Effects of Luminance Contrast on the Looming-sensitive Neuron of the Praying Mantis *Tenodera aridifolia*

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Abstract

Responses of the looming-sensitive neurons to visual stimuli were recorded extracellularly from the cervical connective of the mantis *Tenodera aridifolia*. Responses to looming stimuli were affected by the contrast polarity between objects and background. Although the looming-sensitive neuron responded to looming objects both darker and lighter than the background, the maximum spike frequency during the presentation of a white looming circle on black background was significantly lower than that of a black-on-white looming circle. On the checkerboard background, which had the similar average luminance to gray, the maximum spike frequencies in response to a white looming circle were significantly smaller than that to black and gray looming circles. Finally, responses to black and gray looming circles on checkerboard background appeared to be similar: there was no significant difference in the maximum spike frequency between them.

Key words: Looming, Contrast, Collision detection, Vision, Mantis

Introduction

Many animals show defense behaviors against approaching objects.[1–4] These objects generate specific visual stimuli called looming. Neurons sensitive to looming stimuli have been reported in many animals, such as pigeons,[5] frogs,[6] fishes,[7] crabs,[8] locusts,[9] and mantises.[10]

The locust brain possesses two looming sensitive neurons: lobula giant movement detectors 1 and 2 (LGMD1 and LGMD2).[11] The LGMD1 is excited by the approach of objects both lighter and darker than the background.[9] In contrast, the LGMD2 is only excited by approaching objects darker than the background.[12] It has been reported that the mantis brain also possesses, at least, one looming-sensitive neuron.[10] However, its responses to approaching lighter objects and the effects of contrast have not been sufficiently studied.

In the present paper, we reported the response property of the descending neuron sensitive to looming stimuli in the mantis *Tenodera aridifolia*, focusing on the effects of luminance of objects and the background. The results indicated that the mantis looming-sensitive neuron was excited by looming stimuli both lighter and darker than the background, suggesting similar response properties to LGMD1.

Materials and methods

Animals and preparation

Experiments were performed on adult females of the mantis *T. aridifolia* from our laboratory colony. After cold anaesthesia, a mantis was fastened upside down to a holder using dental wax and its thorax, abdomen and legs were stabilized. Six mantises were used for each experiment.

Extracellular recordings

Extracellular recordings were made using the methods previously described.[10] The recordings were made with the wire electrodes. Two tiny holes were made with an insect pin along the midline on ventral prothorax anterior to the left coxa of foreleg. A silver wire (200-µm in diameter) was inserted through each hole. The anterior and posterior wires acted as minus and plus electrode, respectively, so that descending spikes could be discriminated from ascending spikes. These wire electrodes were connected to the probe of an AC-amplifier (Nihon Kohden, MEG-6108). Data were collected and analyzed using a CED 1401 System running with Spike2 v5 (Cambridge Electronic Design). A high-pass filter (>400 Hz) was used to enhance axonal spikes against muscle potentials. The spikes were classified by the template matching implemented in Spike2 v5. Because the simultaneous firing of several different neurons occasionally formed exceptionally large spikes, such spikes were not used in the analysis.

In the extracellular recordings from cervical connectives, we distinguished spikes of the looming-sensitive neuron according to following criteria: the largest spike in the recording; the best response to looming stimuli; and the increase in the firing rate as the object approached.[10]

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Visual stimuli

Methods for presenting visual stimuli were the same as previous studies.[10] Visual stimuli were displayed on a thin film transistor (TFT) liquid crystal display (Sharp, LL-T1512W) and generated by a computer running a custom-written Visual Basic (Microsoft) program. The refresh rate of the display was 60 Hz. The display was placed parallel to the longitudinal axis of the mantis body at a distance of 8 cm from the left eye. A transparent, electrically conductive film (TORAY) covered the screen of the display to reduce electrical interference in neural recordings. The square part (90°×90°) of the screen was used as a background for visual stimulation and the position of the mantis was adjusted so that the left eye was located at the center of the background. The luminance of white and black on the screen was 99.8 and 5.3 cd/m^2 (Konica Minolta, LS-110), respectively. Contrast between black and white on the screen was 0.899, calculated as: (background luminance – object luminance)/ (background luminance + object luminance).

In the first experiment, we examined the effects of contrast polarity. We presented three types of visual stimuli with different contrast polarity: black object on a white background (black-on-white) and white object on a black background (white-on-black). First, the looming or receding circle. This simulated an 8-cm circle moving towards or away from the mantis over a distance of 3 m at a constant velocity of 2 m/s. Second, a gradually darkening or lightening circle. This was an 8-cm circle that gradually changed its luminance from white to black or vice versa, so that the time course of the luminance change approximated that produced by a looming or receding circle. Last, a linearly expanding circle. This was a circle that altered in size at a constant edge speed of 30°/s.

In the second experiment, we examined the effects of object luminance. We used a black, gray, and white looming circles, whose luminance was 5.3, 64.9 and 99.8 cd/m^2, respectively. The circle was presented on checkerboard backgrounds, whose average luminance (63.6 cd/m^2) was almost the same as gray circle. The size of squares comprising checkerboard pattern was 0.3 mm or 10.4 mm. Since pixel size on the display was 0.3 mm, it was the minimum size that could be generated on the display.

We expected that the mantis would hardly detect luminance change during the presentation of a looming gray circle on a 0.3-mm checkerboard. The visual subtense of 0.3-mm square at the center of screen is 0.213° seen from the mantis, and this subtense is smaller than the estimated highest resolution of the mantis compound eye (0.6° in fovea).[13] Hence, theoretically, it is hard to discriminate between gray and 0.3-mm checkerboard when they have the same average luminance. In contrast, we considered that the mantis could detect the luminance change in a looming gray circle on a 10.4-mm checkerboard. The visual subtense of 10.4-mm square is 3.98° at the peripheral part of the background, which is larger than the estimated lowest resolution of the mantis compound eyes (2.5° in the edge region).[13]

The inter-stimulus interval (ISI) was more than 60 s for each experiment.

Data analysis

We estimated the instantaneous spike frequency by convolving the spike trains with a Gaussian window (time resolution = 1 ms; width σ = 20 ms). Then, the maximum spike frequency was found for each presentation of stimuli. The differences in the maximum spike frequency among stimuli were analyzed with the Friedman two-way analysis of variance by ranks and the Wilcoxon signed rank test by using SigmaPlot 10 and SigmaStat 3.5 for Windows (Systat Software).

Results

Effects of contrast polarity

In all extracellular recordings from cervical connectives, we discriminated the spike unit which matched the criteria of looming sensitivity (see Methods). The response properties of the looming-sensitive unit to black looming stimuli on white backgrounds and other black-on-white stimuli were similar to those reported in previous studies.[10] In brief, the looming-sensitive unit showed strong excitation to a black looming circle and transient excitatory responses to a receding, gradually darkening and lightening circles (Fig. 1A). It showed a sustained excitation to the linearly expanding circle, but its spike frequency declined gradually during presentation.

To examine the effects of contrast polarity, we recorded the responses of the looming-sensitive units to white looming stimuli on black backgrounds and other white-on-black stimuli. Although their responses to white-on-black stimuli were similar to those to black-on-white stimuli, their firing patterns were different (Fig. 1B). The maximum spike frequency during presentation of a white looming circle was significantly lower than that of a black looming circle (z = –4.855, P < 0.001; Fig. 2). In addition, intermittent bursts of spikes occurred more prominently during presentation of a white looming circle than a black one. The unit showed transient excitation to the white-on-black linearly expanding circle, and the spike frequency appeared to decline more rapidly than that of a black-on-white one. The unit showed transient excitatory responses to the white-on-black receding circle, but its maximum spike frequency was significantly lower than that to a black-on-white one (z = –2.624, P = 0.009).

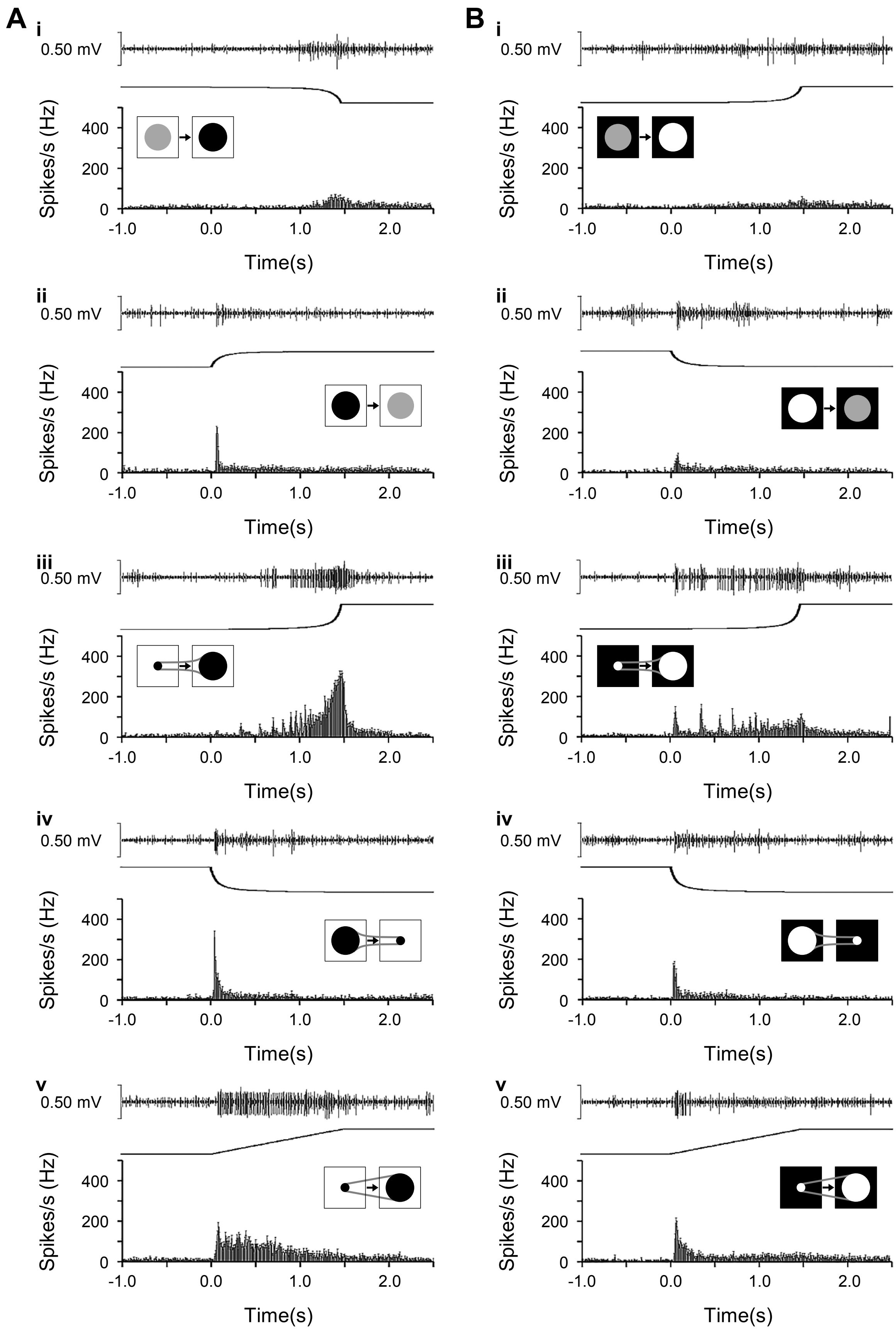

Fig. 1. Sample recordings of responses of the looming-sensitive unit to black-on-white (**A**) and white-on-black (**B**) stimuli. The top trace is an extracellular recording from the left cervical connective. The largest spikes were from the looming sensitive unit. The unit showed responses to gradually darkening (**Ai** and **Bii**), lightening (**Aii** and **Bi**), looming (**iii**), Receding (**iv**), and linearly expanding (**v**) circles. Middle traces indicate the circle subtense (**iii**, **iv**, and **v**) or circle luminance (**i** and **ii**). PSTHs (bin, 10ms) indicate the mean spike frequency and SE of the unit recorded from six presentations to each of the six mantises (n = 36).

Effects of the object luminance

Since the luminance of both object and background were changed in the first experiment, it remained unclear which visual parameters affected the response of the looming sensitive neuron. Thus, we examined the effects of object luminance by keeping an average luminance of backgrounds constant in the second experiment.

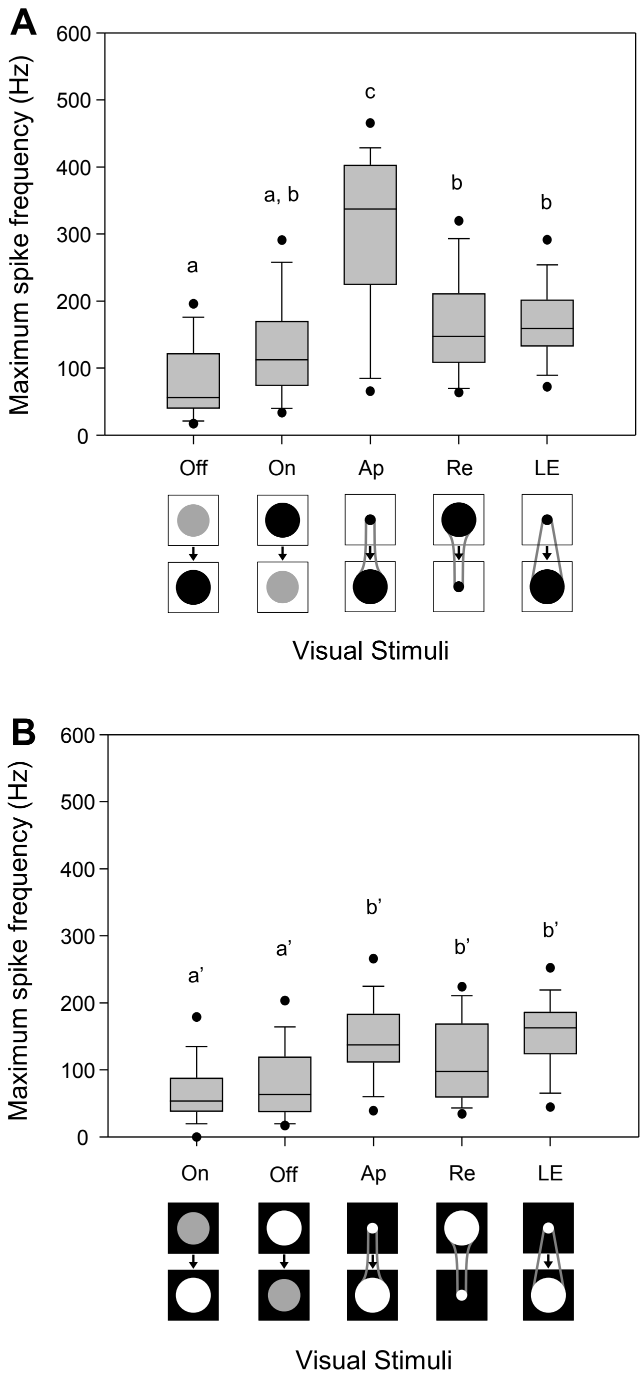

Fig. 2. The maximum spike frequencies of the looming sensitive unit in response to gradually darkening (Off), lightening (On), looming (Ap), Receding (Re), and linearly expanding (LE) circles on white (**A**) and black backgrounds (**B**). Boxes show the 25th and 75th percentiles, and bisecting lines show the median value. Whiskers indicate the 10th and 90th percentiles, and dots indicate the 5th and 95th percentiles. Different letters in each plot indicate the significant differences in mean values between them.

The looming sensitive unit showed strong excitation to all looming circles (Fig. 3), irrespective of the circle luminance (black, gray, or white) and the background (0.3 or 10.4 mm checkerboard). Responses to the black looming circle on 0.3-mm checkerboard were similar to those to the black-on-white looming in the first experiment.

The size of the checkerboard in the background did not seem to affect the maximum responses to looming circles: there were no significant differences in the maximum spike frequencies between 0.3-mm and 10.4-mm checkerboards in responses to a black, gray, and white looming circles (Fig. 4; $P > 0.05$ for each). However, early responses appeared to be different. For example, the unit responded during the early stage of the presentation of a black looming on the 0.3-mm checkerboard but not on the 10.4-mm checkerboard.

In contrast, the object luminance affected the responses of the looming-sensitive unit, and the unit responded more strongly to black and gray looming circles than to the white one. The maximum spike frequencies of the responses of the looming-sensitive unit to a white looming circle were significantly smaller than that to black and gray ones (Fig. 4; $P < 0.05$ for 0.3-mm checkerboard; $P < 0.05$ for 10.4-mm). There were no significant differences in the maximum spike frequencies between black and gray looming circles ($P > 0.05$ for 0.3-mm checkerboard; $P > 0.05$ for 10.4-mm).

Discussion

The results of present study suggested that contrast polarity between objects and backgrounds affected the responses of the looming-sensitive unit in the mantis. When objects were brighter than backgrounds, the responses of the neuron appeared to be small. The preference for objects darker than backgrounds might be adaptive because it is less likely that the approaching predator is brighter than the background.

In addition, intermittent bursts of spikes occurred more prominently during presentation of a white looming circle (Fig.1Biii) than a black one (Fig.1Aiii). These bursts were an artifact of the low screen refresh rate, since it was elicited as a new stripe was added to the edge of the circle.[10] It is possible that the unit responded more strongly to the ON stimuli generated at the edge of the white looming circle than to the OFF stimuli generated by the black looming circle.

When the edge of objects had lower luminance than background, the luminance difference between objects and backgrounds may not affect the responses. For example, there was no significant difference in the responses between the black and gray looming on the gray (checkerboard) backgrounds. In addition, response patterns of the black-on-white visual stimuli were similar to those of the black-on-gray (checkerboard) stimuli.

However, when the edge of the objects was brighter than the backgrounds, background luminance seemed to have affected the responses. For example, responses to white-on-black looming circles appeared smaller than those to white-on-checkerboard ones. To test this possibility, further studies manipulating the luminance of the object and the background are required.

Not only the luminance but also the background texture affected the firing patterns of the unit. The unit showed little excitation during the early stage of the presentation of a black looming on the 10.4-mm checkerboard (Fig. 3Bi). In this case, we considered that the unit could not detect the luminance change during the early stage of presentation because the black circle was hidden by the black squares of the checkerboard.

Although we expected that the unit would hardly detect luminance change during the presentation of a looming gray circle on a 0.3-mm checkerboard, the unit strongly responded at the late stage of the presentation (Fig. 3Aii). This can be explained as follows. Possibly because the luminance of the screen changes from white to gray faster than from black to gray, the dark strip was temporarily observed at the edge of the looming gray circle (Fig. 5). The motion of this dark edge might have elicited such a strong excitation. Responding to the small luminance change at the edge of the object may facilitate the detection of predators or prey.

Conclusion

The looming-sensitive unit in the mantis showed excitation to looming objects both lighter and darker than backgrounds and responded to darker looming objects more strongly than lighter ones, suggesting that the unit had similar response properties to LGMD1 rather than LGMD2.

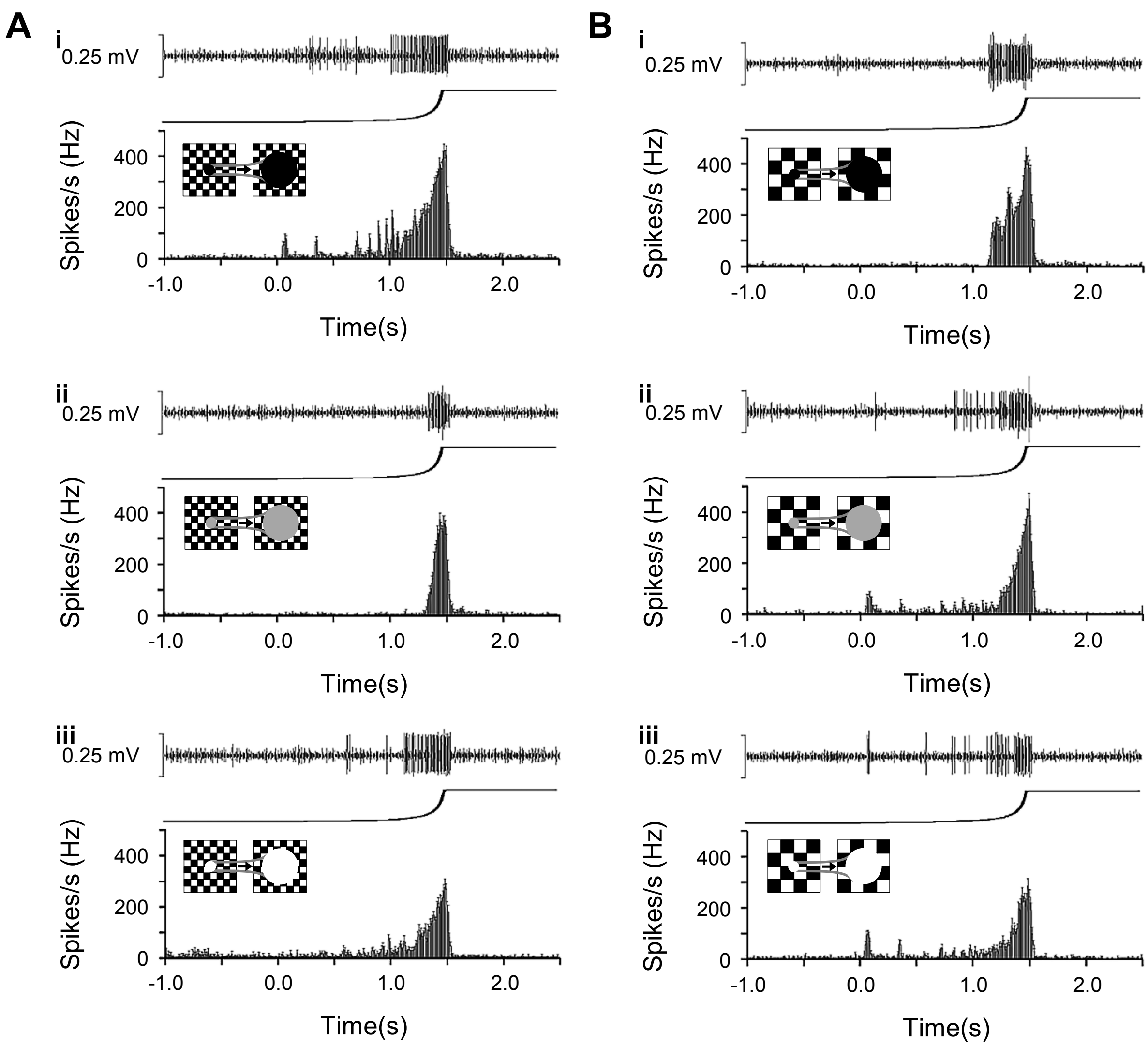

Fig. 3. Sample recordings of responses of the looming-sensitive unit to black (5.3 cd/m^2, **i**), gray (64.9 cd/m^2, **ii**), and white (99.8 cd/m^2, **iii**) looming circles on 0.3-mm checkerboard (**A**) and 10.4-mm checkerboard (**B**) backgrounds. Average luminance of checkerboard was similar to that of gray. The top trace is an extracellular recording from the left connective, and the largest spikes were from the looming sensitive unit. Middle traces indicate the circle subtense. PSTHs (bin, 10ms) indicate the mean spike frequency and SE of the unit recorded from six presentations to each of the six mantises (n = 36).

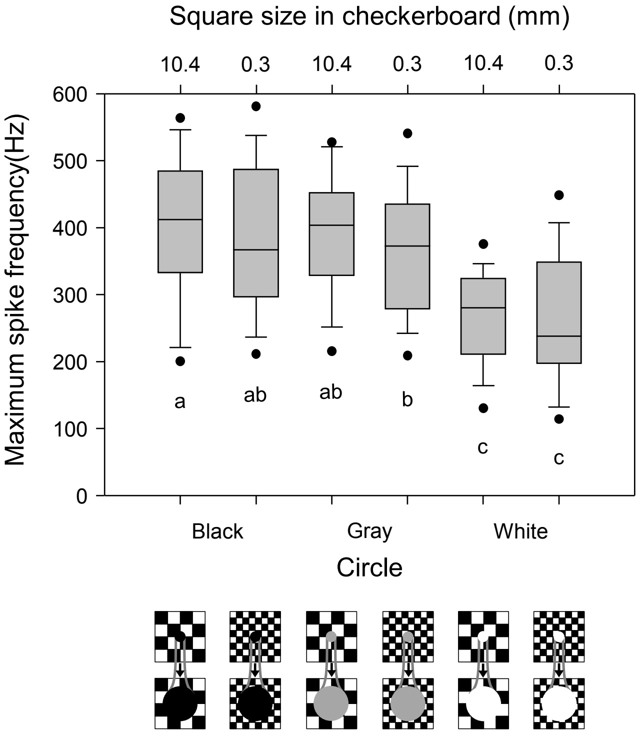

Fig. 4. The maximum spike frequencies of the looming sensitive unit in response to black, gray, and white looming circles on 0.3-mm and 10.4-mm checkerboard backgrounds. Different letters indicate the significant differences in mean values between them.

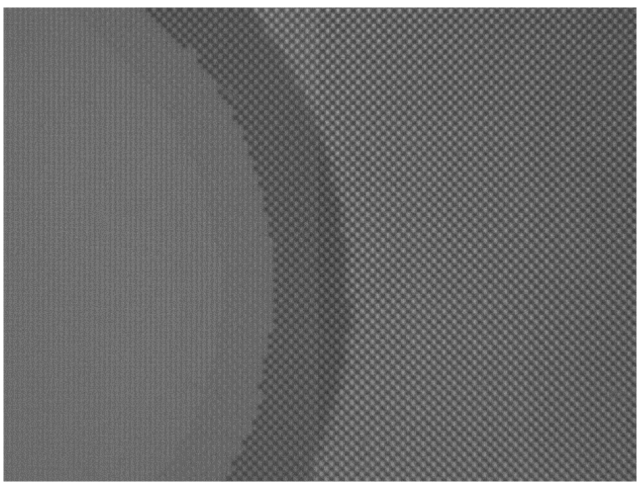

Fig. 5. A sample image of the display during presentation of a gray looming circle on the 0.3-mm checkerboard background. Although the 0.3-mm checkerboard had similar average luminance to the gray circle, a dark stripe was observed on the edge of the circle.

Acknowledgments

This work was supported by Global Science Campus from JST and Marie Skłodowska-Curie Actions Research and Innovation Staff Exchange Scheme (STEP2DYNA).

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オオカマキリ衝突検出ニューロンの応答に対するコントラストの影響

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要旨

オオカマキリの腹髄から衝突検出ニューロンの応答を細胞外記録した．衝突検出ニューロンの応答は物体と背景の間のコントラストの方向に影響された．衝突検出ニューロンは背景よりも明るい接近刺激と暗い接近刺激ともに応答したが，黒背景白図形の接近刺激を提示した時の最大スパイク頻度は白背景黒図形のものに比べて有意に低かった．平均の明るさが灰色とほとんど等しい市松模様を背景にした場合，白色の接近刺激に対する応答の最大スパイク頻度は，黒色・灰色の接近刺激に対するものと比べて有意に低かった．市松模様背景における黒色と灰色の接近刺激に対する応答は似ており，最大スパイク頻度の間には有意差が見られなかった．

重要語句：接近，コントラスト，衝突検出，視覚，カマキリ

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