of only a few hundreds of thousands of neurons, but is capable of visually-controlled turning flights with a rotational speed of 5300°/s [1]. It has the ability of autonomous takeoff, hovering, collision avoidance, and tracking of stationary and nonstationary obstacles [2]. These abilities are based on visual perception of luminance changes in the visual field resulting from object motion or egomotion.

The basic algorithm for detecting visual motion from the insects’ assembly of ommatidia, the compound eyes, has been referred to as the elementary motion detector (EMD) and has been studied as an attractive model system for visual motion detection for a long time. In the 1950s, a phenomenological model for motion perception was developed by Hassenstein and Reichardt to account for optomotor responses of the weevil Chlorophanus [3]. In Hassenstein–Reichardt (HR) model, the signals from two neighboring ommatidia were multiplied after one of them had been delayed effectively amounting to calculating the autocorrelation of a luminance change moving over the array of photoreceptors. When a motion stimulus is given to the HR model system with a time difference equal to the time delay of the element, the downstream response is maximally enhanced. This is considered as a “preferred direction enhancement” that strongly responds to stimuli in a specific direction. This model has been frequently implemented in robot vision using customized devices for simple collision avoidance, for example, improving the behavior of autonomous agents [4, 5].
model. This model is based on the finding in rabbit reti-
nal ganglion cells that the response to the null direction 
(the direction opposite to the preferred direction) was 
significantly reduced [6, 7] in the 1960s. In the BL model, 
the motion-sensitive neuron has an excitatory input and 
a delayed inhibitory input that have spatially separate re-
ceptive fields. This model uses the mechanism of “null 
direction suppression.” In these two EMD models, the 
detection of visual motion based on transitions from dark 
to light (ON-edge) and from light to dark (OFF-edge) re-
quires different logic.

For a long time, our understanding of the actual physi-
oclogical mechanism in the insect brain underlining their 
motion detection ability was limited to abstract, phe-
nomenological models of EMDs. However, developments 
of systematic experimental neuroscience technique that 
includes genetic engineering, neuroinformatics, and elec-
tron and optical microscopy in the 21st century gave us 
some lines of cues on the real optic lobe circuit in the 
Drosophila.

It was revealed that separate circuits for ON- and 
OFF-edge detection are present in the fly optic lobe [8, 9] 
via genetic manipulation and electrophysiological record-
ing in output neurons of the optic lobe at 2010. In addi-
tion, it has been shown that neurons detecting ON-edges 
(T4 cells of the medulla) and those detecting OFF-edges 
(T5 cells of the lobula) converge in four direction selec-
tive regions in the lobula plate (an area specialized in vi-
sual motion processing) and can respond to a wide range 
of frequencies (0.1 Hz to 10.0 Hz) with a response max-
imum around 1 Hz [10] based on the transgenic fly lines 
and two photon Ca$^{2+}$ imaging on the T4/T5 terminal on 
the lobula plate. The existence of both circuits, HR sys-
tem and BL system, in the optic lobe of Drosophila is also 
suggested by anatomical, electron microscope based stud-
ies by Takemura and his colleagues in their works [11, 12] 
about ON-pathway and physiological studies [13, 14] in 
ON- and OFF-pathways. In the columnar medulla neu-
rons, prominent directional selectivity for luminance in-
formation was only found in T4 and T5 cells (ON- and 
OFF-edge motion detection, respectively). Therefore, 
some computational feedforward neural circuits models 
that consist of HR and BL, ON- and OFF-pathways that 
are integrated at T4 or T5 cells to produce a directional se-
lectivity were suggested [15–17]. Some feedforward ab-
stract models that account for EMD function in the optic 
lobe were suggested. They assumed a square-wave signal
from the visual receptors should be divided into low and 
high pass filtered channels and finally integrated at the T4
synapses [14, 15, 18].

However, the reported Transmission Electron Micro-
scope (TEM) connectome of the optic lobe in [11, 12] is 
more complex than a simple feedforward model. It 
includes some feedback neurons, and some neurons’ roles 
are not classified into ON- or OFF-pathways or HR/BL 
pathways. Therefore, we now try to construct a simula-
tion model of the optic lobe faithfully according to the 
connectome. We focus on the ON-pathway in this study 
because a detailed connectome of this pathway is avail-
able [11, 19, a] and the activities of most ON-pathway 
neurons have been recorded [20]. We compare between 
our simulation results and the existing knowledge of the 
properties of each cell and clarify the role of each cell in 
motion detection.

2. Method

In this study, we used the NEURON simulator 
ver. 7.6 [21, b] with Python 2.7.16 [c]. We implemented 
awrapper program in python for our simulation for in-
creasing readability of the simulation code and simplifying 
the administration of parameter files. The simulation is 
completely controlled through NEURON’s Python in-
terface after all required files that describe the individual 
on-channel dynamics (mod format files) are compiled for 
NEURON. For our usage, the input data format of the cell 
information such as transmitter types, location, network, 
physiological properties, and simulation settings was ad-
ministrated in json format parameter files. Our simula-
tion wrapper is provided on Github [d]. In this program, 
parallel processing can be performed by Message Passing 
Interface (MPI). The simulation was carried out on a PC 
cluster computer with 2 × Intel Xeon E5-2680 v4 in our 
lab or on the K computer (RIKEN, Kobe, Japan). Usu-
ally, our simulations that include 1600 neurons were per-
formed with 24 or more processes. However, 6400 neu-
rons were included for the simulation detecting moving 
object in the wide visual field (Fig. 9 in Section 3.3).

2.1. Constructing an ON-Pathway Circuit Model of 
the Fly Optic Lobe Based on the Connectome

In Drosophila, visual information is transferred from 
the retina, the photoreceptor cells, to the optic lobe 
consisting of lamina, medulla, lobula, and lobula plate 
(Fig. 1(a)) [22].

We tried to construct a neural circuit simulation model 
based on the one column connectome by [19] that can re-
produce directional selectivity of T4 a-d cells. Photore-
ceptors are modeled according to [23]. Most of the neu-
rons in the optic lobe of the Drosophila brain except pro-
jection neurons to the central brain and feedback neurons 
from central brain are supposed to operate as non-spiking 
neurons producing only graded potentials [24–27]. Thus, 
we did not include voltage sensitive sodium channels in 
our simulation model.

Lamina cells were modeled using information 
from [28]. The Morris–Lecar model [29], which has been 
widely used for modeling non-spiking neurons 
(that have no sodium spikes), was adapted to simulate 
medulla neurons. Details of the cell models are described 
in Appendix A. In our simulation model, we included 
the following cell types: L1, L2, L3, L4, L5 as the 
lamina neurons, Mi1, Tm3, Mi4, Mi9, C2, C3 as the 
medulla neurons, and T4a, T4b, T4e, T4d in each layer of 
T4-cells as the major components involved in ON-edge 
motion detection, as described in [11, 19]. We assumed
Connectome Based Simulation of Fly’s ON-Edge Motion Detector

(a) Drosophila’s visual system. Retina with ommatidia containing the photoreceptors and optic lobe containing lamina, medulla, and lobula complex composed of lobula and lobula plate. Lamina, medulla, and lobula have a columnar structure that corresponds to the ommatidia.

(b) Conceptual network connections to one T4 cell in our ON-edge detecting simulation. All neurons except T4 are columnar neurons that have their axon in a range of a column and have connections only to neighboring columns.

Fig. 1. Schematic representation of Drosophila’s visual system for ON-edge detection.

(a) Model structure of visual field in our simulation. Left: 10 × 10 column structure. The black column (5, 5) was mainly observed. Right: Wider scale column structure (20 × 20) was used for a circular object stimulus.

(b) Connections to a T4a cell corresponding to the center of a compound eye observed by electron microscope reported in [18]. The number shows the number of the synaptic connections from the cell at each coulomb. Connections can be listed like (Tm3 → T4a) is [3, 17, 9, 2, 0, 6, 3, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0] (see Table 1).

Fig. 2. Coordinate system in the visual field and columns.

A single receptor cell (R-cell) per column for simplicity and omitted the neural superposition mechanism of the fly retina/lamina system. We assumed synaptic weights between the described neurons to be proportional to the number of the synaptic boutons between the neurons observed by electron microscopy [19].

The network connection schema is shown in Fig. 1(b). Regarding the network of the cells, we used 100 (10 × 10) or 400 (20 × 20) columns in a hexagonal lattice (Fig. 2(a)), imitating the structure of the compound eye. The structure of a column is shown in Fig. 2(a). Each column contains R, L1, L2, L3, L4, L5, Tm3, Mi1, Mi4, Mi9, C2, C3, T4-cells respectively. Some types of cells have synaptic connections with adjacent columns. Especially the important connections of T4 as described in [19] are shown in Fig. 2(b). In this study we omitted the wide field neurons in the optic lobe and feedback neurons from central brain areas that affect both ON- and OFF-pathways. Projection neurons to the central brain were also excluded. Visual stimulation to R-cells is applied as a simulated current injection (see Appendix B).

2.2. Graded Synapse Model

All synapses in our current simulation were implemented as graded synapses. We implemented a model of graded synaptic transmission using the following equation.

\[ i(t) = g(t - \tau)(V_{post}(t) - V_{re}), \]

\[ g(t) = \begin{cases} \max(g_{sat}, k \times N_{syn}(V_{pre}(t) - V_{th})) & \text{if } V_{pre}(t) > V_{th}, \\ 0 & \text{otherwise.} \end{cases} \]

Here, \( i(t) \) is the transmembrane current of the post-synaptic cell at time \( t \), \( g \) is the synaptic conductance in
the postsynaptic cell, $V_{\text{post}}(t)$ and $V_{\text{pre}}(t)$ are membrane potentials of the post- and pre-synaptic neuron, respectively, $\tau$ is the time delay of the synapse, $N_{\text{syn}}$ is the number of synapses between the two neurons, $g_{\text{sat}}$ is the upper limit of conductance, set to 1, $V_{th}$ is the threshold membrane potential for transmitter release of the presynaptic neuron, and $V_{re}$ is the reversal potential of the postsynaptic current.

The number of synapses $N_{\text{syn}}$ was set with reference to the ultrastructural information of [11, 19, 30], shown in Table 1. $V_{re}$ was determined by the excitatory and inhibitory properties given by [31]. The time delay $\tau$ is set according to [17]. The remaining parameters were determined by simulation with the criterion to prevent saturation of activity in the network (Table 2). First, $k$ was set to $k=0.01$ as almost of synaptic strengths will not be saturated. $V_{th}$ was set at first in R-cells. Second, in L1–L2 and at the third medulla cells it was set as about 5 mV lower than the minimum value of steady state membrane potential of the presynaptic cell. At last, minimum change of $V_{th}$ was executed as whole cells activities are not saturated. All cell parameters used in our simulations are described in Table 2.

All cell parameters used in our simulations are described in Table 2.

3. Results

3.1. Simulated Moving Grating Visual Stimulus

For our first model, we stimulated visual motion stimulation by a 100% contrast moving grating using square-wave current injection into R-cells and investigated the resulting responses of the simulated neurons in the network. The responses of Mi1, Tm3, Mi9, Mi4, C3, and T4 cell (T4a) to R-cell activation at temporal frequencies of 0.1, 1.0, 10.0 Hz, which correspond to 3, 30, 300°/s on the visual field we set (Fig. 2(b)), for the square waves, are shown in Fig. 3. In this result the activities shown in T4 from the corresponding ommatidium are carried through Mi4 that was a nearly direct copy of R and Tm3 that have been modified by many neurons activities. Mi9 and Mi4 send delayed information though inhibitory synapses to T4 cells of adjacent columns from opposite sides. Mi4 enhances the signals of a moving ON-edge in the preferred direction because the phase of activities in Mi4 is reversed with respect to R. Similarly, Mi9 plays a role in null direction suppression.

When the temporal frequency was 1.0 Hz, the maximum and minimum membrane potential of T4a was $-41.5$ mV and $-51.1$ mV, and the difference of the maximum membrane potential was $9.6$ mV. The maximum membrane potential of each T4-cell (T4a, T4b, T4c, T4d), when the simulated grating stimulus was given at an orientation from 0° to 330° with 30° interval, is shown in Fig. 4. Each simulated T4 cell displayed direction selectivity (T4a: 180°, T4b: 0°, T4c: 90°, T4d: 270°) qualitatively similar to the experimental data of [10]. Real T4 cells have the capability to respond to a wide range of temporal frequencies of 0.1–10.0 Hz, and have a peak

<table>
<thead>
<tr>
<th>Pre cell</th>
<th>Post cell</th>
<th>$N_{\text{syn}}$</th>
<th>$\tau$ [msec]</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>L1</td>
<td>200</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>L2</td>
<td>200</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>L3</td>
<td>60</td>
<td>1</td>
</tr>
<tr>
<td>L1</td>
<td>L5</td>
<td>[90]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tm3</td>
<td>[120, 50, 50, 50, 50, 50]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi4</td>
<td>[5]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi9</td>
<td>[3]</td>
<td>1</td>
</tr>
<tr>
<td>L2</td>
<td>L4</td>
<td>[5, 0, 0, 3, 5, 0]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>L5</td>
<td>[48]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Mi4</td>
<td>[5]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi9</td>
<td>[65]</td>
<td>1</td>
</tr>
<tr>
<td>L3</td>
<td>Mi1</td>
<td>[28]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi4</td>
<td>[1]</td>
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<td></td>
<td>Mi9</td>
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<td>C3</td>
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<td>L4</td>
<td>[4, 2, 3, 0, 0, 0, 1]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>L5</td>
<td>[2, 2, 5, 0, 0, 0, 0]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>L1</td>
<td>[32]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>L2</td>
<td>[7]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>L5</td>
<td>[2]</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tm3</td>
<td>[30]</td>
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</tr>
<tr>
<td></td>
<td>Mi1</td>
<td>[44]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi4</td>
<td>[21, 3, 4, 2, 8, 0]</td>
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</tr>
<tr>
<td></td>
<td>Mi9</td>
<td>[65]</td>
<td>1</td>
</tr>
<tr>
<td>L5</td>
<td>Mi1</td>
<td>[28]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi4</td>
<td>[1]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Mi9</td>
<td>[65]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>C3</td>
<td>[7]</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 2. Synaptic parameters of the simulation.

Table 1. Synaptic parameters of the simulation.
Table 2. Cell parameters of the simulation.

<table>
<thead>
<tr>
<th>Cell</th>
<th>Vr [mV]</th>
<th>Vth [mV]</th>
<th>C [F]</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>−80</td>
<td>−53</td>
<td>9.42 × 10⁻¹³</td>
</tr>
<tr>
<td>L1</td>
<td>−80</td>
<td>−52</td>
<td>6.28 × 10⁻¹³</td>
</tr>
<tr>
<td>L2</td>
<td>−20</td>
<td>−55</td>
<td>6.28 × 10⁻¹³</td>
</tr>
<tr>
<td>L3</td>
<td>−20</td>
<td>−40</td>
<td>6.28 × 10⁻¹³</td>
</tr>
<tr>
<td>L4</td>
<td>−20</td>
<td>−35</td>
<td>6.28 × 10⁻¹³</td>
</tr>
<tr>
<td>L5</td>
<td>−20</td>
<td>−42</td>
<td>6.28 × 10⁻¹³</td>
</tr>
<tr>
<td>Tm3</td>
<td>−20</td>
<td>−83</td>
<td>3.14 × 10⁻¹³</td>
</tr>
<tr>
<td>Mi1</td>
<td>−20</td>
<td>−76</td>
<td>3.14 × 10⁻¹³</td>
</tr>
<tr>
<td>Mi4</td>
<td>−80</td>
<td>−65</td>
<td>4.71 × 10⁻¹⁷</td>
</tr>
<tr>
<td>Mi9</td>
<td>−80</td>
<td>−72</td>
<td>4.71 × 10⁻¹⁷</td>
</tr>
<tr>
<td>C2</td>
<td>−80</td>
<td>−75</td>
<td>3.14 × 10⁻¹³</td>
</tr>
<tr>
<td>C3</td>
<td>−80</td>
<td>−81</td>
<td>2.51 × 10⁻¹⁷</td>
</tr>
<tr>
<td>T4</td>
<td>−20</td>
<td>−55</td>
<td>3.14 × 10⁻¹³</td>
</tr>
</tbody>
</table>

Fig. 3. The response of Mi1, Tm3, Mi9, Mi4, C3, and T4a, for square wave current stimulation of the photoreceptors to simulate a moving grating.

response at 1.0 Hz [10, 18, 20]. Here, we confirmed the temporal frequency characteristics using our simulation model. The maximum potential difference of a T4-cell (T4a), when stimuli of 0.1, 0.3, 0.6, 1.0, 3.0, 6.0, 10.0 Hz temporal frequency are applied, is shown in Fig. 5. In our simulation, a decrease in response was observed on the higher frequency side, but the response was maintained on the lower frequency side. Thus, our simulation could reproduce the capability to respond to a wide range of frequencies.

3.2. Introducing Sensory Adaptation in the Receptor Cells

We could mimic the frequency characteristics of T4 cells at higher frequencies over 1 Hz in the previous section. However, in the frequency range below 1 Hz, physiological data show a stronger response decrease in T4 [10, 20] or other optic lobe neurons [18, 32].

Our effort through modifications of the parameters in our synapse and cell models could not reproduce this re-
response reduction at low frequencies. However, the low response in the low frequency domain is nearly identical to slowly decreasing responses in time domain, which is equivalent to adaptation that is a commonly observed phenomenon in single neurons and networks [33–35]. The motion at low frequency, that is slow movement, takes a longer time to detect, so it may be conceivable that adaptation is present to reduce the energy cost per unit time. The time course of adaptation is often referred to as optimal for energy saving under the limitation to preserve input information in the neural circuit [36].

We introduced the decreasing activity as sensory adaptation in R-cells. A decreasing current in the fast phase is injected according to physiologically observed sensory adaptation in fly photoreceptors [23] as described in Appendix B.

In the modified simulation introducing receptor currents with adaptation, the directional selectivity and the temporal frequency characteristics were investigated. For the input stimulus, the square wave was adjusted to include adaptation for the plateaus corresponding to light-on conditions. The response of the cells in the network is shown in Fig. 6. By adopting adaptation for R-cells, the response of R-cell was changed as compared with Fig. 3. The response on the low frequency side was large, and the response of T4-cell at 0.1 Hz was decreased. This is because the attenuation due to the adaptation is faster than the time difference of the signals input from the adjacent columns at low frequencies, so that the preferred direction enhancement is reduced. On the other hand, at 10 Hz, the response of R-cell remained almost unchanged. Therefore, it is considered that the response on the high frequency side was not significantly affected.

Each T4-cell (T4a, T4b, T4c, T4d) showed directional tuning slightly changed from conditions without sensory adaptation (Fig. 7). The frequency characteristic of responses to stimuli of the temporal frequencies from 0.1 to 10.0 Hz was also investigated. Responses of the T4-cell (T4a) are shown in Fig. 8. The decrease of responses both at lower frequencies and at higher frequencies in the improved simulation shows that adaptive activities in this circuit are important to mimic qualitatively temporal frequency characteristics of T4-cells.

Comparing the responses of the cells (Mi1, Tm3, Mi9, Mi4, C3) which are connected to T4-cells, it was found that when the sensory adaptation was introduced, the responses of Mi4 and Mi9 decreased at 10.0 Hz. At 0.1 and 1 Hz, decreased activities of Mi4, Mi9, and C3 were also observed. At 0.1 Hz, the response of Tm3 decreased.

3.3. Edge Detection of a Moving Object

We evaluated the representation of a bright moving circular object in the visual field by four T4 cells in the improved simulation. The result is shown in Fig. 9. We could confirm that the leading edge of a moving object can be detected well by this circuit. Of course, it is the most important information when animals want to interact with moving objects.

When the circular object is moved, the column where the cell potential exceeds the threshold ($V_{th}$: −45 mV for R, −42.5 mV for T4a, −44.7 mV for T4b, −43.2 mV for T4c, −44.5 mV for T4d) was displayed in white. T4 cells responded strongly at the edge of the movement of the circular object. This indicates that the simulation model detected a change from dark to light. When the circular object was moved upward, T4a and T4c responded, and when it was moved downward, T4a and T4d responded. Since the response of T4a is strong, it appears in both, but the simulation model showed the motion detection ability of T4c and T4d that respond in the vertical direction. Then, when the circular object was moved diagonally to

![Fig. 6](image_url)

*Fig. 6.* The response of L1–L5, Mi1, Tm3, Mi9, Mi4, C3, and T4a, for input stimulus including adaptation.
Connectome Based Simulation of Fly’s ON-Edge Motion Detector

(a) Directional selectivity described as maximum membrane potential in T4 cells.

(b) Directional selectivity described normalized responses. The minimum value of the axis was set to 0.5 in left figure (left: this work, right: replotted from Maisak et al. [10]).

Fig. 7. Directional selectivity of T4-cells, in the case of input stimulus of square wave. 0° is the horizontal motion in forward direction.

Fig. 8. Response of T4a to temporal frequency, in the case of input stimulus adopted the adaptation. \( V_{\text{max-diff}} \) is maximum difference of membrane potential. The dotted line is replotted from Maisak et al. [10].

The maximum potential difference is shown in Fig. 10.

The responses of T4, in the case of silencing of Mi1/Tm3, dropped significantly for stimuli between 1.0 and 10.0 Hz. In the case of Mi4 silencing and Mi9 silencing the effect on response amplitude is slight. The frequency characteristics of our simulations (middle of Fig. 10) differ from Stroger’s results [20] that Mi4 and Mi9 have opposite effects in the higher frequency range and from the assumption in [15] that Mi4 (presumptive BL pathway) is more sensitive than Mi9 (presumptive HR pathway) in the higher frequency range. Further studies that include more detailed modeling and a characterization using a wider variety of stimuli are required to resolve this apparent contradiction.

For the models with silencing, the directional selectivity at 1.0 Hz was also evaluated (Fig. 11). Silencing of Mi3 and Tm3 that inhibited the activity of T4 over a wide frequency range slightly changed directional selectivity. Moreover, it was observed that both silencing of Mi4 that
is suggested to convey delayed signals compatible with the BL model in the fly optic lobe and Mi9 that is suggested to convey delayed signals in the HR mode in the fly optic lobe had reduced, but not abolished directional selectivity. This means that even if some cells do not respond due to silencing, the function of directional selectivity was retained by alternative pathways. This may suggest that the EMD in optic lobe is more than a simple combination of HR and BL detectors and that it is more robust and sophisticated to be adaptive for being suitable for processing various complex visual stimuli.

When silencing was applied to C3, for the frequency dependence of the response, there was no significant difference in the maximum potential difference compared to the case where silencing was not applied (Fig. 10). Regarding the directional selectivity, anisotropy in the 180° direction appeared even when silencing was applied to C3, and it was found that the directional selectivity was maintained (Fig. 11). It is considered that it may not play a major role in ON-edge moving object detection. However, since the information on the downstream side was not modeled in this simulation, it is possible to have a role on the downstream side.

4. Concluding Remarks

We created a simulation of the ON-edge motion detection neural circuit in the fly optic lobe using the connectome of Drosophila. Our network model was built incorporating the actual number of synapses between optic lobe neurons and their electrophysiological parameters. We showed the directional selectivity and frequency characteristics as responses to motion stimuli of fly visual system can be qualitatively reproduced by our simulation when the adaptative neural circuit properties were introduced through the adaptation of the photoreceptor current. Our simulation is innovative in the point that it is physically realistic because it is based on the connections of neurons of real fly brain and modeling is based on its biophysical properties. Therefore, we can compare this simulation to many experimental results that were performed, investigating various aspects beyond the limited scopes of more conceptual computational models.

However, our model is still relatively simple in terms of neural circuit simulation using biophysical modeling. The model of graded synaptic transmission in this study essentially directly transmits the membrane voltage over a threshold to the postsynaptic region with a time delay, though graded synapses of real neurons display spontaneous transmitter release with vesicles that depends on the internal calcium concentration of the presynaptic region.
More detailed modeling with smooth time cores of miniature postsynaptic current will allow reproducing more realistic and smooth activity patterns of optic lobe neurons. The dendritic integration, the transmission of voltage signals in non-spiking neurons, and the Ca$^{2+}$ dynamics in the intracellular space can be included in our model by the extension of our model as each neuron has its own morphology and many synaptic boutons, necessitating multi-compartment neuron models. Moreover, cell adaptation of each optic lobe neuron based on the biophysical properties of the cable theory will naturally be introduced. Of course, these extensions will increase the number of biophysical parameters. We will require some automatic solver to determine individual parameters. The combination of evolutionary algorithms and well-organized large-scale simulations in a massively parallelized computational environment is one candidate to solve this problem [37]. This can also improve the modeling of the reliability of some neurons for which physiological data are not yet available.

Advancements in the opposite direction are also possible. Recent neuromorphic technology that involves the combination of analog and digital circuits may allow implementations of ours or a variant simulation with high energy efficiency and high speed [38, 39]. Our simulation does not involve high calculation and communication costs. The calculation cost of our simulation will be reduced further if exponential decays of membrane potential can be handled by capacitive analog circuits. The communication cost of synaptic transmission implemented via MPI is not currently a bottleneck because the delay of each synaptic transmission allows the simulation at a sufficient communication time. Using specific hardware with low energy consumption and highly configurable devices has the potential to implement simulations like the one presented here in mobile autonomous vehicles and UAVs using visual information under the limitation of power sources [40, 41]. Even before implementing the OFF-edge detection algorithm, the moving edge detector as an application of our simulation may be useful for autonomous machine moving in night because it works for avoiding and tracking moving objects, the egomotion estimation and so on without detailed scene analysis.

From the biological aspect this study enabled us to evaluate the role of individual neurons in the optic lobe. The virtual silencing of Mi4 and Mi9, which were proposed to be crucial for the EMDs in the optic lobe, significantly decreased directional selectivity but did not have a fatal impact on ON-edge detecting function. This may suggest that the motion detection in the fly optic lobe has more robustness and is more sophisticated than a simple combination of HR and BL systems suggested in [15]. Our simulation shows less directional selectivity than the reported experiment results before adopting receptor adaptation and adopting receptor adaptation slightly decreased directional selectivity in T4 cells in our simulation. It may be affected by the fact we currently introduced adaptive properties only into the receptor cell instead of each optic lobe neurons. Further studies using an advanced version of this simulation and systematic wide range stimuli in line with naturalistic environments and behaviors may bring us a clearer understanding of the function of all cells, including cells like C3. Especially we note that our current study does not make attend to the spatial resolution and range in the visual stimuli. Moreover, the physiological, anatomical, and theoretical analysis of the OFF-pathway is an important topic recently [42–44]. The suggested systems are similar to the ON-pathway but we note that 1) T5 cells receive the information at a more distant position from medulla. 2) The interaction from the lobula neural circuit may modify the calculation in the OFF-pathways. Therefore, the simulation of the OFF-pathway based on biophysically detailed model should be considered as a multi-compartment model with more detailed information on the lobula.

In the near future, we will create and verify a more detailed connectome-based model by adjusting parameters, implementing adaptive properties of each neuron in a multi-compartment model, adding the OFF-pathway to the model, and adding wide-field neurons that affect both ON- and OFF-pathways.

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References:


\[
\begin{align*}
y_1' &= \alpha_1(V)(1 - y_1) - \beta_1(V)y_1, \\
y_2' &= \alpha_2(V)(1 - y_2) - \beta_2(V)y_2, \\
y_3' &= \alpha_3(V)(1 - y_3) - \beta_3(V)y_3, \\
y_4' &= \alpha_4(V)(1 - y_4) - \beta_4(V)y_4. \\
\alpha_1(V) &= \frac{1}{\tau_1(V) (1 + \exp(-0.153(V + 6)))}, \\
\beta_1(V) &= \frac{1}{\tau_1(V) - \alpha_1(V)}, \\
\alpha_2(V) &= \frac{1}{\tau_2(V) (1 + \exp(0.117(V + 31.35)))^{1/2}}, \\
\beta_2(V) &= \frac{1}{\tau_2(V) - \alpha_2(V)}, \\
\alpha_3(V) &= \frac{1}{\tau_3(V) (1 + \exp(-0.098(V + 32.52)))}, \\
\beta_3(V) &= \frac{1}{\tau_3(V) - \alpha_3(V)}, \\
\alpha_4(V) &= \frac{1}{\tau_4(V) (1 + \exp(-0.153(V + 6)))^{1/2}}, \\
\beta_4(V) &= \frac{1}{\tau_4(V) - \alpha_4(V)}, \\
\tau_1(V) &= 3.5 \left(1 + \frac{V + 80.01}{18.34} \right)^{2.0998}, \\
\tau_2(V) &= \frac{1}{115} \left(1 + \frac{V + 74.46}{26.44} \right)^{2.018}, \\
\tau_3(V) &= \frac{1}{6.4} \left(1 + \frac{V + 19.13}{26.01} \right)^{2.0817}, \\
\tau_4(V) &= 890. \\
\end{align*}
\]

Here, \( C \) is a membrane capacitance, \( \overline{g_{sh}} \) is a maximal conductance of Shaker \( K^+ \) channel, \( y_1 \) is a rate of opening activation gate, \( y_2 \) is a rate of opening inactivation gate of Shaker \( K^+ \) channel, \( \overline{g_{dr}} \) is a maximal conductance of delayed rectifier \( K^+ \) channel, \( y_3 \) is a rate of opening activation gate, \( y_4 \) is a rate of opening inactivation gate of the delayed rectifier \( K^+ \) channel, \( g_{K_{\text{leak}}} \) is a conductance of leak \( K^+ \) channel, \( V_K \) is an equilibrium voltage of \( K^+ \) ion, \( \overline{g_{Ca}} \) is a maximal conductance of the \( Ca^{2+} \) channel, \( V_{Ca} \) is an equilibrium voltage of \( Ca^{2+} \) ion, \( g_{leak} \) is a conductance of leak channel, \( V_{leak} \) is a reversal potential of leak channel, and \( i \) is an extracellular current.

For Tm3, Mi1, Mi4, Mi9, C2, and C3 in the medulla, we use the Morris–Lecar model [29] setting the parameters not to generate spikes. We used the model including potassium channel and calcium channel. Here, \( C \) is a membrane capacitance, \( \overline{g_{Ca}} \) is a maximal conductance of \( Ca^{2+} \) channel, \( V_K \) is an equilibrium voltage of \( K^+ \) ion, \( \overline{g_{Ca}} \) is a maximal conductance of the \( Ca^{2+} \) channel, \( V_{Ca} \) is an equilibrium voltage of \( Ca^{2+} \) ion, \( g_{leak} \) is a conductance of leak channel, \( V_{leak} \) is a reversal potential of leak channel, and \( i \) is an extracellular current.

\[
\begin{align*}
\frac{dV}{dt} &= C(-g_{leak}(V - V_{leak}) - g_K(V - V_K) + i), \\
g_K &= \overline{g_{Ca}} \times n, \\
g_{Ca} &= 0.5 \overline{g_{Ca}} \times \left(1 - \tanh \left(\frac{V + 1}{15}\right)\right), \\
\frac{dn}{dt} &= 0.5 \times \left(1 + \tanh \left(\frac{V + 50}{1}\right)\right) - n \\
&\quad \times 0.0025 \times \cosh \left(\frac{V + 50}{2}\right). \\
\end{align*}
\]

For T4-cells, we used the passive membrane model following [15]. Here, \( C \) is a membrane capacitance, \( g_{leak} \) is a conductance of leak channel, \( V_{leak} \) is a reversal potential of leak channel, and \( i \) is an extracellular current.

\[
\frac{dV}{dt} = C(-g_{leak}(V - V_{leak}) + i).
\]

### Appendix B. Stimuli

#### B.1. Square Wave Stimulation to Simulate a Moving Grating

In this study, the transduction currents of R-cells were simulated by directly injecting current to R-cell as following.
Two-dimensional plane wave.

At the time)

Equation.

Sudden fluctuations in the membrane potential, the edges

Given as an input stimulus. To prevent the noise due to

Here).

B.2. Stimulation that Imitates an Adaptation

In order to apply an adaptation, we created the current by multiplying the function $f(t)$ to the input current $A$.

$$
i(x,y,t) = \begin{cases} A \times f(t), & \text{position} \leq \frac{\omega}{2} \text{ or position} > \frac{1}{SF} - \frac{\omega}{2}, \\ 0, & \text{otherwise}, \end{cases}$$

$$f(t) = \frac{1}{1 + \exp\left(\frac{t - t_{sp}}{500}\right)} + 0.3.$$  

Here, $t_{sp}$ is the time to start the stimulation periodically.

B.3. Stimulation that Imitates a Moving Object

In order to confirm the moving object detection ability of the simulation model, we created stimulus for the movement of a circular object. The current $i(x,y,t)$ was given as an input stimulus. To prevent the noise due to sudden fluctuations in the membrane potential, the edges of the circular object were smoothed as the following equation.

$$i(x,y,t) = \begin{cases} I_{th}, & f(x,y,t) > I_{th}, \\ f(x,y,t), & \text{otherwise}, \end{cases}$$

$$f(x,y,t) = A \exp\left(-\frac{D}{2\sigma^2}\right),$$

$$D = \frac{3(x - cx)^2}{4} + \left(\frac{x}{2} + y - \frac{cy}{2}\right)^2.$$  

Here, $(cx, cy)$ is the center coordinates, $\sigma$ is the variance of the Gaussian distribution, $A$ is the amplifier, $I_{th}$ is the threshold of the current. In this work, we use $\sigma = 2, A = 3, I_{th} = 1$.  

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