

# Signaling of Object Approach by the DCMD Neuron of the Locust

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**Rind, F. Claire and Peter J. Simmons.** Signaling of object approach by the DCMD neuron of the locust. *J. Neurophysiol.* 77: 1029–1033, 1997. The locust descending contralateral motion detector (DCMD) responds to movements anywhere within a wide visual field, but responds most strongly to the images of approaching objects. It has been claimed that the response peaks before the end of an approach movement, providing a signal that anticipates collision. However, we find that when the locust eye is presented with appropriate computer-generated images of approaching objects, the response builds up until after movement has stopped. Premature peaking in the response is due to failure to stimulate the eye with sufficiently small and frequent jumps in image edges. We conclude that the DCMD signals impending collision by tracking edge motion throughout object approach.

## INTRODUCTION

Neural mechanisms for anticipating collision and triggering avoidance movements are not well understood. Recently, Hatsopoulos et al. (1995) described a novel mechanism for anticipating collision, in which the response of the descending contralateral motion detector (DCMD) neuron of the locust peaks and declines before an object finishes its approach toward the eye. They claim this peak would provide a cue for the timing of escape behavior.

The DCMD is a widefield visual neuron that responds briskly to any novel movement, but only generates maintained vigorous responses when an object approaches the eye (Rind and Simmons 1992). Increases in both the extent and the velocity of travel of image edges across the eye are critical cues for the selective responses to approaching objects (Simmons and Rind 1992). Our previously published recordings (Rind 1996; Rind and Simmons 1992) have not shown that the response by the DCMD to object approach declines before the end of movement, and we have therefore repeated and extended our previous experiments. We cannot substantiate the central finding of Hatsopoulos et al. (1995), and suggest that the graphics computer system they employed had insufficient temporal resolution to generate the illusion of an approaching object for the DCMD.

## METHODS

In general, methods were similar to those described previously (Rind and Simmons 1992). Stimulus conditions are summarized in Fig. 1A. The right eye of a locust, usually *Locusta migratoria* but occasionally *Schistocerca gregaria*, viewed a monitor screen while the left eye was shielded with black card. Image size was monitored by the output of a digital to analog converter (DAC). In 10 experiments, the monitor screen was a Kikusui COS1611 X-Y display (100 × 80 mm; P31 phosphor) at 100 mm from the eye. Usually, the background had an intensity, measured at the eye, of

16  $\mu\text{W}/\text{cm}^2$ , and dark shapes of 4  $\mu\text{W}/\text{cm}^2$  in intensity moved against it. Stimuli were controlled with a Cambridge Research Systems VSG2/1 board and RG2 raster generator, providing a refresh rate of 200 Hz, at a resolution of 437 lines by 438 dots.

In 17 experiments, the locust viewed a Sony VDU monitor controlled by a Silicon Graphics Indigo-2 Computer. Images were refreshed at 72 Hz and screen resolution was  $1,024 \times 1,248$  pixels. In 14 of these experiments the eye was 150 mm from the screen, which subtended  $99 \times 86^\circ$  at the eye. Dark squares of intensity measured at the eye of 25  $\mu\text{W}/\text{cm}^2$ , moved against a green (540 nm) background of 32  $\mu\text{W}/\text{cm}^2$  in intensity. In a further three experiments the stimulus conditions matched those used by Hatsopoulos et al. (1995). The eye was 70 mm from the screen, which subtended  $149 \times 129^\circ$  at the eye. Dark squares of intensity measured at the eye of 0.02 or 6.49  $\mu\text{W}/\text{cm}^2$  moved against a green background of either 8.05 or 14.54  $\mu\text{W}/\text{cm}^2$ , respectively.

Spikes were recorded extracellularly and converted to 0.1-ms pulses with a height discriminator. They were collected to disk in real time and analyzed with the use of Cambridge Electronic Design "Spike2" Software. Different types of stimuli were interleaved at intervals of 90 s.

## RESULTS

Previously (Rind and Simmons 1992) we employed images of approaching rectangles, so that the corners of the images move much faster over the retina than the center of each straight edge. We have now also generated images of circular disks, in which all movements over the retina are at an equal speed, and we find that, for a variety of object sizes (Fig. 1, *B* and *C*) and speeds, the DCMD response continues until several tens of milliseconds after the end of image movement. In these stimuli, like those of rectangles we have used previously, the image stops expanding before its edges reach the limit of the screen, so that the object appears to stop moving when it reaches the screen rather than coming closer to the locust (see Fig. 1A). We have also recorded responses to images of rectangles that expand to the limit of the screen. For objects smaller than the screen, this mimics the approach by the object to within a few milliseconds of collision (Fig. 1A). Again, for a variety of speeds (Fig. 1, *D–F*) and sizes of object, the response usually continues to increase after movement has ended. Even at slow simulated approach speeds, the response shows little decline until well after movement has stopped (Fig. 1D). Neither image contrast nor the absolute brightness of the background (up to 35  $\mu\text{W}/\text{cm}^2$ ) affects this feature of the response.

When we displayed images on a graphics computer VDU screen, we found that for squares up to 40 mm across the response also continued to increase after the end of movement. However, for larger squares, although the response

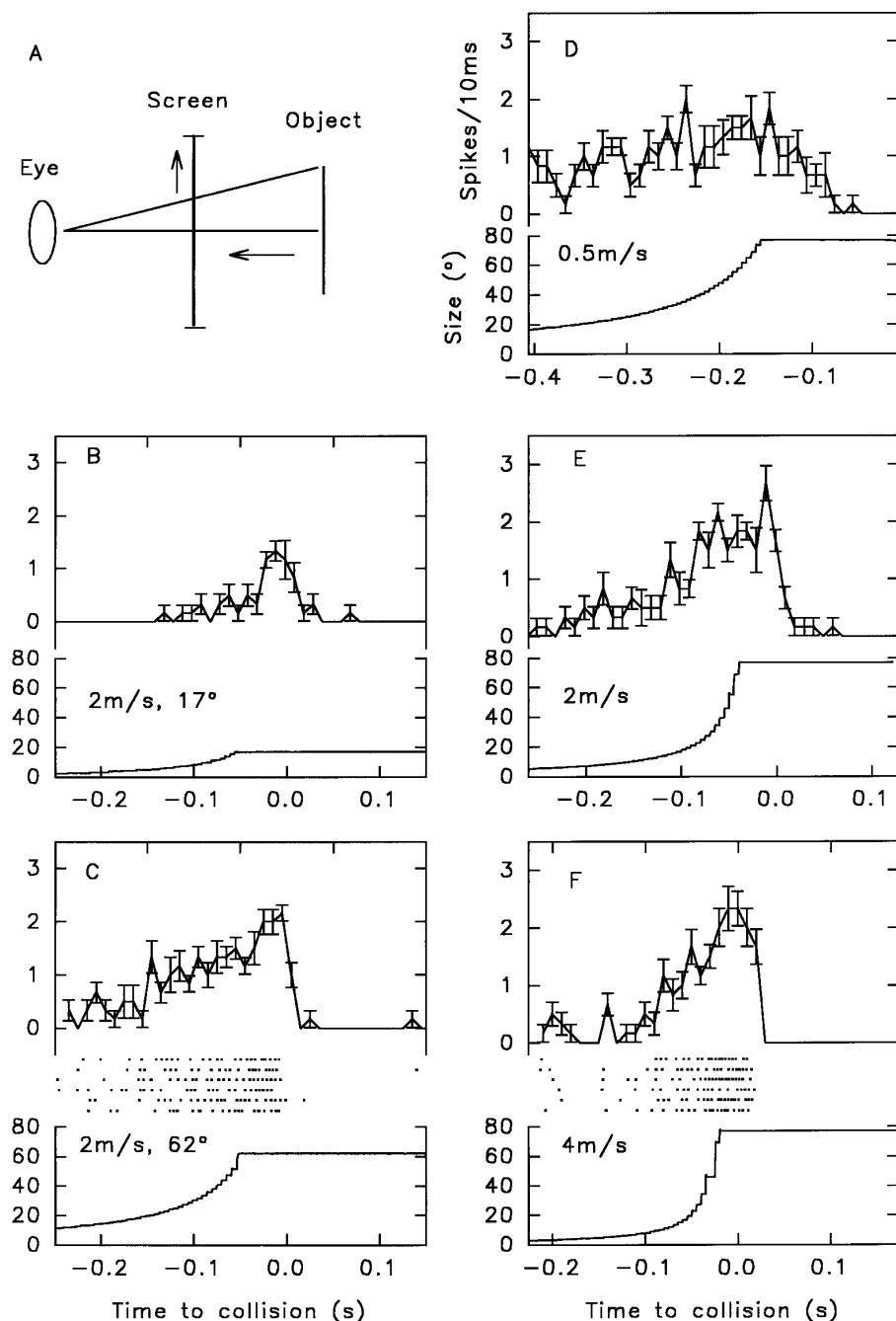


FIG. 1. Responses by the descending contralateral motion detector (DCMD) to simulated, approaching objects presented on a screen refreshed at 200 Hz. A: diagram of stimulus configuration. As the simulated object approaches the eye, its image size on the screen grows. Movement stops either when the image reaches a specific size or when the image size equals the screen size. Image size was calculated as (object size)  $\times$  (distance from eye to screen)/(distance from eye to object). B and C: responses to 6 simulated approaches of circular disks that subtended 17 or 62° at the eye at the end of movement. The continuously recorded response to each approach is shown for the approach of the larger disk (C, middle). D–F: responses in a different locust to simulated approach of a rectangle of 30  $\times$  40 mm. Three different speeds of approach from a distance of 4 m are shown. The time axis is labeled relative to when collision would have occurred. In each recording, the bottom trace is a monitor of image size and the top trace is the DCMD response during 10-ms bins (6 repetitions, mean  $\pm$  SE). F, middle: continuously recorded response to each approach.

began earlier during the movement, it also started to decline at about the time movement ended. In Fig. 2A, the mean number of spikes during each display frame is shown for squares 40 and 70 mm across, approaching at 2.5 m/s to 100 mm from the eye. For the 70-mm square, there was a clear reduction in response during the last few frames of movement (note that the latency of response to movement is  $\geq 60$  ms, or nearly 5 frames) (Simmons and Rind 1992). However, when we examined the pattern of response in more detail, we found that whenever the subtense of images grew in jumps of  $\sim 3^\circ$  or more, the response by the DCMD became locked to the frame repetition rate and declined in vigor (Fig. 2, B and C). Locking of response to each successive

frame was particularly clear for the 60- and 70-mm squares (final image subtenses 38.6 and 38.4°), and was seen for a range of speeds of approach. When images were displayed on the faster X-Y monitor, no locking of response to screen refresh was seen for images up to a final subtense of  $\geq 60^\circ$  (Fig. 1, C and F). In the relation between square size and total spike number for each approach there was a discontinuity at a square size of 40 mm. Responses to smaller squares depended on square size, but squares larger than 40 mm generated equal responses (Fig. 3). The size of square at which the locking of response to individual frames first became apparent was 40 mm (final frame, Fig. 2B). When we duplicated the stimulus conditions described by Hatso-

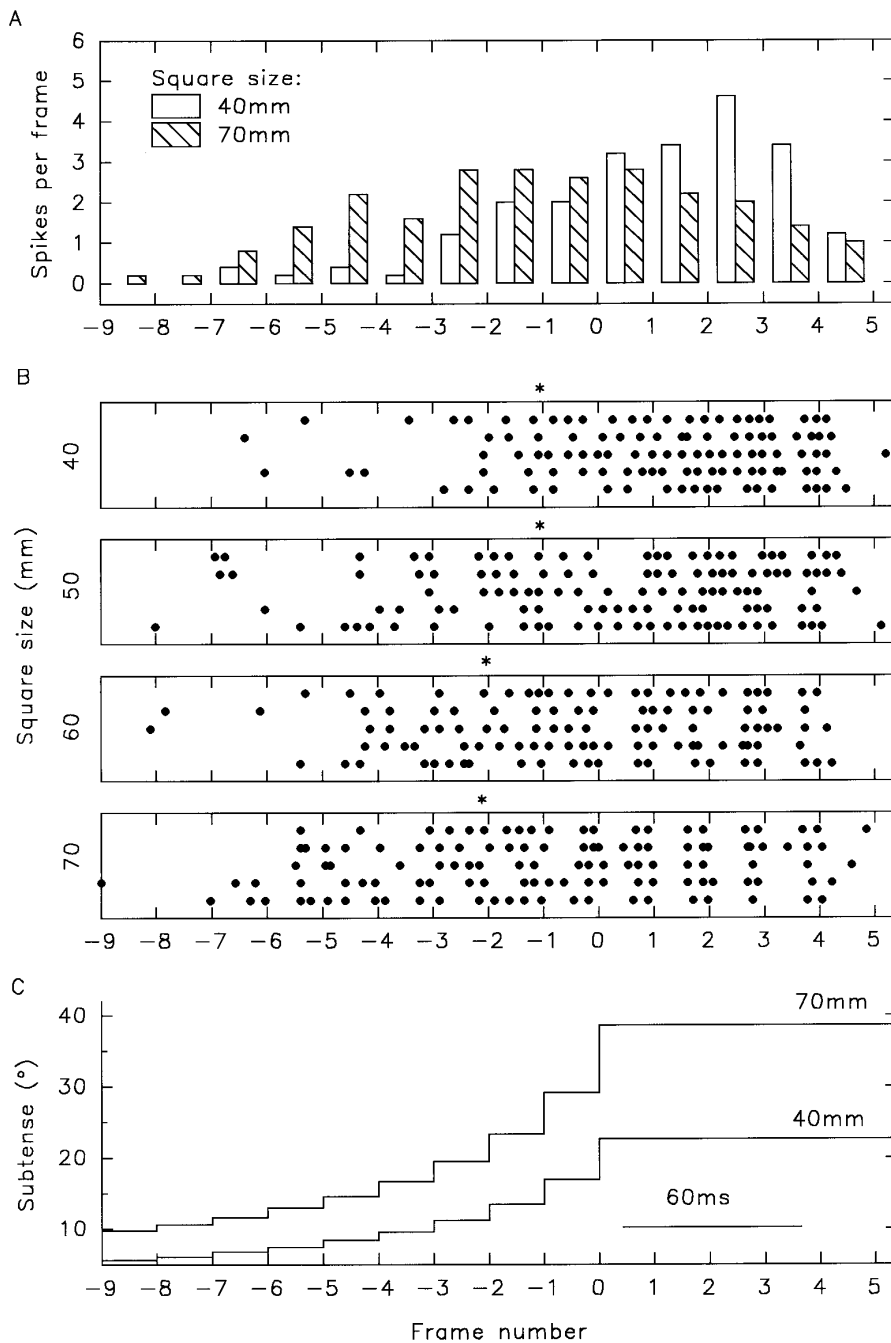


FIG. 2. Responses by the DCMD to images of approaching squares displayed on a graphics computer VDU screen, refreshed at 72 Hz. *A*: responses during the approach of squares with sides of 40 and 70 mm. Each square approached to a simulated 100-mm distance from the eye at 2.5 m/s. The mean number of spikes per frame of simulation is plotted for 5 repetitions of each stimulus. *B*: spike occurrence for 5 repetitions of the approach of 4 different sizes of square at 2.5 m/s. For each square size, asterisk indicates the 1st jump in image size  $>3^\circ$ . *C*: monitor of image size for the 40- and 70-mm squares. On the X-axes in A–C, times of frame refresh are shown, labeled relative to the final frame of movement.

poulos et al. (1995), we found that the response of the DCMD to an approaching 120-mm square declined before the end of the approach (Fig. 4A). In this simulation, collision would have occurred at the last frame: image size was limited by the angle subtended by the screen on the eye (see Fig. 1A). Inspection of the timing of the individual DCMD spikes during object approach revealed that they first became locked to each image frame and then failed completely. This type of response was also found for smaller squares, and decreasing the contrast of the stimuli led to earlier frame locking and failure of the response (Fig. 4B). The effect of contrast was particularly evident with the 120-mm square. Phase locking and decline in response occurred some 60 ms

after image jumps increased above  $3^\circ$ . For the DCMD neuron an illusion of continuous motion requires image edges to move over neighboring or near-neighboring ommatidia. The stimuli used by Hatsopoulos et al. (1995) clearly fail to do this in the latter stages of object approach.

#### DISCUSSION

Previously we have shown that responses by the DCMD to computer-generated, simulated movements of a single edge at a constant velocity are sensitive to the size of jumps with which the edge moves across the eye (Simmons and Rind 1992). Single edges that jump in steps of  $10^\circ$  generate

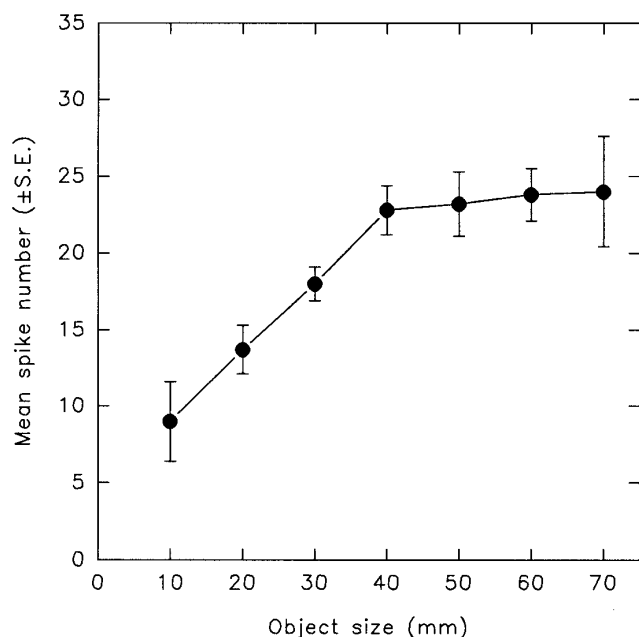


FIG. 3. Plot of square size against mean response from 5 repetitions. Details as in Fig. 2.

responses that are less than half those to edges that move the same distance and at the same velocity in jumps of  $3^\circ$ . Generally, Hatsopoulos et al. (1995) presented locusts with large images (subtense  $82^\circ$  in their Fig. 2A). They employed a Hewlett-Packard Graphics workstation, where the screen was refreshed at 72 Hz. It is inevitable that their stimuli involved large jumps in image size, although they do not provide a monitor of image size. Our results have shown, first, that the DCMD can follow individual screen refreshes at 72 Hz and, second, that large image jumps generate relatively poor responses. When images are large on the screen, approach movements must be represented by simultaneous change in intensity of relatively large areas of the screen, and this causes breakdown of the illusion of smooth movement for the DCMD. We suggest therefore that the premature peaking in DCMD response reported by Hatsopoulos et al. (1995) is an artifact, rather than a true description of the response characteristics of the DCMD.

Hatsopoulos et al. (1995) claim that the responses by the DCMD to approaching objects are described by an equation that represents the product of the instantaneous angular velocity of the image and an exponential function of the size of the image. The equation includes a constant, the delay between stimulus and response, which was set to 0–40 ms. In fact, the latency of response to a moving object (at  $20^\circ\text{C}$ )

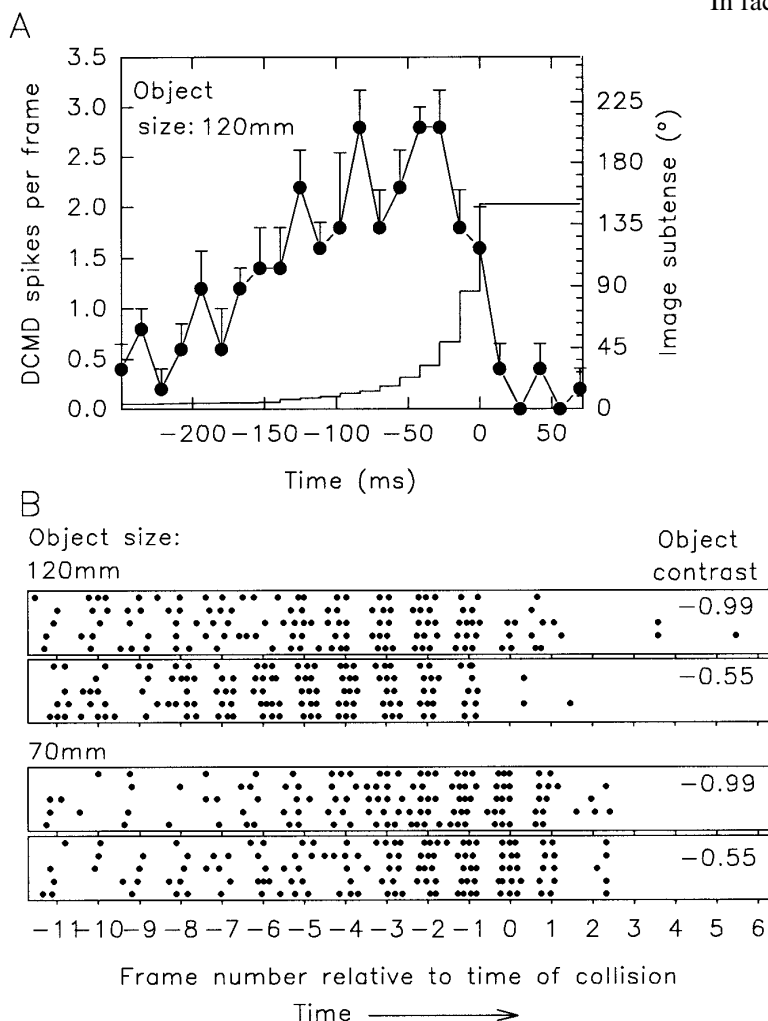


FIG. 4. Responses by the DCMD to images of approaching squares displayed on a graphics computer VDU screen, refreshed at 72 Hz. The screen was 70 mm from the eye; images simulated square objects approaching the eye at 2.5 m/s. *A*: number of spikes per frame of simulation (mean  $\pm$  SE) plotted for 5 approaches of a square with 120-mm sides and contrast  $-0.99$ . Conditions match those in Fig. 2A and those in Fig. 3Cii of Hatsopoulos et al. (1995). *B*: times of spike occurrence for 5 repetitions of the approach of a square with sides measuring 120 or 70 mm. For each object size, experiments were conducted at contrasts of  $-0.99$  and  $-0.55$  (top and bottom, respectively). The timing of each 13.9-ms frame is indicated; collision would have occurred at time 0.

is  $\geq 60$  ms, and varies with speed of the image across the retina (Simmons and Rind 1992). The equation of Hatsopoulos et al. fails to account for some of the important properties of the DCMD, particularly for responses to receding objects, which are intense but brief periods of excitation followed by inhibition (Rind 1996; Rind and Simmons 1992). The equation of Hatsopoulos et al. (1995) predicts a mirror image of the response to approaching objects. We have proposed (Simmons and Rind 1992) that the input organization of the DCMD neuron can be represented as a critical race between excitation as image edges reach successive retinotopic units and inhibition that spreads both laterally between these units and forward around them. A model based on this organization simulates the responses by the DCMD and its presynaptic neuron to many types of visual stimuli (Rind 1996; Rind and Bramwell, 1996), and is consistent with the known physiological organization of the optic lobe. Although the equation of Hatsopoulos et al. (1995) generates a function that could be used to warn of collision, it cannot adequately describe the input organization of the DCMD.

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## REFERENCES

- HATSOPoulos, N., GABBIANI, F., AND LAURENT, G. Elementary computation of object approach by a wide-field visual neuron. *Science Wash. DC* 270: 1000–1003, 1995.
- RIND, F. C. Intracellular characterization of neurons in the locust brain signalling impending collision. *J. Neurophysiol.* 75: 986–995, 1996.
- RIND, F. C. AND BRAMWELL, D. I. Neural network based on the input organization of an identified neuron signalling impending collision. *J. Neurophysiol.* 75: 967–985, 1996.
- RIND, F. C. AND SIMMONS, P. J. Orthopteran DCMD neuron: a reevaluation of responses to moving objects. I. Selective approaches to approaching objects. *J. Neurophysiol.* 68: 1654–1666, 1992.
- SIMMONS, P. J. AND RIND, F. C. Orthopteran DCMD neuron: a reevaluation of responses to moving objects. II. Critical cues for detecting approaching objects. *J. Neurophysiol.* 68: 1667–1682, 1992.