IS THE LOCUST DCMD A LOOMING DETECTOR?

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To a prey, a salient visual characteristic of an approaching predator is 'looming', a figure of average subtended visual angle increasing as some function of time. If the approach is at constant velocity, two important characteristics of the looming figure are an ever increasing velocity (i.e. acceleration) of sideways motion of edges away from the centroid of the figure, and the opposed motion of opposite edges. These characteristics make looming objects distinct from translation of single objects across the visual field, so that the visual looming characteristics may have value in warning of approaching predators. In the locust, a visual neurone, the DCMD (descending contralateral movement detector) in the ventral nerve cord forms an important input to the interneurones triggering the jump response in the locust (Pearson, Heitler & Steeves, 1980; Pearson & Robertson, 1981). Thus it is of considerable interest to determine whether the DCMD responds preferentially to looming visual stimuli.

The responses of the DCMD have been characterized quantitatively and in considerable detail (Palka, 1967; Rowell, O'Shea & Williams, 1977; Pinter, 1977, 1979). The DCMD responds vigorously to translation movements across the visual field of small objects (subtending 2–10° of visual angle at the surface of the compound eye) within the receptive field of approximately a hemisphere. The polar axis of this hemispheric visual field runs approximately lateral to and through the centre of the animal's contralateral compound eye. Movements of large textured objects, or of the animal itself in a textured visual environment elicit only weak DCMD responses. Schlotterer (1977) measured the response of locust DCMD to looming and translating objects, and found that looming objects were more potent stimuli than translating stimuli. However, we have found that translating objects are as potent stimuli as looming objects.

We have examined this question in a series of experiments on *Schistocerca americana*, both male and female from the University of Washington colony, and on a male from the University of British Columbia colony. The ventral nerve cord was exposed between the first and second thoracic ganglia and gently hooked with a silver-wire

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electrode, insulated with Vaseline; a ground electrode was placed in the abdomen. I̶ the data presented here, the interstimulus interval (ISI) was 30 s, with the two initial trials of a run of one stimulus type discarded to lessen effects of habituation. (Similar results were confirmed with 60 s ISI's.) The ipsilateral eye and the three ocelli were covered with opaque acrylic paint and the ears were waxed closed. Control experiments were run with an optical window to ascertain whether air currents produced by looming stimuli were affecting DCMD responses. In no case were air-current effects found.

In these experiments the animal's compound eye was presented with looming and translating stimuli made from black paper and attached to an arm joined to the moving carriage of an $X-Y$ recorder which was driven by function generators. The light background behind these dark stimuli was white illustration board illuminated by two 15 W d.c.-powered fluorescent lamps with reflectors, at a distance of approximately 1·5 ft. The luminosity of this background was approximately that under daylight from an overcast sky.

For the looming stimulus of a black circular object (disc) approaching the animal, the possible range of approach velocity and size change is limited by the apparatus and difficulties of interpretation of spike trains over widely differing stimulus intervals. The range utilized was a maximum of 5–135° in 1 s. Then translating stimuli were chosen on the basis of this visual size range. The velocity of translation was chosen on the basis of the sideways (i.e. perpendicular to the axis of approach) motion of the edge of a looming stimulus. This velocity is

$$\frac{d\Theta}{dt} = \frac{(57\cdot3)\,vy}{x^2+y^2} \quad \text{deg of visual angles/s,}$$

where v is the constant velocity of approach, x the distance at any point in the loom between the looming object and the compound eye, and y the distance from centre (axis of approach) to edge of the looming object, each in consistent units. For a disc of 2 cm radius looming from 10 to 67·5° in 1 s at a constant velocity v cm/s the visual angular velocity has a range of 3°/s at size 10° to 173°/s at size 67·5°. This accelerated motion was also used for translated stimuli in some experiments, and it was generated by a nonlinear rising function synthesized with electronic multipliers and operational amplifiers.

In Fig 1 the spike train recorded from the DCMD is shown for a single trial of both a typical looming stimulus (parameters as in Schlotterer, 1977) and a comparable translating stimulus. The time histograms of spikes for 10 trials of these same responses are shown in Fig. 2A, with spike frequency counts (peak and average) shown in Table 1. In the sequence of conditions the looming followed the translating stimulus, but this entire experiment, lasting for 3·75 h, was without decrement in sensitivity to. control stimuli. It can be seen that looming is not a more potent stimulus than translation. All experiments on other animals verified this result. In addition, looming stimuli of larger range (5–90° and 6–135° over 1 s) could not be shown to be more potent than comparable translating stimuli. Table 2 shows that looming of sectors of dark discs (one-half and one-quarter) centred on the eye were as potent as looming

Fig. 1. DCMD spike traces (A) Response to rapidly approaching dark circular object (looming) on a light uniform background; loom begins at left edge of trace and continues for 1 s, the size changing from 10 to 67·5° of visual angle in that period; trajectory of loom is directly medial toward the centre of the animal's compound eye; the velocity in anterior and posterior directions of the respective edges of the looming object at its final size (67·5°) is 173°/s, (B) DCMD spike train in response to an 8° dark square on the same light background as (A), moving with constant velocity of 90°/s on a trajectory in the anterior–posterior direction, directly lateral to the animal; the extent of travel of the square is +45° to −45° (0° is directly lateral to the animal on a line through the centre of the compound eye, and positive angles are anterior of 0°) during 1 s; calibration bar 100 ms, temperature 25–26 °C, Exp. 7/8/81.

Table 1. *Peak and average spike frequency, means and standard deviations over ten trials following two trials discarded to reduce effects of habituation*

	Looming disc 10–67·5°	Translation of 8° square, 90°/s
Peak spike frequency/s	107 ± 26	117 ± 24
Average spike frequency/s	19 ± 6	21 ± 5
Data of figure	1A, 2Ai	1B, 2Aii

Average spike frequency based on count for period of stimulation to 1·1 s from stimulus initiation. Peak spike frequency based on count for a 30 ms period set by an electronic peak detector. Inter-stimulus interval 30 s. These counts are for the data of Figs. 1 and 2A.

of entire circles, and accelerated motion of edges of both fixed and expanding size was not more effective than constant-velocity motion. Thus looming is not a more potent stimulus than translation. Furthermore, the salient components of the looming stimulus such as acceleration of edges (in units of visual angle) and opposed motion of opposite edges are not especially potent DCMD stimuli. Schlotterer's (1977) conclusion, that looming stimuli are more potent than translating stimuli, results from his choice of a rather weak translating stimulus, one whose velocity never approaches that achieved by the edges of the looming stimulus.

Examination of Fig. 2A will show that the looming response is bimodal (as in Schlotterer, 1977), and that the later peak is larger than the earlier peak. This hiatus in activity is a robust property of the DCMD response, and is not a function of the frequency of spike firing during the first peak. Since the later peak is the larger, we examined the relative effects of looming and translation on it. These results are demon-
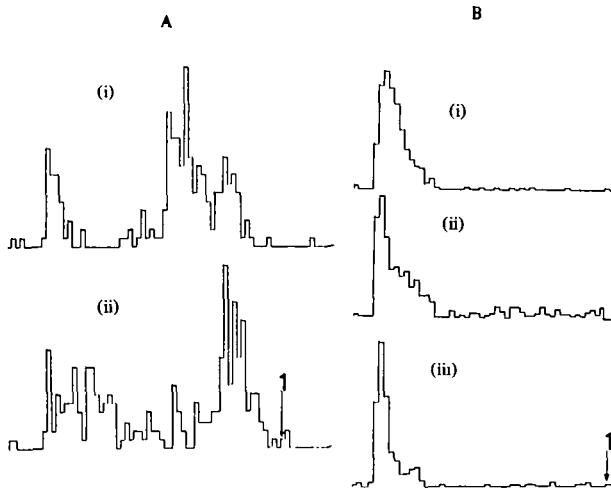
Fig. 2. (A) Time histograms of the DCMD spike response for ten trials of the experiment of Fig. 1, A(i) Looming response to size change 10–67·5°. A (ii) Translation response to moving 8° square. Stimulus begins at left edge of traces, time bins are 20 ms. Calibration at arrow, one spike. All parameters as in Fig. 1. Exp 7/8/81. (B) Time histograms of DCMD spike response to the last 200 ms of a 10–67·5° loom and to comparable translations. B (i) response to loom of dark circular object, size changing from 32 to 67·5° in 200 ms, beginning at left edge of the trace. B (ii) response to 8° dark square moving from directly lateral to a posterior position, from 0° to −35°, at 173°/s for 200 ms. B (iii) Response to 67·5° circular object translating as in B (ii). Time bins, 20 ms. Arrow, calibration level for one spike. Temperature, 22 °C. All other parameters as in Fig. 1. Expt 21/8/81.

Table 2. *Peak and average spike frequencies, means and standard deviations over 10 trials.*

	Full-disc loom	Hemi-disc loom	Quadrant-disc loom
Peak spike frequency/s	167 ± 33	167 ± 33	167 ± 33
Average frequency/s	48 ± 25	52 ± 18	51 ± 15

	60° tongue translation accelerated	15° tongue translation accelerated	expanding edge, 0–67·5°, accelerated	expanding edge, 0–67·5°, 30°/s
Peak spike frequency/s	133 ± 33	100 ± 33	167 ± 33	167 ± 33
Average spike frequency/s	26 ± 24	25 ± 15	42 ± 19	48 ± 13

Full disc, hemi-disc and quadrant disc are dark looming stimuli on light background, centred on the looming trajectory through the centre of the compound eye directly lateral to the animal, and are respectively a full circular object, a half circular and a quarter of a circular object. The looming size change in each case is 10–67·5° centre to outer edge of the object, over 1 s. The 60° and 15° circular-edge tongues were advanced from directly lateral to posterior, 0° to −30°, in accelerated motion obtained by a fit of the function $(ax^2 + bx^4)$ to the actual sideways (normal to looming trajectory) velocity of the edge of the 10–67·5° looming stimulus; initial velocity of accelerated motion was 17°/s and final velocity 200°/s; the tongue edge moved over the 30° in 0·9 s. This same accelerated motion was given the 0–67·5° expanding edge, as well as the constant velocity of 30°/s in the last entry. Peak frequency numbers have round-off errors of approximately the standard deviation in this case. Temperature 24 °C, Expt 30/7/81, other parameters as in Table 1.

Table 3. *Comparison of peak and average spike frequency means and standard deviations for the experiment of Fig. 2B*

	Looming disc $32–67\cdot5°$	Translation of 8° square, $173°/s$	Translation of 67° square, $173°/s$	Looming disc $10–67\cdot5°$
Peak spike frequency/s	307 ± 38	297 ± 29	327 ± 26	203 ± 40
Average spike frequency/s	100 ± 20	92 ± 4	71 ± 19	76 ± 10
Data of Fig. 2	B (i)	B (ii)	B (iii)	(Experiment of Fig. 2 B)

For the $32–67\cdot5°$ loom, 8° square translation and 67° square translation the average spike frequency count period is 300 ms. All other parameters as in Table 1 and Fig. 2B.

strated in Fig. 2B and Table 3, where again no preference for looming over translations of objects can be inferred. Fig. 2B also demonstrates a possible systematic relationship between edge size and preferred velocity, but that is the subject of a separate investigation. The peak spike frequency certainly does increase with the velocity of a moving edge, but not with acceleration (Tables 2, 3). The increase of peak frequency at higher velocity may be a function of 'lack of time' to set up lateral inhibition (Rowell *et al.* 1977; Brodie, Knight & Ratliff, 1978 (in *Limulus*)), as can be demonstrated from quantitative models, such as the Hartline–Ratliff equations in their complete time- and space-dependent form (Brodie *et al.* 1978).

The form and magnitude of the DCMD response to looming and translation varies with stimulus location in the receptive field, but within any given region no preference for looming could be found. Further, no preference can be found for looming stimuli for parameters beyond those stated above, e.g., very small size expanding rapidly or very large size expanding slowly.

The existence of looming and changing-size responsive neurones is an old and intriguing question. They have been demonstrated and their properties measured in visual cortex of the cat (Regan, Beverley & Cynader, 1979). However, our results do not confirm Schlotterer's (1977) suggestion that the locust DCMD responds preferentially to looming stimuli.

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