

Orthopteran DCMD Neuron: A Reevaluation of Responses to Moving Objects. I. Selective Responses to Approaching Objects

F. CLAIRE RIND AND PETER J. SIMMONS

Division of Neurobiology, School of Neuroscience, University of Newcastle upon Tyne, Newcastle upon Tyne NE1 7RU, United Kingdom

SUMMARY AND CONCLUSIONS

1. The "descending contralateral movement detector" (DCMD) neuron in the locust has been challenged with a variety of moving stimuli, including scenes from a film (Star Wars), moving disks, and images generated by computer. The neuron responds well to any rapid movement. For a dark object moving along a straight path at a uniform velocity, the DCMD gives the strongest response when the object travels directly toward the eye, and the weakest when the object travels away from the eye. Instead of expressing selectivity for movements of small rather than large objects, the DCMD responds preferentially to approaching objects.

2. The neuron shows a clear selectivity for approach over recession for a variety of sizes and velocities of movement both of real objects and in simulated movements. When a disk that subtends $\geq 5^\circ$ at the eye approaches the eye, there are two peaks in spike rate: one immediately after the start of movement; and a second that builds up during the approach. When a disk recedes from the eye, there is a single peak in response as the movement starts. There is a good correlation between spike rate and angular acceleration of the edges of the image over the eye.

3. When an object approaches from a distance sufficient for it to subtend less than one interommatidial angle at the start of its approach, there is a single peak in response. The DCMD tracks the approach, and, if the object moves at 1 m/s or faster, the spike rate increases throughout the duration of object movement. The size of the response depends on the speed of approach.

4. It is unlikely that the DCMD encodes the time to collision accurately, because the response depends on the size as well as the velocity of an approaching object.

5. Wide-field movements suppress the response to an approaching object. The suppression varies with the temporal frequency of the background pattern.

6. Over a wide range of contrasts of object against background, the DCMD gives a stronger response to approaching than to receding objects. For low contrasts, the selectivity is greater for objects that are darker than the background than for objects that are lighter.

INTRODUCTION

As an object moves on a path directly toward the eyes, the size of the image on each eye and the disparity between the images on the two eyes increase. Neurons or psychophysical channels that respond selectively to one direction of motion in depth have been shown to be sensitive either to changes in image size (Regan and Beverley 1978; Regan and Cynader 1979; Zeki 1974) or to binocular disparity (Cynader and Regan 1978, 1982; Hong and Regan 1989; Orban et al. 1986; Pettigrew 1973; Poggio and Talbot 1981; Roy and Wurtz 1990). In this paper we demonstrate that

an identified neuron in the visual system of the locust, the "descending contralateral movement detector" or DCMD (Rowell 1971a) responds more vigorously to the images of an object that is approaching toward, rather than receding from, its eye. Another identified visual neuron, the "lobula giant movement detector" or LGMD (O'Shea and Williams 1974) is the major source of synaptic input to the DCMD, and each spike in the DCMD follows a spike in the LGMD, up to frequencies of at least 400 Hz (Rind 1984). The only cues used by these neurons are monocular, which means that changing image size or *looming* is the effective stimulus, rather than binocular retinal disparity.

The LGMD/DCMD neurons are two of the most widely known visual neurons. The generally accepted view of the function of these neurons, given for example in the textbook "*Neurobiology*" (Shepherd 1988), is that they respond optimally to rapid movements of small objects in the visual field. This classical interpretation of the preferred stimulus for the LGMD/DCMD neurons arose historically from the experiments of Palka (1967a,b), who used luminance changes (light ON or OFF) of an area of retina whose size was altered with the use of an iris diaphragm: as the size of the area increased, the response (measured as spike numbers) declined. Palka concluded that the optimal stimulus was dimming of a small target. Other investigators (Rowell et al. 1977) repeated the experiment with the use of light ON or light OFF stimuli and confirmed the preference for small size stimuli. The response of the LGMD/DCMD neurons for moving stimuli of various sizes was not systematically investigated. A moving dark target was considered to be mimicked by a succession of light OFF stimuli (Edwards 1982; Rowell 1971). Motion of periodic stimuli such as moving striped patterns, confirmed the preference of the DCMD for small ($<30^\circ$) stimuli (Rowell et al. 1977; O'Shea and Rowell 1975). The DCMD gave little or no response to stimuli when they subtended $>30^\circ$. Periodic stimuli were also found to suppress the response of the DCMD to a previously excitatory stimulus. This suppression was found to depend on the spatial separation of the two stimuli and was thought to confirm the presence of lateral inhibition between input elements to the LGMD.

The organization of the inputs onto the LGMD neuron in the lobula, responsible for generating such response preferences, have as yet only been studied indirectly. The dendritic fan of the LGMD is thought to receive excitatory inputs from a retinotopic array of small-field units responding both to light ON and to light OFF. Lateral inhibitory

interactions occur between neighboring units and were thought to confer on the LGMD a preference for small over large objects (Edwards 1982; O'Shea and Rowell 1975; Rowell et al. 1977). The synapses from these small-field units onto the LGMD are likely to be the sites for habituation shown in the response by the LGMD to repeated stimulation of the same area of retina (Rowell et al. 1977). Lateral inhibition among the units protects the synapses onto the LGMD from habituation by movement, of the whole visual field, or of large objects. In addition to these excitatory inputs, the LGMD is thought to receive inhibitory inputs at synapses on discrete dendritic branches of the LGMD proximal to the convergence of the excitatory inputs on the main dendritic fan (O'Shea and Rowell 1976; Rowell et al. 1977), although Rind (1987) noted that the LGMD2, which lacks any such dendritic branches, also receives large inhibitory postsynaptic potentials (IPSPs), which appear to have a similar origin to those seen in the LGMD.

In a challenge to the prevailing view that the DCMD is selective for movements of small objects, Schlotterer (1977) compared its responses to approaching and receding disks. He found that the stronger responses were given to the approaching disks, with the strongest responses at an image subtense normally thought to inhibit the DCMD. Pinter et al. (1982) repeated Schlotterer's experiments but found no greater response to an approaching object, compared with a translating one. In this study we used the video Star Wars to challenge the LGMD/DCMD neurons with a range of visual scenes filmed from the viewer's perspective. Star Wars contains sequences showing the following: rapidly approaching objects that were either on a collision course or passing over the viewer; translatory movement of

small objects or of edges within a horizontal or vertical plane; and flow fields that would be created by the rapid movement of the viewer forward through textured surroundings. Real and computer-generated images of approaching or receding objects led to the identification of the optimal stimulus for the DCMD as a rapidly approaching object.

METHODS

Experiments were performed on 97 adult *Locusta migratoria*, obtained from a commercial supplier. Locusts were mounted dorsal side up, and hook electrodes were manipulated under the cervical connectives to make extracellular recordings from the axon of the DCMD. In a few experiments, intracellular recordings were also made from the axon of the DCMD to confirm the response preference of the neuron. The head was immobilized but not otherwise disturbed. Stimuli were monocular and separated by intervals of at least 40 s. Spikes were recorded extracellularly and discriminated by a spike processor (Digitimer), which converted each DCMD spike into a pulse. The pulses were then displayed and analyzed. Temperature was maintained above 24°C throughout the experiments.

Three different kinds of visual stimuli were used. In our initial experiments, locusts viewed an edited version of the video of the film Star Wars. A color television monitor (160 × 140 mm) was placed parallel to the longitudinal axis of the body, 100 mm lateral to one compound eye. The electroretinogram flicker fusion frequency (Pinter 1972) and the impulse response and angular acceptance curves of locust photoreceptors (Howard et al. 1984; Wilson 1975) indicate that they would not resolve each individual half frame of a video, so that this method presents realistic scenes. DCMD spikes were converted to pulses by a window circuit (Digitimer) and were dubbed onto the copy of the video made simultaneously, by splitting the signal between the television monitor that

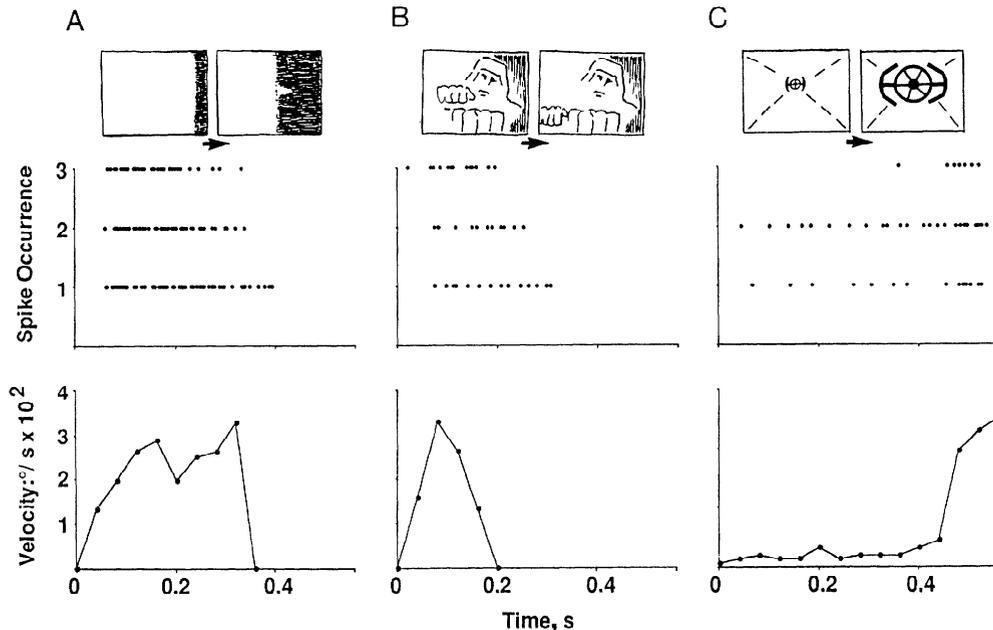


FIG. 1. Descending contralateral movement detector (DCMD) neuron gave consistent responses to particular scenes in a video recording of the film Star Wars. For each of 3 scenes (A–C), the movement that the locusts viewed is depicted by 2 sketches of individual frames during the movement. *Middle panels*: times of occurrence of DCMD spikes in each of 3 locusts (1, 2, and 3). *Bottom panels*: angular velocity of the movement of an edge or object across the eye. A: sudden movement of an extended dark edge from right to left [contrast, -0.71 ; contrast = $(I_{\text{Object}} - I_{\text{Background}})/I_{\text{Background}}$]. B: brief translating movement, from right to left (contrast, ≤ 0.2). C: approaching object (contrast, ≤ 0.2).

the locust viewed and a second video recorder. This preserved the temporal relation of the DCMD spikes and the stimuli on the video that elicited them. These spikes were subsequently related to events on the screen by monitoring movements in the scene with a photocell. Each 0.56-s segment of video analyzed contained 28 individual half frames. During each segment, edge movement was restricted to the single object or area indicated in each scene.

The second visual stimulus consisted of a black disk mounted on the arm of an x - y plotter, moving at a uniform velocity directly toward, or away from the locust. Movements were controlled by a microcomputer and were monitored by using a photocell. Disks of four different radii were used: 10, 16, 25, and 75 mm. Each disk was moved at three speeds: 0.53, 0.41, and 0.27 m/s. The trajectory of the movement was at 45° to the longitudinal axis of the locust, directed posteriorly and directly toward the eye. Each movement was repeated five times at 1-min intervals. A removable shield prevented the contralateral eye viewing the stimulus, and a glass window prevented air currents from stimulating the DCMD during disk movement. Movement of the x - y plotter arm without a disk evoked only 1–2 spikes in the DCMD. For each combination of disk size and approach velocity, the response of the DCMD was filmed and the response divided into bins each representing disk travel of 24.3 mm ($1/10$ of the total travel). The bins were equivalent to intervals of 46 ms at a disk speed of 0.57 m/s; 60 ms at 0.41 m/s; and 92 ms at 0.27 m/s. The spikes occurring in each interval were counted and mean spike numbers for each interval calculated. The subtense of the disk on the eye, γ , was then calculated with the use of the formula $\gamma = 2 \tan^{-1}(r/z)$, where r is the radius of the disk and z is the distance of the disk from the eye. The response of the DCMD could then be related temporally to a specific image size. In addition, these measurements allowed a comparison of the DCMD response to disks of the same image size but with different angular velocities. The data are presented as groups of offset histograms generated by the use of graphics programs written with "Spike 2" software. The angular subtense of the disk is shown at the bottom of each stack of histograms.

The third type of stimulus was a computer-generated image displayed on a 608 Monitor Screen (Tektronix). The screen was parallel to the long axis of the locust, with its center 100 mm from the locust's right eye. Screen dimensions were 120 by 100 mm. Unless otherwise stated, the background screen intensity was

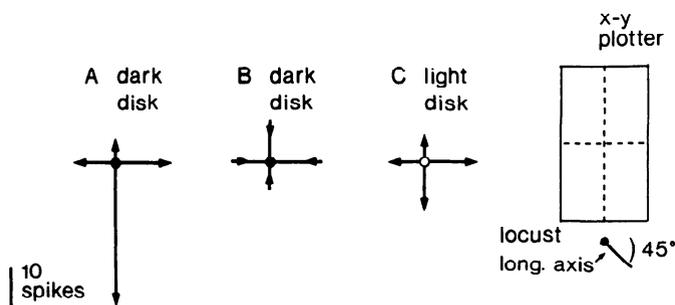


FIG. 2. Comparison of responses by the descending contralateral movement detector to approaching, translating, and receding disks. Diagram on the right depicts the relationship between the locust and the x - y plotter. Filled circle indicates the locust's head, and dotted lines indicate the paths along which the disks traveled. A: a dark disk was initially positioned 210 mm from the eye, at the center of the x - y plotter. Numbers of spikes produced in response to equivalent movement by the disk in each of the 4 directions shown by arrowheads are indicated by the lengths of the lines (means of 3 repetitions; standard errors lay within the extent of an arrowhead). B: as A, except that movements of the disk were toward the center of the x - y plotter. C: responses to movements of a light disk away from the center of the plotter, as A. Each movement of the disk was 110 mm, at a velocity of 0.5 m/s. Initially the disk subtended 13.6° at the eye.

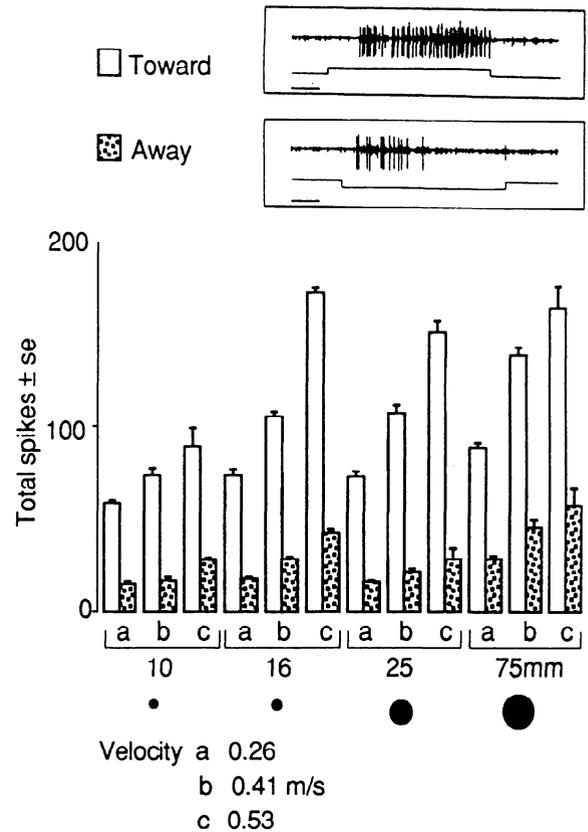


FIG. 3. Directional response of the descending contralateral movement detector (DCMD) neuron to motion of a black disk toward and away from the eye. Spikes were elicited by a black disk moving against a white background. Four different sizes of disk were used, radii 10, 16, 25, and 75 mm; and each disk was moved at 3 different velocities (a, b, c). Disks were mounted on the arm of an x - y plotter, driven by ramp voltage changes. For each movement type, the mean \pm SE of the total number of spikes/second produced over 5 repetitions is shown. Inset: extracellularly recorded DCMD response to the motion of a 16-mm radius disk at 0.4 m/s toward, or away from, the eye (top trace). Motion of the disk toward or away from the eye is indicated by an upward or downward step on the bottom trace. Scale bar represents 100 ms.

4.12×10^{-2} mW/cm², and objects, which moved against this background, had an intensity of 1.64×10^{-3} mW/cm². The screen has a standard P30 (green) phosphor. The refresh rate for the screen was 100 Hz, and an "RG1" board (Cambridge Research Systems, Sidcup, Kent, UK) generated a raster with 200 horizontal lines. This refresh rate is unlikely to cause appreciable flicker on a locust's photoreceptors (Howard et al. 1984; Pinter 1972; Wilson 1975) and enables a resolution of 1,024 parts along each of the horizontal lines. Images were generated on a VSG2 board (Cambridge Research Systems), fitted in a microcomputer. Most images generated on the screen were of expanding or contracting rectangles. A rectangle was a window created in one visual grating, through which a second grating can be seen. In most experiments the visual gratings consisted of a field of uniform intensity. A trace that provides a monitor of the image size was generated by a D-to-A converter on the VSG2 board, controlled by our software. Rectangles were made to expand by sequentially adding strips to the circumference, and to contract by sequentially removing strips. Rectangles or disks can also be made to expand by overdrawing previous windows, but this method suffers from two serious drawbacks. First, it cannot be applied to contracting shapes, because it is necessary to erase completely one shape before replacing it with a smaller one, and this creates flicker in the image. Second, it can take several screen refresh cycles to generate

a large window. The main advantages of this method of visual stimulation are as follows: first, objects can be made to appear to approach from a considerable distance away from the locust [subtending <1 interommatidial angle (Horridge 1978)] to 100 mm away (subtending up to 55°); second, intensities of both the background and the object can be set at will and independently of each other; and, third, either the background, or the object, or both can be a moving grating instead of a uniform field of color. The simulations of approaching and receding rectangles were realistic to a human observer. Only for the final stage of approach at high speed do the image changes become quite irregular and large, as shown by the monitor of image size. Stimuli were separated by intervals of 40 s, which was a compromise between reducing the effects of habituation and the effects of changes in responsiveness of the neuron. Mean responses (with standard errors) are from six repetitions of identical stimuli in single experiments. Data were analyzed with the use of Spike 2 software (Cambridge Electronic Design, Cambridge, UK).

RESULTS

Responses to Scenes in Star Wars

We initially recorded the responses of the DCMD neuron to a wide variety of images of moving objects and edges. Twenty locusts viewed a videotape recording of the film *Star Wars*. *Star Wars* was chosen because it contained a variety of scenes with different sizes of objects moving at many speeds. We particularly examined responses to movement as follows: directly toward the screen; toward the screen and not on a collision course with the viewer; across the screen; and scenes with flow fields simulating self mo-

tion. The DCMD consistently responded well to sudden, rapid motion of both large and small objects. It was excited by the same scenes in which edges (Fig. 1A) or objects (Fig. 1B) moved rapidly across the screen, and it always responded vigorously to the rapid approach of a spaceship on an apparent collision course with the viewer (Fig. 1C). The DCMD was not excited by the following: objects receding from the eye; objects that passed slowly across the screen; objects that appeared to move over the top of a viewer; or a flow field such as that experienced by an animal moving forward through a textured surrounding. The response of the DCMD to scenes from the *Star Wars* video confirmed that the neuron responded to rapid, sudden movement of small objects but suggested that it also responded strongly to extensive moving edges and to rapidly approaching objects. The approaching objects elicited the strongest response from the DCMD at image subtenses $>30^\circ$ at the eye.

The experiments with the *Star Wars* video suggested that the DCMD gives a directional response to images of approaching versus receding objects. This preference was examined in the following experiments.

Responses to real motion in depth

The preference for approach over recession of an object has been clearly demonstrated for movement of real objects by using an x - y plotter to move disks toward and away from the eye (Figs. 2–5). We also compared the responses to disks translating across the eye at a uniform velocity with the responses to disks approaching or receding from the eye

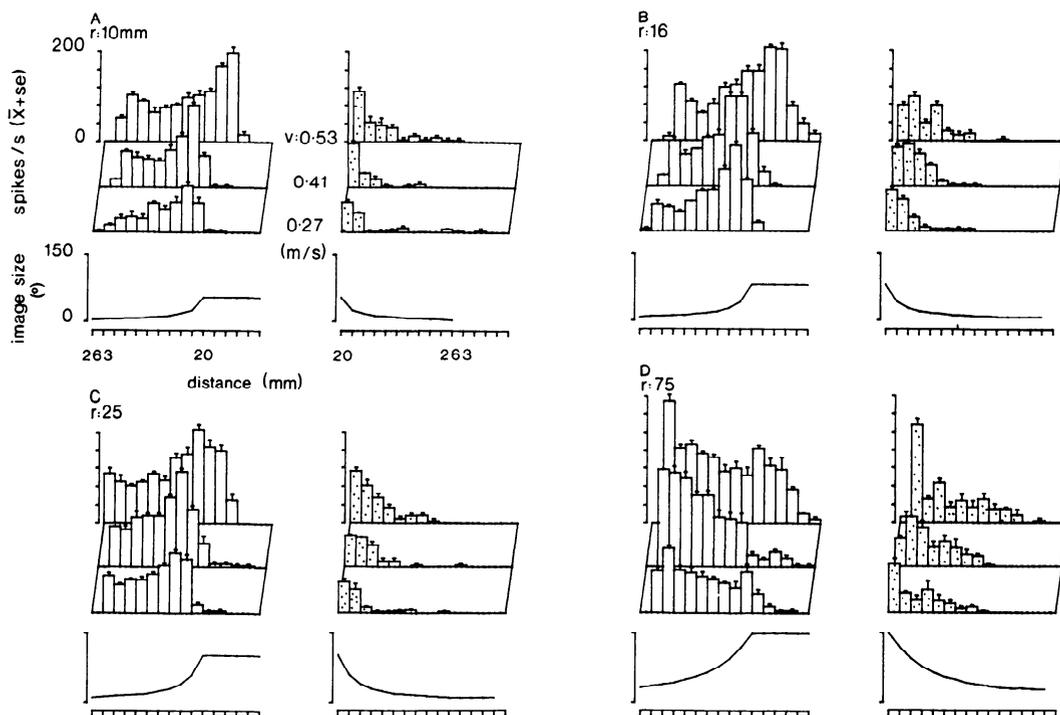


FIG. 4. Changes in the mean spike rate of the descending contralateral movement detector (DCMD) during movement of a black disk toward and away from the eye. Each set of offset histograms, A–D, details the time course of the DCMD response to the movement of a disk of a particular size approaching or receding from the eye at 0.2, 0.4, and 0.5 m/s. Data are from the experiment shown in Fig. 3 and Table 2. In the analysis here, the travel of the x - y plotter arm was divided into 10 equal distances, each of 24 mm. Each bin shows the mean frequency of spikes during travel over 1 of these distances (5 repetitions; error bars are SE). Open bars, disk movement toward the eye; stippled bars, disk movement away from the eye. Subtense of the disk at the eye for each 24-mm interval is shown below each stack of 3 histograms.

at the same velocity (Fig. 2). In the experiment of Fig. 2, a black disk of radius 25 mm was positioned 210 mm from the eye. The disk was moved from this common initial position at a uniform velocity of 0.5 m/s in four different directions: directly toward the eye; directly away from the eye; translating posteriorly; and translating anteriorly. When the disk approached or receded from the eye, it traveled at 45° to the anterior-posterior axis, and the translatory move-

TABLE 1. Directional selectivity in the response of the DCMD to images of approaching versus receding rectangles

Velocity, m/s	Approaching	Receding	Ratio
<i>Experiment 1</i>			
4.2	27.7 ± 0.9	7.2 ± 0.5	3.8
3.2	30.7 ± 1.0	7.3 ± 1.0	4.2
1.8	31.8 ± 1.5	8.5 ± 0.6	3.7
1.0	22.8 ± 2.1	8.5 ± 0.9	2.7
0.4	8.0 ± 2.8	8.0 ± 0.6	2.0
<i>Experiment 2</i>			
10.0	15.0 ± 0.7	1.7 ± 0.3	21.4
5.3	15.8 ± 0.9	1.3 ± 0.5	12.2
4.3	23.5 ± 2.0	1.2 ± 0.3	19.6
2.4	21.7 ± 1.0	2.0 ± 0.8	10.8
1.2	8.3 ± 1.9	3.7 ± 0.5	2.2
0.5	1.2 ± 0.3	1.5 ± 0.6	0.8
<i>Experiment 3*</i>			
10.0	13.3 ± 0.9	4.5 ± 0.6	3.0
5.0	15.2 ± 0.9	4.0 ± 0.4	3.8
3.0	16.0 ± 2.0	4.7 ± 0.5	3.4
2.0	12.3 ± 3.0	4.8 ± 0.1	2.6
1.2	8.8 ± 0.1	4.2 ± 0.1	2.1
0.5	5.8 ± 2.4	6.8 ± 0.1	0.9

Values in Approaching and Receding columns are means ± SE Rectangles moved at a constant velocity, which ranged from 0.4 to 10 m/s. The DCMD response is expressed as the mean number of spikes over the last 0.5 s of movement. In any one experiment, each movement was repeated 6 times. Stimulus details are as described in Fig. 2. DCMD, descending contralateral movement detector. *Experiment plotted in Fig. 2.

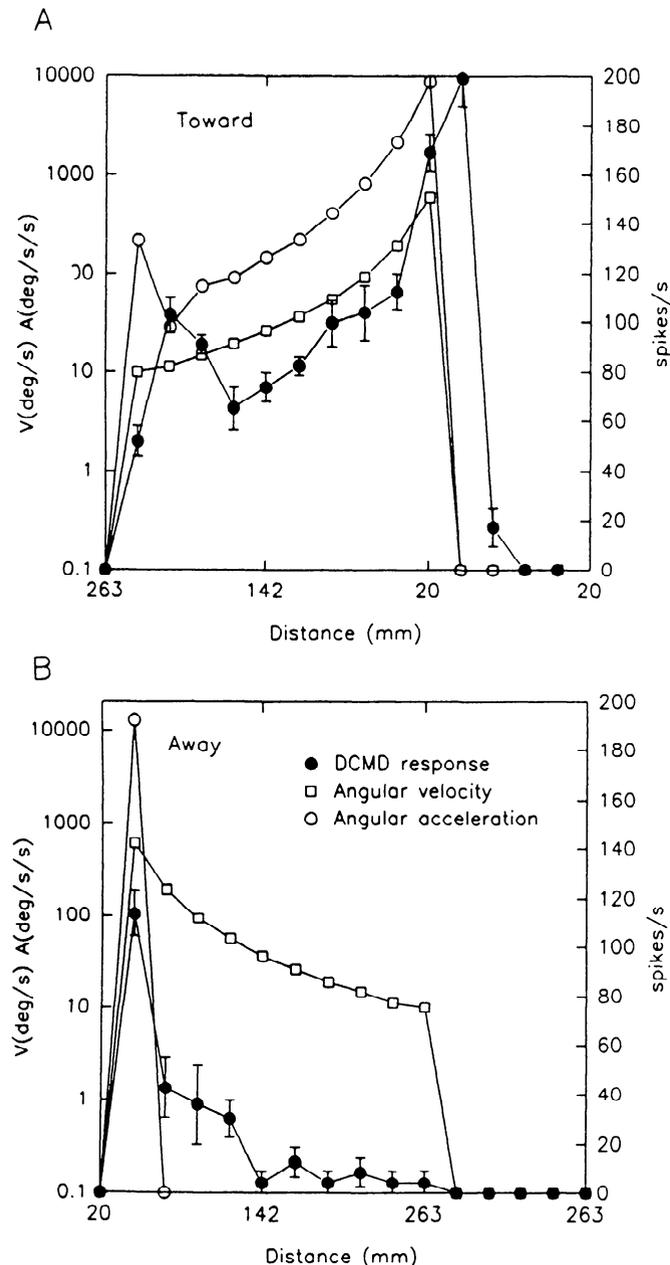


FIG. 5. Descending contralateral movement detector (DCMD) response to approaching or receding disks is well correlated with angular acceleration of image edges. *A*: movement toward the eye. *B*: movement away from the eye. DCMD response (mean spike frequency ± SE); angular velocity; and angular acceleration are plotted against the distance traveled by a disk, radius 10 mm, toward the eye at a velocity of 0.5 m/s. The disk moved between 260 and 20 mm from the eye. Angular velocity (V) and angular acceleration (A) are plotted on a log scale; but the DCMD response is plotted on a linear scale. Angular velocity and angular acceleration were calculated as the change in image subtense ($^{\circ}/s$) and the rate of change in image subtense ($^{\circ}/s/s$), respectively.

ments were along paths at 90° to this direction of travel. The largest response was to the approach toward the eye (37 ± 1.1 spikes, mean ± SE, $n = 3$), and the smallest was to recession from the eye (5.7 ± 1.9 spikes). Translation in the posterior and anterior directions elicited 14.7 ± 0.9 and 11.3 ± 0.7 spikes, respectively. As the velocity of approach was reduced progressively, the response was still greater than that to translating movements, until an approach velocity of 0.2 m/s was reached, which elicited 10.3 ± 0.3 spikes. This experiment clearly shows that a disk that is approaching the eye at a given velocity, and whose image size on the eye is therefore increasing, elicits a greater response than the same disk translating over the eye at the same velocity. A stronger response to approach compared with recession was also found in an experiment where the same dark disk moved toward the initial, common position (Fig. 2*B*), and in an experiment where a light disk moved away from the initial, common position (Fig. 2*C*). In each of these two experiments, the size of the response to approach was between the sizes of the responses to the two translating movements.

For four different sizes and three different velocities of movement of disks, the DCMD showed a clear selectivity for approach over recession. For each size of disk, the strongest response, measured as the mean total number of spikes per stimulus, was evoked by the highest velocity of approach used (Fig. 3). The DCMD responded strongly to the largest size of disk (radius, 75 mm), which subtended 31.8° at the eye at the beginning of the approach. The smallest

responses were to the smallest disk (radius, 10 mm; subtending 4.7° at the beginning of the approach), with numbers of spikes to movements of the three larger disks being about equal for each velocity.

Usually there were two peaks in the spike rate of DCMD during the approach of a disk toward the eye (Fig. 4, A–D). The first peak, which was absent only for the slowest velocity of the smallest disk (Fig. 4A), occurred soon after the start of the approach. After the first peak, the response declined and then, for all but the largest disk (Fig. 4D) increased throughout the duration of the approach. The am-

plitudes of both of the peaks in mean spike frequency during approach increased with disk velocity for each of the four sizes of disk (Fig. 4). The presence of two peaks in the response to approaching disks was also noted by Schlotterer (1977) and is evident in the recordings of Pinter et al. (1982). By contrast, the response of the DCMD to a receding disk shows a single peak, which was sometimes quite strong, at the initiation of disk motion. The latency of the first spike after start of disk movement was consistently smaller for the receding than for the approaching disks. For example, for the smallest disk traveling at 0.3 m/s, the la-

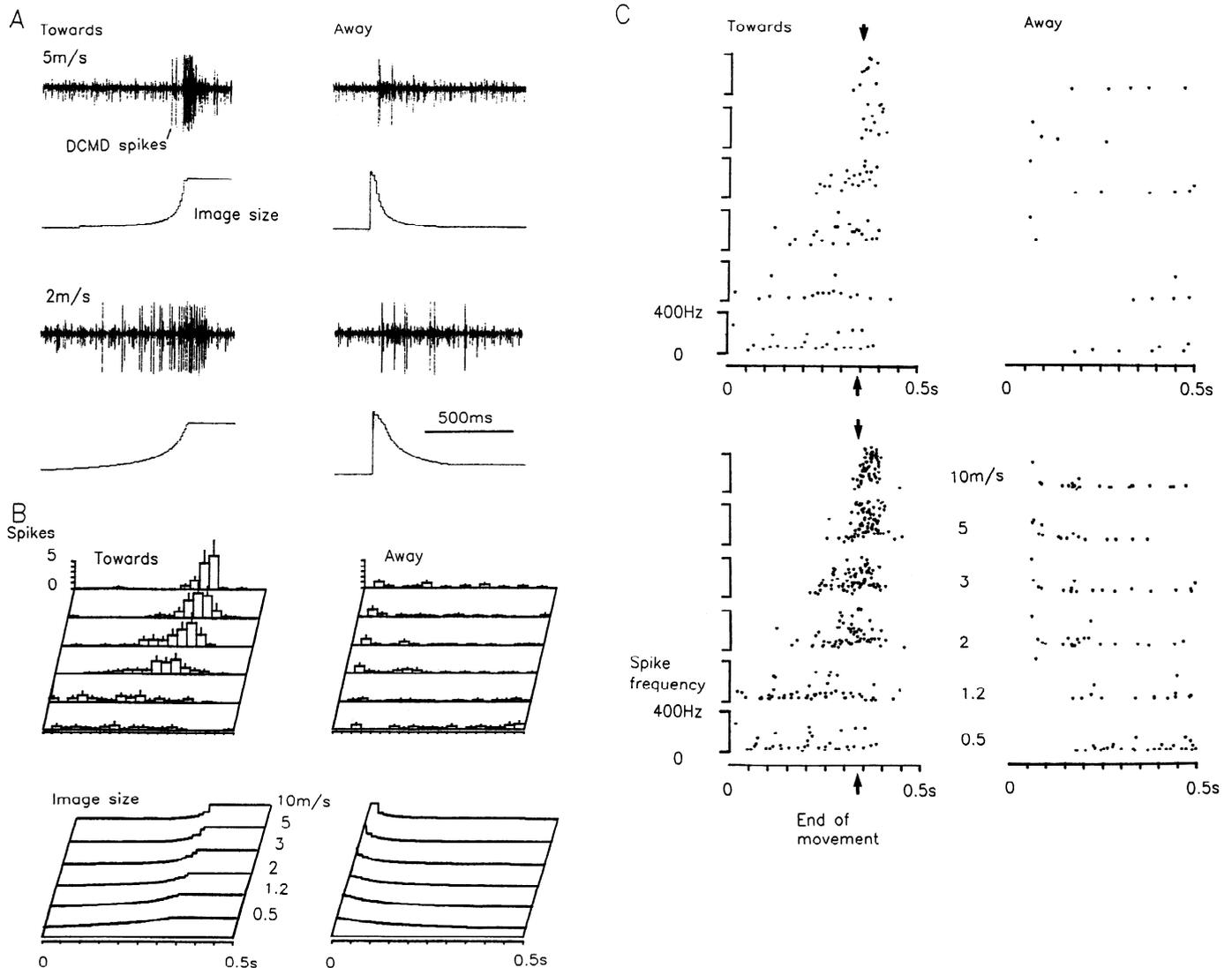


FIG. 6. Descending contralateral movement detector (DCMD) produces directional responses to simulated movements of a rectangle toward or away from the eye. The locust viewed an electrostatic screen 100 mm from its right eye on which the image of a dark rectangle changed between a subtense of $<1^\circ$ and a subtense of $62 \times 53^\circ$ at the eye. Each stimulus was repeated 6 times with a 40-s interval between stimuli. *A*: extracellularly recorded DCMD spikes in response to a rectangle moving at 2 or 5 m/s toward or away from the eye. *Bottom trace* is a monitor of the width on the screen of the rectangle. In the away direction, the monitor trace steps up at the initiation of rectangle movement. *B*: responses of the DCMD to rectangles moving toward or away from the eye at velocities of 0.5, 1.2, 2, 3, 5, and 10 m/s. Each stimulus was repeated 6 times, and the mean \pm SE of the response in 25-ms binwidths is plotted. For movement toward the locust, the records begin 350 ms before the end of the movement, there was no significant response earlier than this. For movements away from the locust, the 1st 500 ms is recorded. Below each set of peristimulus histograms, corresponding monitors of the width of the rectangle are shown. *C*: same responses as *B*, plotted as instantaneous spike frequency. *Top*: responses to single stimuli. *Bottom*: all 6 repetitions of the same stimulus superimposed. On the *left* are responses to simulated movement toward the locust, and on the *right*, responses to simulated movement away from the locust. Abscissa for each graph is to the same scale, with a range 0–400 Hz. Note that these plots are not staggered.

tencies were 110 ± 15.6 (approach) and 25.5 ± 2.3 ms (recession); and for the largest disk, 45 ± 1.7 (approach) and 41.0 ± 0.9 ms (recession). The relatively short latency in the receding direction is consistent with a strong initial excitation of the DCMD.

The response of the DCMD follows angular acceleration of the image much more closely than angular velocity or subtense of the image, during movements both toward (Fig. 5A) and away from (Fig. 5B) the eye. The peaks in the response by the DCMD correlated well with peaks in angular acceleration. As the disk began to move, either toward or away from the eye, there was a brief peak in acceleration, the size of which was largest for movement away from the locust (a 10-mm radius disk starting its recession at 0.5 m/s accelerates from 0 to $600^\circ/\text{s}$ in ~ 50 ms). An initial peak was not reflected in either the subtense or the velocity of the image. After the initial acceleration, angular velocity again increased during approach but decreased during recession. In summary, these results indicate that the DCMD responds strongly to increases in the velocity of the edges of an image over the retina, a salient feature of approaching objects.

Responses to simulated approaching and receding objects

Computer-generated images were used to simulate approach or recession of an object toward or away from the locust at a variety of velocities. The object approached on a collision course with the eye, starting at a sufficient apparent distance for its image to subtend less than one interommatidial angle. As the object approached the eye, the size of its image on the screen, and therefore its subtense on the retina, increased.

Extracellularly recorded responses of the DCMD to the simulated approaches toward or recession from the eye of a

rectangle are shown in Fig. 6A. Responses to two different velocities of simulated movement, 2 and 5 m/s, are shown. Two important characteristics can be seen by inspection of Fig. 6A: first, the response to simulated approach is more vigorous than that to simulated recession; and second, the frequency of DCMD spikes increases during approach. The response of the DCMD was more vigorous and intense to the higher velocity of simulated approach.

Consistently, at all simulated velocities > 1 m/s, images expanding as if they were approaching rectangles elicited more spikes during their movement than did images that contracted as if they were receding rectangles (Fig. 6, A–C; Table 1). The mean numbers of spikes over six repetitions of each stimulus were counted over the final 500 ms during approach, and over the first 500 ms during recession. For velocities > 1 m/s, at least twice as many spikes were produced during approach as during recession. Although the directionality of the response seemed to disappear for velocities of ≤ 0.5 m/s in two of the experiments, the directionality of the response was quite sensitive to the interval between stimuli. For example, in experiment 3 of Table 1, increasing the interval between stimuli from 40 s to 2 min increased the number of spikes elicited by simulated approaches at speeds of ≤ 0.5 m/s, although having little effect on the responses to simulated recession. The number of spikes to a particular stimulus varied between preparations, and in one preparation at different times, especially for recession. The relatively high ratios between spike numbers to approaching versus receding objects in experiment 2 compared with experiments 1 and 3 is largely due to a difference in the vigor of the response to recession.

The DCMD responds throughout the duration of simulated approach, but only for a brief time at the start of simulated recession (Fig. 6, B and C). During approach, only

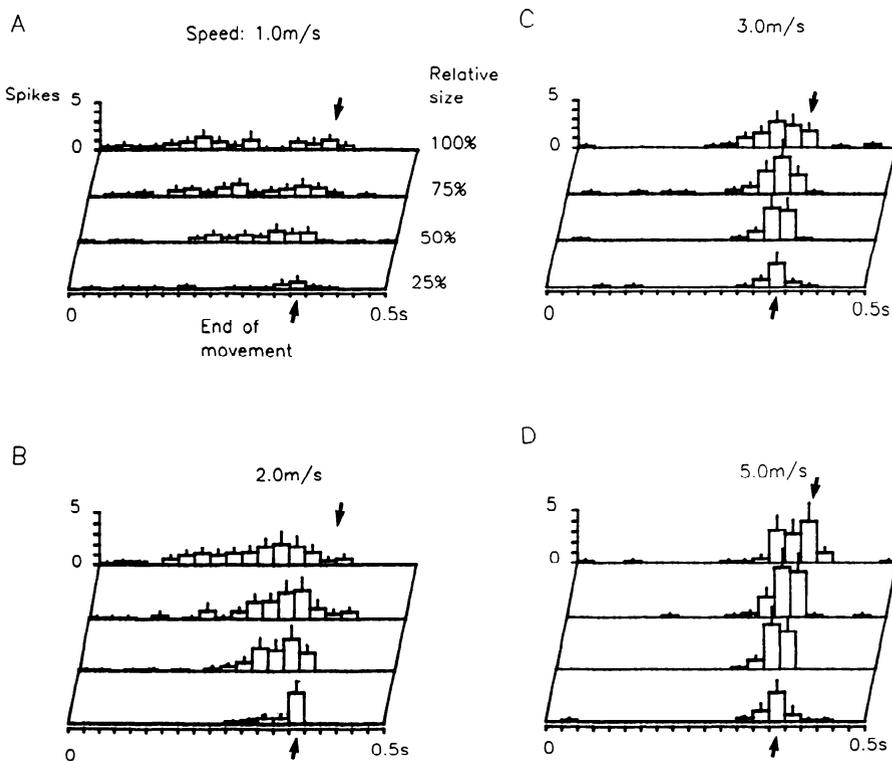


FIG. 7. Responses of the descending contralateral movement detector to the simulated approaches of rectangles of 4 different sizes. Each set of histograms shows responses to approach at one particular velocity: A, 1 m/s; B, 2 m/s; C, 3 m/s; and D, 5 m/s. Relative sizes of the rectangles were as follows: *top histogram* in each set, 1; *2nd histogram*, 0.75; *3rd histogram*, 0.5; and *bottom*, 0.25. The final size on the screen of the largest rectangle was 100×80 mm, and rectangles were darker than the background. Each histogram shows, in 25-ms bins, the mean response \pm SE of 6 repetitions. Each recording begins 350 ms before the end of the approach. Arrows indicate the end of the approaching movement.

one peak in the response was seen in the simulated looms where, unlike the experiments with real movements of disks, the image initially subtended less than one interommatidial angle on the eye and where the initial angular acceleration was low. In the experiment shown in Fig. 6, *B* and *C*, for velocities of approach >2 m/s, the frequency of spikes increased throughout the approach, so that the DCMD tracked object approach. The increase in spike frequency was greatest for the fastest velocities of approach, and the maximum response during an approach, measured either by number of spikes during a 25-ms bin (Fig. 6*B*) or by inspecting records of instantaneous mean frequency (Fig. 6*C*), increased with the speed of approach. Note that these experiments are not directly comparable with those with real movements of disks: contrast of the object against

background and interstimulus intervals were smaller; and the nearest distance of approach to the eye and the velocities of movement were greater.

Responses to approaches of objects of different sizes

A possible function for the DCMD is to provide information on time to collision of an approaching object with the locust. If this is so, then objects of different sizes, approaching at the same speed, should elicit similar responses. For the approach of real disks of different sizes, the clearest effect of increasing object size was to increase the size of the first peak in DCMD response relative to the second peak for each velocity (see Fig. 4). There was no obvious, consistent effect on the amplitude of the second peak. The relationship between the size of the approaching object and re-

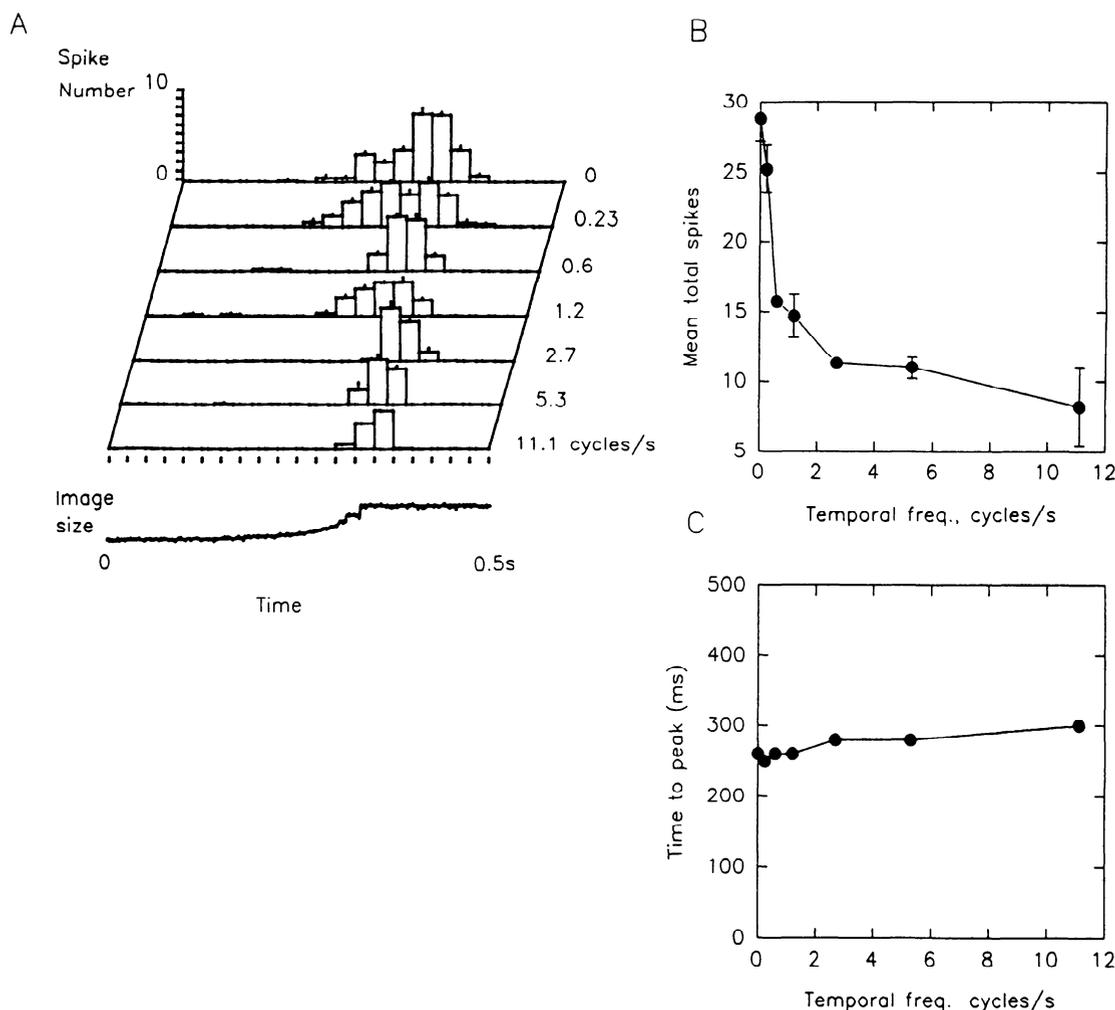


FIG. 8. Suppression of the response by the descending contralateral movement detector (DCMD) to a simulated approach by a drifting grating in the background. The sinewave grating began to move 6 s before the start of the simulated approach of a dark rectangle at 5.5 m/s. The DCMD did not respond to movement of the grating alone. The grating covered the whole of the screen, had a Michelson contrast of 0.78, a spatial frequency of 0.055 ($\lambda = 18.2^\circ$), and moved at a variety of velocities to give temporal frequencies between 0.23 and 11.1 cycles/s (4.2–202°/s). Intensity of the rectangle was the same as the minimum intensity in the grating; casual observations showed that the DCMD also signals approach of a rectangle in the presence of a moving grating when the intensity of the rectangle is the same as the mean intensity of the grating. *A*: histograms of DCMD responses to simulated approaches with gratings of temporal frequency 0, 0.23, 0.6, 1.2, 2.7, 5.3, and 11.1 cycles/s. Records start 350 ms before the end of the approaches. Each 25-ms bin shows mean \pm SE of 6 repetitions. Below the histograms is a monitor of image size. *B*: DCMD response, measured as mean total spike numbers (\pm SE) per stimulus, plotted against temporal frequency of the moving grating. *C*: time to peak of the DCMD response (maximum mean spikes/25 ms) plotted against temporal frequency of the moving grating. Time 0 corresponds with the start of the records in *A*.

sponse was further investigated by the use of simulated movements so that image movement could begin at a very small subtense, without the initial peak in angular acceleration (Fig. 7). The most obvious effect of object size on the

response was that, the larger the object, the sooner the response started and the more gradual was its buildup during approach. Generally, the larger the size of the simulated object, the greater was the total number of spikes elicited by

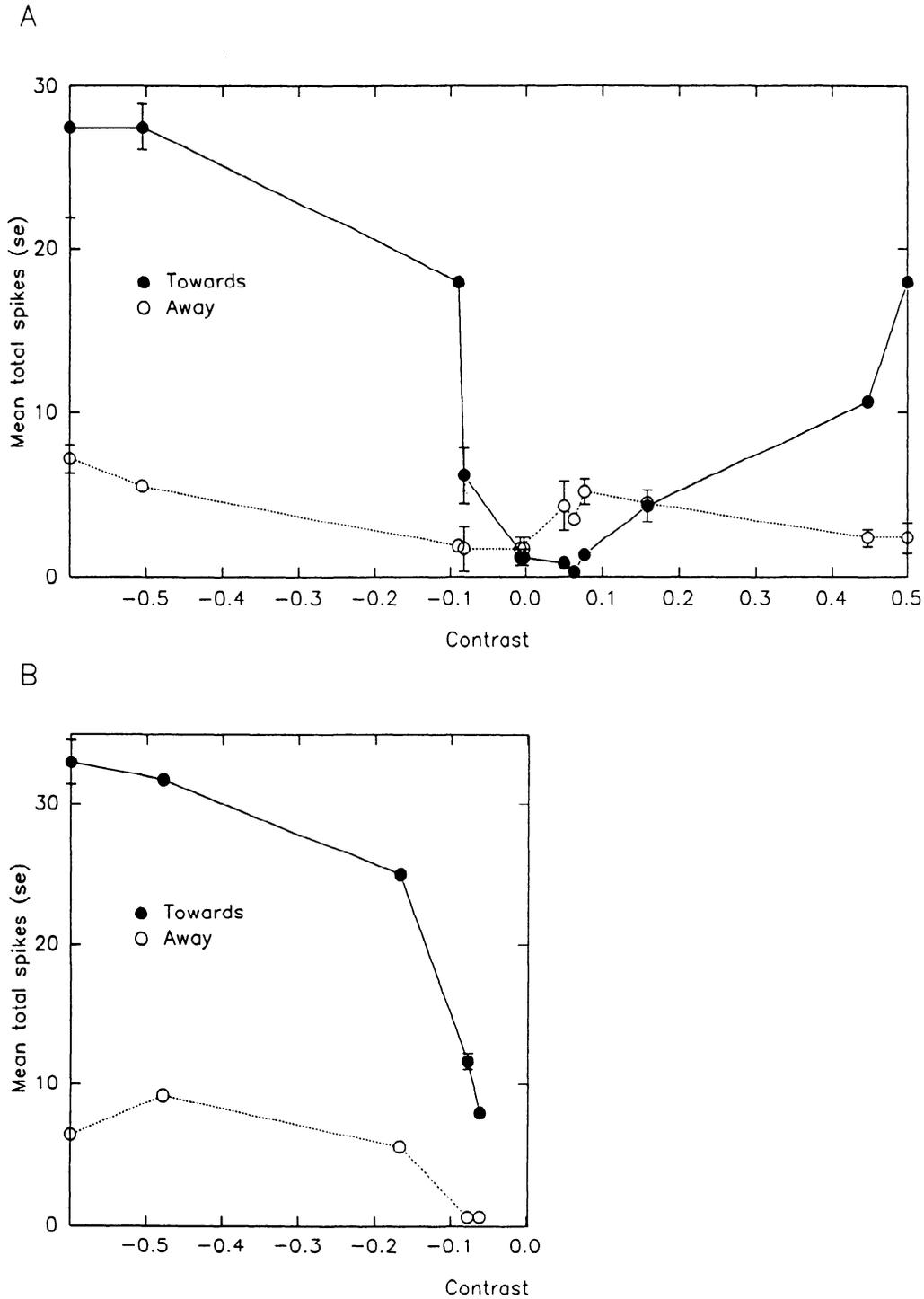


FIG. 9. Effect of contrast of an object against the background on responses by the descending contralateral movement detector to movements toward and away from the eye. Simulated velocity of movements was 5.5 m/s, and the final subtense of the rectangle on the eye was $62 \times 53^\circ$. Contrast is expressed as $(I_{\text{Object}} - I_{\text{Background}})/I_{\text{Background}}$, where I is mean intensity (Michelson contrast is not applicable here because the mean luminance of the screen changes during object movement). *A*: background intensity $1.38 \times 10^{-2} \text{ mW/cm}^2$. Note that, over most of the range of contrasts used, a larger response was obtained for movement toward than for movement away from the eye, for objects both darker and lighter than the background. *B*: brighter background, $1.35 \times 10^{-1} \text{ mW/cm}^2$. Error bars are only shown if they extend beyond the height of the symbol.

an approach at a particular velocity, although the effect of increasing object size was much less marked for larger than for smaller objects. The conclusion that can be drawn here is that the structure of the response to approach at a particular velocity is not independent of the size of an object, and so the DCMD does not, on its own, convey unequivocal information about time to collision.

Suppression of response by wide-field movements

It is well known that the response of the DCMD neuron to a small moving object is suppressed by a moving periodic pattern (O'Shea and Rowell 1975; Pinter 1977, 1979; Rowell et al. 1977). We investigated the effects of a drifting sine-wave grating on the response of the DCMD to the simulated approach of an object (Fig. 8). In the absence of an approaching object, there was no response either to uniform motion, or to the start of motion of the drifting grating. The drifting grating reduced the total number of spikes produced by the DCMD in response to the image of an approaching object (Fig. 8A; simulated approach speed, 5.5 m/s). The inhibition of the DCMD response was dependent on the temporal frequency of the drifting grating, being greatest at the highest temporal frequency used (Fig. 8B). A second feature of the DCMD's response, the timing of the peak in relation to the objects simulated approach, was not systematically altered as temporal frequency of the drifting grating was increased (Fig. 8C).

Effects of image contrast on responses to approaching objects

The DCMD responds more vigorously to dimming than to lightening of small areas (Palka 1967a,b; Rowell 1971), and the directionality that we have observed in the response to approaching compared with receding objects might be simply due to the associated changes in mean luminance. This possibility was ruled out by experiments in which the contrast of the image against the background was altered, and in which the sign of the luminance cue in the stimulus was reversed (Fig. 9). The DCMD could distinguish approach from recession not only of objects that were darker than the background but also of objects that were lighter than the background, although its performance at low contrasts was clearly better for darker objects. For light objects at contrasts <0.1 , the directional preference reversed consistently in three experiments, because of a pronounced decrease in the response to approaching objects together with a small increase in the response to recession (4 or fewer spikes for each stimulus). For dark objects, at all contrasts, there was a greater response to approach than to recession. At very low contrasts near the threshold for a significant directional DCMD response, a human subject could not see the approaching rectangle. For approaching objects, as contrast increased, there was a rapid increase in response by the DCMD at contrasts ~ 0.1 , followed by a more modest rate of increase in response, which reached a plateau level by a contrast of 0.5. The response to receding, dark objects increased only modestly with increased contrast.

DISCUSSION

We have used a wide range of moving visual stimuli to challenge the DCMD neuron, and we conclude that the

optimal stimulus for the DCMD is a rapidly approaching object. The neuron uses monocular cues. The response of the DCMD tracks the expanding image of the object as it approaches on an apparent collision course with the locust. The directional preference for approaching over receding objects is found over a wide range of object sizes, velocities, and contrasts, including objects that are lighter as well as darker than the background. Directionality persists in the presence of a moving background, although the magnitude of the response is reduced. The image feature most closely correlated with the response of the DCMD is angular acceleration of the image edges.

Directional selectivity by the DCMD

In the present investigation we have challenged the DCMD with a wide range of real and simulated moving stimuli. The Star Wars video contained a wide variety of scenes filmed from the viewers perspective, and we found that the DCMD responded in a consistent way to particular scenes. As expected from previous work, the DCMD responded to the rapid or jittery movement of small objects. However, in addition it responded vigorously to the images of extended moving edges and rapidly approaching objects. The velocities with which the edges of these images traversed the eye were undoubtedly higher than the velocities with which the neuron has been challenged in most previous investigations. The response to approaching objects was specifically to objects that were apparently on a collision course with the viewer, and objects that were approaching on a course that would bypass the viewer elicited much weaker responses. The DCMD gave no recordable response to scenes showing a flow field as would be generated by the viewer moving rapidly forward through a textured alley, but a rapid deviation to one side of the alley led to a response in the neuron. Taken together, these observations suggested to us that the neuron is not primarily tuned to movement of small objects, but to rapid movements of edges and, in particular, the edges of approaching objects.

Both for real and simulated objects, we found that the response by the DCMD to objects approaching toward or receding from the eye along the same path was extremely directional, over a wide range of object sizes, and velocities between 0.2 and 10 m/s. A feature of the response to approaching disks moved by the x - y plotter was the presence of two peaks, one immediately after the start of the approach and the second as the object came near to the eye. The size of the first peak in response correlated well with the peak in angular acceleration as the disk on the x - y plotter arm began to approach. In a similar way, the brief peak in response to a disk receding from the locust correlated with the large instantaneous angular acceleration as the disk began to move. The first peak was absent in the responses to simulated approaches of rectangles, which appeared to approach from greater distances than the travel of the x - y plotter. The computer-generated rectangles subtended $<2^\circ$ at the eye at the start of their movement. The mean spike frequency tracked the rectangles during simulated approaches, so that the response increased as both the subtense of the image on the eye and the velocity with which the image edges were traveling across the eye increased.

The DCMD has previously been generally considered to be most excited by movement of a small dark object on an

erratic path in any direction over the receptive field of one eye. This view was challenged by Schlotterer (1977), who noted, in a series of five preliminary experiments, that the DCMD gave a strong maintained response to the expanding image of an approaching disk, whereas its response to a receding disk was weak. In Schlotterer's study the disk was moved on the arm of an x - y plotter at a uniform velocity of 0.2 m/s for 1.25 s, changing its subtense on the eye from 10 to 67°. Schlotterer found that, in comparison with the response to an approaching disk, the response to a disk that subtended 10° at the eye and translated vertically at 0.2 m/s was much briefer and consisted of fewer spikes. This result is the same as the one that we obtained when we compared responses to approaching and to translating disks moving at 0.5 m/s. Schlotterer also reported that the response to the translating disk fatigued more rapidly with repetition than the response to the approaching disk. The conclusion that Schlotterer drew, that the optimal stimulus for the DCMD is an approaching, or looming, object, was subsequently refuted by Pinter et al. (1982), who compared responses to approaching objects with responses to translating objects but did not report any data on the responses to receding objects. Unlike Schlotterer or ourselves, Pinter et al. did not compare the responses to approaching and translating disks that moved at the same velocity, but they employed disks that translated at higher velocities than the velocity of approach, to achieve an angular velocity during translation that was close to the angular velocity at the end of approach. Inspection of their published records reveals that the responses are dominated by an initial peak in spike numbers, both to translating and to approaching objects, and that the response of the DCMD did not track the approach of objects in the way in which was shown both by Schlotterer (1977) and by the present study. The responses that they obtained are, therefore, likely to be largely to the initial angular acceleration as the stimulus started to move. Neither Schlotterer (1977) nor Pinter et al. (1982) report the absolute size or the distance between the eye and the translating disk. This information is important because the velocity with which the image of the disk moved over the eye would not have been uniform, particularly if the path of movement was near to the eye. The velocity would probably increase and then decrease, in the same way as the edges of an image that first approached and then receded from the eye. It is very likely, therefore, that the translating stimuli that these authors employed, contained an element of "loom." We conclude that the course of travel for an object that elicits the strongest response from the DCMD is on a collision course directly toward the eye. This conclusion is reinforced by the demonstration in the next paper (Simmons and Rind 1992) that two salient features of the images of approaching objects, an increase in the amount of edge, and a continual increase in edge velocity are critical image cues for the DCMD.

Role of the DCMD in behavior

How do the types of stimuli that we employed compare with stimuli that the locust might naturally encounter; and what kinds of natural stimuli would excite the DCMD most strongly? Our results show that the DCMD is well suited to signaling the rapid approach of an aerial avian predator such as a fiscal shrike, a known predator of locusts in Africa

(Cramp 1977). Like several other insectivorous birds, the Fiscal Shrike dives toward its prey from an elevated perch 3–4 m above the ground. As a shrike approached a locust, its dark silhouette would expand rapidly over the locust's retina. The DCMD responds strongly over the range of angular velocities that would be generated by such an expanding image, and the DCMD would certainly be able to track the approach of the bird (Table 2). Although the frequency of DCMD spikes would increase as the bird came nearer and nearer, it is unlikely that the neuron would signal unequivocally the time to collision, because our results show that the response depends both on the speed and absolute size of an approaching object. However, a role for the DCMD in estimating time to collision cannot be ruled out until the way in which the output from the DCMD is integrated has been examined in detail, taking into account the kinds of changes in spike frequency that accompany the approaches of objects. Because it is responsive to accelerating movements, the DCMD will also respond strongly to the sudden appearance of an object in the visual field, as might happen if an animal came into sight from behind vegetation or a rock close to the locust. We observed a strong response by the DCMD to such a stimulus during one experiment when a bird flew over a skylight above the preparation. Objects that suddenly appear would elicit a strong initial response, but the response would not be maintained or increased unless the objects were approaching the locust.

The connections that the DCMD is known to make with motoneurons and interneurons that are involved in jump-

TABLE 2. Comparison of the angular characteristics of a swooping avian predator with those of a computer-generated approaching object

D, m	V, m/s	Tc, ms	Deg	V, °/s
<i>Avian predator</i>				
4	0	629	2.1	0
3	4.4	403	2.9	3
2	6.3	243	4.3	9
1	7.7	113	8.6	33
0.8	7.9	87	10.7	77
0.6	8.1	63	14.3	144
0.4	8.3	39	21.3	292
0.2	8.7	16	28.1	862
<i>Computer-generated object</i>				
4	10	400	1.4	2
3	10	200	1.9	5
2	10	200	2.9	10
1	10	100	5.7	2.8
0.8	10	80	7.2	75
0.6	10	60	9.5	115
0.4	10	40	15.0	275
0.2	10	20	28.0	650

Calculations were based on the approach of a common African locust predator the fiscal shrike, *Lanius collaris humeralis*, (Cramp 1977), the bird swoops from a 3 to 4-m elevated perch. The bird was represented by a 0.75-m circle, accelerating downward at 9.8 m/s². The computer-generated image was a 0.07 × 0.1/m rectangle approaching at a constant velocity of 10 m/s to within 0.1 m of the locust. D, distance to the locust; V, m/s, object velocity; Tc, projected time to collision; Deg, angular subtense of the image on the eye; V, °/s, angular velocity of 2 diverging edges of the image.

ing are consistent with a role for the DCMD in detecting the rapid approach of a predator (Burrows and Rowell 1973; Gynther and Pearson 1989; Pearson 1983; Pearson and Goodman 1981; Pearson et al. 1980). In these studies, accelerating and prolonged bursts of DCMD spikes were not employed. A description of the integrative processes that can trigger a jump must take into consideration the pattern of spikes that the DCMD produces in response to a rapidly approaching object. One reason the pattern of spikes may be important is that the thoracic terminals of a DCMD are subject to presynaptic inhibition from a variety of sources, including from itself and the contralateral DCMD, and from leg proprioceptors (Steeves and Pearson 1982). The presynaptic inhibition has been suggested to ensure that the DCMD only triggers a jump in the correct behavioral context, and this context might include the kind of accelerating burst of spikes that the DCMD produces in response to a rapidly approaching object. Another aspect of the escape jump that requires consideration is its latency, which can be several hundred milliseconds because of the time required for the extensor tibiae muscle to develop sufficient tension to launch the locust (Heitler 1974), and it may be important for the response by the DCMD to continue throughout this development of tension, which it would do for an approaching object.

The DCMD also makes extensive connections with flight motoneurons ipsilateral to its axon (Simmons 1980). There are particularly strong connections onto a motoneuron that elevates the forewings, and this might be important in initiating flying as an escape response in a stationary locust. In an airborne locust the response of the DCMD to approaching objects would make it suitable for collision avoidance. Forward flight creates a velocity gradient, or image flow field, over the retina. The DCMD does not respond to such wide-field visual movements, but we have shown that it can signal approach of an object out of a moving background by presenting simulated approaches of a rectangle against a high-contrast drifting grating in the background. Production of spikes in the DCMD is suppressed by an amount proportional to the temporal frequency (velocity) of the drifting grating, but the timing of the peak in the response is not altered. The contrast and spatial frequency of the grating we employed were both relatively high, probably greater than those that a locust would experience while flying through natural surroundings. We do not know whether there is any central alteration of responsiveness in the DCMD during flight. Although the DCMD is not suppressed during walking (Rowell 1971b), it is strongly suppressed during a saccade in the optomotor response (Zaretsky 1982; Zaretsky and Rowell 1979). During the saccade, retinal image velocities of $300^\circ/\text{s}$ are generated in <100 ms, potentially a very effective stimulus for the DCMD.

In a stationary locust, there is a gradient of responsiveness over the eye, with stimuli presented to the posterior part of the eye generally eliciting larger responses than stimuli to the anterior part (Palka 1967a,b; Rowell 1971a; Rowell et al. 1977; Schlotterer 1977; results in this paper to translating stimuli). This might suggest that a DCMD would be most sensitive to objects that are approaching from behind. However, this gradient in sensitivity would be offset during forward flight by an oppositely directed gra-

dient of image motion (the flow field), and thus of suppression of the DCMD. In flight, therefore, the DCMD response will be least suppressed over the part of the eye that faces the direction in which the locust is heading, which is also the direction in which potential collision with a stationary or moving object is most likely.

Comparison with other detectors of looming stimuli

The DCMD clearly responds to approaching objects with the use of monocular cues, looming. The direction of motion is signaled by the DCMD independently of luminance cues. In the human visual system, Regan and Beverley (1978) demonstrated a psychophysical channel for the perception of motion in depth with a specific sensitivity to looming. This pathway is not affected by specific deficits that sometimes occur in the binocular disparity pathway for depth perception (Hong and Regan 1989). Regan and Cynader (1979) investigated the physiological basis for specific sensitivity to looming by recording from 56 neurons in area 18 of the cat visual cortex, which responded selectively to one direction of motion in depth. In 19 neurons this selectivity could be explained by a response to luminance cues that accompany the looming stimulus; and in a further 20 neurons the selectivity changed with a change in the position of the stimulus on the retina. Only one neuron distinguished unequivocally the direction of motion independent of luminance cues or the position on the retina. They concluded that, at the level of the primary visual cortex, the cat's ability to detect looming objects was based on the statistical distribution of activity across many neurons. In both the monkey (Zeki 1974) and the cat (Regan and Cynader 1979) the opposite motion of *two* edges was either necessary, or at least greatly enhanced, the selectivity of the response to stimuli corresponding to particular directions of motion in depth. Zeki did not test whether the ability of the monkey neurons to discriminate direction of motion in depth was independent of luminance cues. In a subsequent paper (Simmons and Rind 1992), we show that the divergent motion of opposite edges is not a critical image cue for a directional response from the DCMD.

The DCMD follows angular velocities and accelerations of image motion higher than those used in these classical vertebrate studies, although well within the range that a locust would encounter naturally. In their studies on psychophysical channels in humans, Regan and Beverley (1978, 1979) employed as a stimulus a square whose image grew and shrank repeatedly, as if it was the image of an object moving between two positions in depth. The image changed with a constant angular velocity (0.64 min arc/s). Similarly, in their electrophysiological studies in the cat visual cortex, Regan and Cynader (1979, 1982) employed edges moving at constant angular velocities. Looming neurons, or channels, in vertebrates are tuned to detecting speeds of approach that are slower than those detected by the binocular disparity system (Regan and Beverley 1978, 1979, 1983; Regan and Cynader 1979, 1982), but as yet they have only been challenged with low angular velocities or small accelerations. As vertebrate looming neurons, or channels, are able to track changes in image size down to minutes of arc, an object can be detected as approaching when it is still distant. The locust eye in contrast, has a minimum resolution of $1-2^\circ$. This means that the image of

an object the size of an insectivorous bird can not be detected as approaching by the DCMD until the bird is within 4–5 m of the locust and subtends more than one interommatidial angle (see Table 2). At this distance such an image will be moving rapidly, with increasing acceleration across the retina. The existence of looming, or size change, neurons like the orthopteran DCMD shows that it is possible for individual visual neurons to encode the rapid increase in angular velocity shown by the image of an approaching object on a collision trajectory.

C. Rind is a Royal Society University Research Fellow.

This work was supported by a grant from the Science and Engineering Research Council (UK).

Address for reprint requests: F. C. Rind, Division of Neurobiology, School of Neuroscience, Ridley Bldg., University of Newcastle upon Tyne NE1 7RU, UK.

Received 12 March 1992; accepted in final form 23 June 1992.

REFERENCES

- BURROWS, M. AND ROWELL, C. H. F. Connections between descending visual interneurons and metathoracic motoneurons in the locust. *J. Comp. Physiol.* 85: 221–234, 1973.
- CRAMP, S. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic.* New York: Oxford Univ. Press, vols. 1–5, 1977.
- CYNADER, M. AND REGAN, D. Neurons in cat parastriate cortex sensitive to the direction of motion in three-dimensional space. *J. Physiol. Lond.* 274: 549–569, 1978.
- CYNADER, M. AND REGAN, D. Neurons in cat visual cortex tuned to the direction of motion in depth: effect of positional disparity. *Vision Res.* 22: 967–982, 1982.
- EDWARDS, D. H. The cockroach DCMD neurone. I. Lateral inhibition and the effects of light- and dark-adaptation. *J. Exp. Biol.* 99: 61–90, 1982.
- EDWARDS, D. H. Response vs. excitation in response-dependent and stimulus-dependent lateral inhibitory networks. *Vision Res.* 23: 469–472, 1983.
- GYNTHNER, I. C. AND PEARSON, K. G. An evaluation of the role of identified interneurons in triggering kicks and jumps in the locust. *J. Neurophysiol.* 61: 45–57, 1989.
- HEITLER, W. J. The locust jump: specializations of the femoral-tibial joint. *J. Comp. Physiol.* 89: 93–104, 1974.
- HEITLER, W. J. AND BURROWS, M. The locust jump. I. The motor programme. *J. Exp. Biol.* 66: 203–220, 1977a.
- HEITLER, W. J. AND BURROWS, M. The locust jump. II. Neural circuits of the motor programme. *J. Exp. Biol.* 66: 221–242, 1977b.
- HEITLER, W. J. AND BURROWS, M. The locust jump. II. Neural circuits of the motor programme. *J. Exp. Biol.* 66: 221–242, 1977b.
- HONG, X. AND REGAN, D. Visual field defects for unidirectional and oscillatory motion in depth. *Vision Res.* 29: 809–819, 1989.
- HORRIDGE, G. A. The separation of visual axes in apposition compound eyes. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 285: 1–59, 1978.
- HOWARD, J., DUBS, A., AND PAYNE, R. The dynamics of phototransduction in insects. A comparative study. *J. Comp. Physiol.* 154: 707–718, 1984.
- ORBAN, G. A., SPILEERS, W., GULYAS, B., AND BISHOP, P. D. Motion in depth selectivity of cortical cells revisited. *Soc. Neurosci. Abstr.* 12: 584, 1986.
- O'SHEA, M. AND ROWELL, C. H. F. Protection from habituation by lateral inhibition. *Nature Lond.* 254: 53–55, 1975.
- O'SHEA, M. AND ROWELL, C. H. F. The neuronal basis of a sensory analyzer, the acridid movement detector system. II. Response decrement, convergence, and the nature of the excitatory afferents to the fan-like dendrites of the LGMD. *J. Exp. Biol.* 65: 289–308, 1976.
- O'SHEA, M. AND WILLIAMS, J. L. D. The anatomy and output connections of a locust visual interneurone: the lobula giant movement detector (LGMD) neurone. *J. Comp. Physiol.* 91: 257–266, 1974.
- PALKA, J. An inhibitory process influencing visual responses in a fibre of the ventral nerve cord of locusts. *J. Insect. Physiol.* 13: 235–248, 1967a.
- PALKA, J. Head movement inhibits locust visual units response to target movement (Abstract). *Am. Zool.* 7: 728, 1967b.
- PEARSON, K. G. Neural circuits for jumping in the locust. *J. Physiol. Paris* 78: 765–771, 1983.
- PEARSON, K. G. AND GOODMAN, C. S. Presynaptic inhibition of transmission from identified interneurons in locust central nervous system. *J. Neurophysiol.* 45: 501–515, 1981.
- PEARSON, K. G., HEITLER, W. J., AND STEEVES, J. D. Triggering of locust jump by multimodal inhibitory interneurons. *J. Neurophysiol.* 43: 257–278, 1980.
- PETTIGREW, J. D. Binocular neurons which signal change of disparity in area 18 of cat visual cortex. *Nature Lond.* 241: 123–124, 1973.
- PINTER, R. B. Frequency and time domain properties of reticular cells of the desert locust (*Shistocerca gregaria*) and the house cricket (*Acheta domesticus*). *J. Comp. Physiol.* 77: 383–397, 1972.
- PINTER, R. B. Visual discrimination between small objects and large textured backgrounds. *Nature Lond.* 270: 429–431, 1977.
- PINTER, R. B. Inhibition and excitation in the locust DCMD receptive field: spatial frequency, temporal and spatial characteristics. *J. Exp. Biol.* 80: 191–216, 1979.
- PINTER, R. B., OLBERG, R. M., AND ABRAMS, T. W. Is the locust DCMD a looming detector? *J. Exp. Biol.* 101: 327–331, 1982.
- POGGIO, G. F. AND TALBOT, W. H. Mechanisms of static and dynamic stereopsis in foveal cortex of rhesus monkey. *J. Physiol. Lond.* 315: 469–492, 1981.
- REGAN, D. AND BEVERLEY, K. I. Looming detectors in the human visual pathway. *Vision Res.* 18: 415–421, 1978.
- REGAN, D. AND BEVERLEY, K. I. Binocular and monocular stimuli for motion-in-depth: changing-disparity and changing-size inputs feed the same motion-on-depth stage. *Vision Res.* 19: 1331–1342, 1979.
- REGAN, D. AND BEVERLEY, K. I. Visual fields for frontal plane motion and for changing size. *Vision Res.* 23: 673–676, 1983.
- REGAN, D. AND CYNADER, M. Neurons in area 18 of cat visual cortex selectively sensitive to changing size: nonlinear interactions between responses to two edges. *Vision Res.* 19: 699–711, 1979.
- REGAN, D. AND CYNADER, M. Neurons in cat visual cortex tuned to the direction of motion in depth: effect of stimulus speed. *Invest. Ophthalmol. Visual Sci.* 22: 535–550, 1982.
- RIND, F. C. Non-directional, movement sensitive neurones of the locust optic lobe. *J. Comp. Physiol.* 161: 477–494, 1987.
- RIND, F. C. A chemical synapse between two motion detecting neurones in the locust brain. *J. Exp. Biol.* 110: 143–167, 1984.
- ROWELL, C. H. F. The orthopteran descending movement detector (DMD) neurones: a characterisation and review. *Z. Vgl. Physiol.* 73: 167–194, 1971a.
- ROWELL, C. H. F. Variable responsiveness of a visual interneurone in the free-moving locust and its relation to behaviour and arousal. *J. Exp. Biol.* 55: 727–748, 1971b.
- ROWELL, C. H. F., O'SHEA, M., AND WILLIAMS, J. L. D. Neuronal basis of a sensory analyzer, the acridid movement detector system. IV. The preference for small field stimuli. *J. Exp. Biol.* 68: 157–185, 1977.
- ROY, J.-P. AND WURTZ, R. H. The role of disparity-sensitive cortical neurons in signalling the direction of self-motion. *Nature Lond.* 348: 160–162, 1990.
- SCHLOTTERER, G. R. Response of the locust descending movement detector neuron to rapidly approaching and withdrawing visual stimuli. *Can. J. Zool.* 55: 1372–1376, 1977.
- SHEPHERD, G. M. *Neurobiology.* New York: Oxford Univ. Press, 1988.
- SIMMONS, P. J. Connexions between a movement-detecting visual interneurone and flight motoneurons of a locust. *J. Exp. Biol.* 86: 87–97, 1980.
- 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.
- STEEVES, J. D. AND PEARSON, K. G. Proprioceptive gating of inhibitory pathways to hind leg flexor motoneurons of the locust. *J. Comp. Physiol.* 146: 507–515, 1982.
- WILSON, M. Angular sensitivity of dark and light adapted locust retinula cells. *J. Comp. Physiol.* 97: 323–328, 1975.
- ZARETSKY, M. Quantitative measurements of centrally and retinally generated saccadic suppression in a locust movement detector neurone. *J. Physiol. Lond.* 328: 521–533, 1982.
- ZARETSKY, M. AND ROWELL, C. H. F. Saccadic suppression by corollary discharge in the locust. *Nature Lond.* 280: 583–585, 1979.
- ZEKI, S. Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *J. Physiol. Lond.* 242: 827–841, 1974.