

THE LOCUST DCMD, A MOVEMENT-DETECTING NEURONE TIGHTLY TUNED TO COLLISION TRAJECTORIES

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Summary

A Silicon Graphics computer was used to challenge the locust *descending contralateral movement detector* (DCMD) neurone with images of approaching objects. The DCMD gave its strongest response, measured as either total spike number or spike frequency, to objects approaching on a direct collision course. Deviation in either a horizontal or vertical direction from a direct collision course resulted in a reduced response. The decline in the DCMD response with increasing deviation from a collision course was used as a measure of the tightness of DCMD tuning for collision trajectories. Tuning was defined as the half-width of the response when it had fallen to half its maximum level. The

response tuning, measured as averaged mean spike number *versus* deviation away from a collision course, had a half-width at half-maximum response of 2.4° – 3.0° for a deviation in the horizontal direction and 3.0° for a deviation in the vertical direction. Mean peak spike frequency showed an even sharper tuning, with a half-width at half-maximum response of 1.8° for deviations away from a collision course in the horizontal plane.

Key words: locust, *Locusta migratoria*, DCMD, identified neurone, movement detection, direction selective, visual system, motion in depth.

Introduction

The image of a rapidly approaching object is a powerful stimulus eliciting avoidance reactions in many animal species (Gibson, 1958; Holmqvist and Srinivasan, 1991; Schiff *et al.* 1962). Specific cues, such as the ratio between the rate of image expansion and image size, are perceived by the visual system and used to predict the time to collision of an approaching object or image feature (Lee, 1980; Lee and Reddish, 1981; Lee *et al.* 1992, 1993; Wagner, 1982; Wang and Frost, 1992). In the pigeon *Columba livia*, particular neurones use such image cues to signal a collision course and to estimate the time to collision. Wang and Frost (1992) recorded from neurones in the nucleus rotundus in the pigeon that were maximally excited by objects approaching the animal and found that many of these neurones showed extremely tight tuning to a collision trajectory. Tuning was defined as the half-width of the response when it had fallen to half its maximum level. The excitatory response of the neurones centred on a 0° azimuth straight in front of the animal, with a mean response half-width at half response height of 3.3° and a mean above-baseline width of 16° . In the visual system of the locust, two neurones, the *lobula giant movement detector* (LGMD, O'Shea and Williams, 1974) and its postsynaptic partner the *descending contralateral movement detector* (DCMD, Rind, 1984), have been found to respond most strongly to images of

a rapidly approaching object (Schlotterer, 1977; Rind and Simmons, 1992). The LGMD is the sole source of input from compound eye to the DCMD, and a spike in the LGMD produces a spike in the DCMD at spike frequencies up to 400 Hz (Rind, 1984). DCMD spikes are easily recorded extracellularly from the ventral nerve cord and provide a monitor of the output of both neurones. The response of the LGMD/DCMD neurones builds up throughout the approach of an object, reaching a peak only after a collision would have occurred (Rind and Simmons, 1992, 1997; Simmons and Rind, 1992; Rind, 1996).

A neural network based on the input organisation of these neurones responds in the same way as the locust LGMD neurone (Rind and Bramwell, 1996). The network responds directionally when challenged with approaching and receding objects and reveals the importance of a critical race, between excitation passing down the network and inhibition directed either laterally or forward, for the rapid build-up of excitation in response to approaching objects. The excitatory response of the network is greatest for objects approaching within 3° of a collision course. In the present study, we test the predicted tuning of the LGMD/DCMD neurones for collision trajectories and reveal a very tight tuning, particularly for deviations in the horizontal plane.

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Materials and methods

Experiments were performed on 14 adult locusts (*Locusta migratoria*). The head was stabilised in a way that preserved the vertical axis of the eye. Extracellular recordings were made from the axon of the DCMD in the cervical connectives while the animal viewed the monitor of a Silicon Graphics Indigo 2 workstation fitted with two Extreme Graphics boards. The screen of the 19 inch Sony multi-scan monitor was placed parallel to the long axis of the locust, 150 mm from its right eye. The monitor was used with only the green gun active. At its maximum intensity, emission was centred on 540 nm, measured using a Jena Glaswerk Schott and Gen monochromator fitted with a Veril B200 no. b-731515 filter. The emission that overlapped the peak sensitivity of the locust green photoreceptors (Bennett *et al.* 1967) remained centred on 540 nm as intensity was altered.

Initially we assessed the suitability of the Silicon Graphics workstation for stimulating the LGMD/DCMD before exploiting the larger screen size of the computer monitor to investigate the tuning of the LGMD/DCMD for objects approaching on a variety of near-miss trajectories. These preliminary experiments were necessary as the large-size monitor, which allowed the simulation of near-miss trajectories with their attendant large shifts in image position, had the disadvantage of a 72 Hz refresh rate compared with the rate of 100–200 Hz with a small electrostatic monitor (Rind and

Simmons, 1992). A recent claim made by Hatsopoulos *et al.* (1995), that the LGMD/DCMD response to a rapidly approaching object peaks before collision allowing the locust to use the timing of this peak to make an escape before collision, has been shown to be based on an artefact generated by the low (72 Hz) refresh rates of the computer screen they used (Rind and Simmons, 1997). The peak in DCMD response measured by Hatsopoulos *et al.* (1995) occurred when the jump size on the monitor first exceeded approximately 3° . Throughout this study, we limited stimulus size so that image jumps remained below 3° . The approaching square travelled a simulated distance of 1900 mm at a fixed velocity (Fig. 1). The orientation of the square remained parallel to the screen throughout the approach. A monitor of image size was provided by a digital-to-analogue converter (DAC) connected to the serial port of the computer. In the first experiment, a 50 mm×50 mm square approached on a collision course with the locust, and stimulus contrast, calculated from (intensity of object minus intensity of background)/intensity of background, was varied over the range 0.0 to -0.4. Approaching squares at each contrast were presented six times in a random order, with a minimum interval of 30 s between each presentation. The effect of stimulus velocity was measured using a 50 mm×50 mm square approaching at constant velocities ranging from 0.5 to 5 m s⁻¹. The DCMD response was divided into 50 ms bins, and the mean number of spikes in each bin was calculated for five stimulus repetitions.

Eleven locusts were used to investigate the response of the DCMD to 30 mm×30 mm squares approaching on collision and

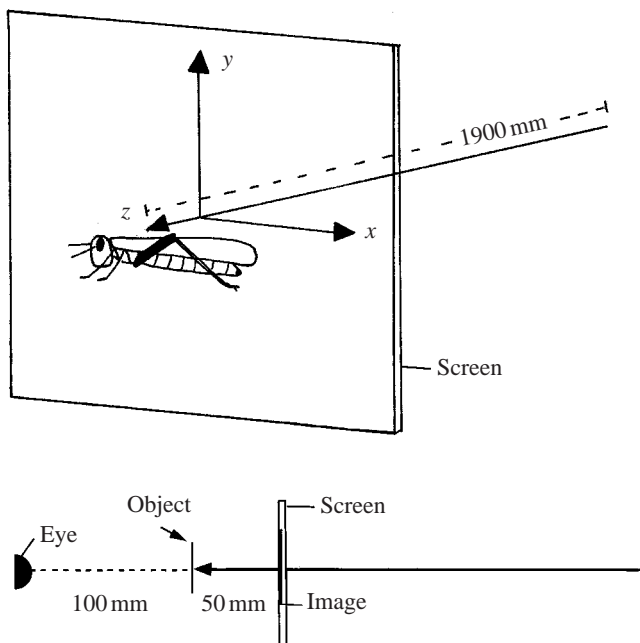


Fig. 1. Stimulus configuration. The locust was positioned side-on to the monitor with its right eye 150 mm from the centre of the screen. On the screen, images were shown of either a 50 mm×50 mm or a 30 mm×30 mm square approaching the locust on a direct path from a point 2000 mm distant, to within 100 mm of the eye. At the beginning of the approach, both the 50 mm×50 mm and 30 mm×30 mm squares subtended less than 1° at the eye. At the end of the approach, the subtense had increased to 28.1° for a 50 mm×50 mm square and to 17.1° for a 30 mm×30 mm square. During the approach, the orientation of the square remained parallel to the plane of the screen.

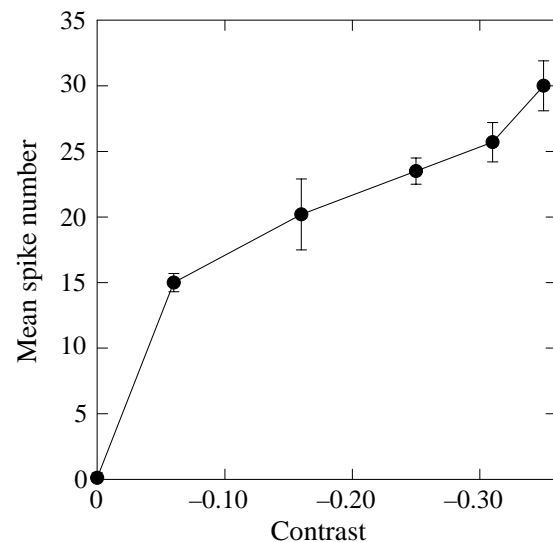


Fig. 2. Effect of the contrast [(intensity of object minus intensity of background)/intensity of background] of an object against the background on the responses of the descending contralateral movement detector (DCMD) neurone to movements towards the eye. Mean spike numbers per approach were calculated as in Rind and Simmons (1992). Background light intensity measured at the eye, in the absence of a simulated object on the monitor screen, was $18.71 \mu\text{W cm}^{-2}$. Objects were 50 mm×50 mm in size and approached at 2.5 m s^{-1} . Details of the stimuli are given in the Material and methods section. Values are means \pm S.E.M., $N=6$.

non-collision trajectories. As in the previous experiments, the square moved towards the locust along a path in the z -direction from a point 2000 mm away. However, the trajectory could be offset from a direct path in either the x -direction (horizontal plane) or the y -direction (vertical plane) (Fig. 1). Stimuli with trajectories deviating from a direct collision path in the horizontal plane were presented to five animals with six stimulus repetitions for each animal. The final positions of the squares were 0, 20, 40, 60, 80, 100, 120, 140 and 160 mm to the right of the central axis. At the eye, each 20 mm deviation represents a 0.6° shift of the midpoint of the square away from the central axis. Stimuli with trajectories deviating from a direct collision path in the vertical plane were presented to six animals with six stimulus repetitions for each animal. The final positions

of the squares were 0, 10, 20, 30, 40, 50, 60, 80 and 100 mm above the central axis. At the eye, each 10 mm deviation represents a 0.3° shift of the midpoint of the square away from the central axis. The response of the DCMD to this size of stimulus showed no synchronisation to the 72 Hz refresh rate of the screen during the approach (Rind and Simmons, 1997).

Results

Responses to objects approaching on a direct collision course: relationship with object contrast and approach velocity

The first experiments were performed to test the adequacy of the monitor in exciting the LGMD/DCMD neurones. The DCMD responded directionally to objects approaching on a direct

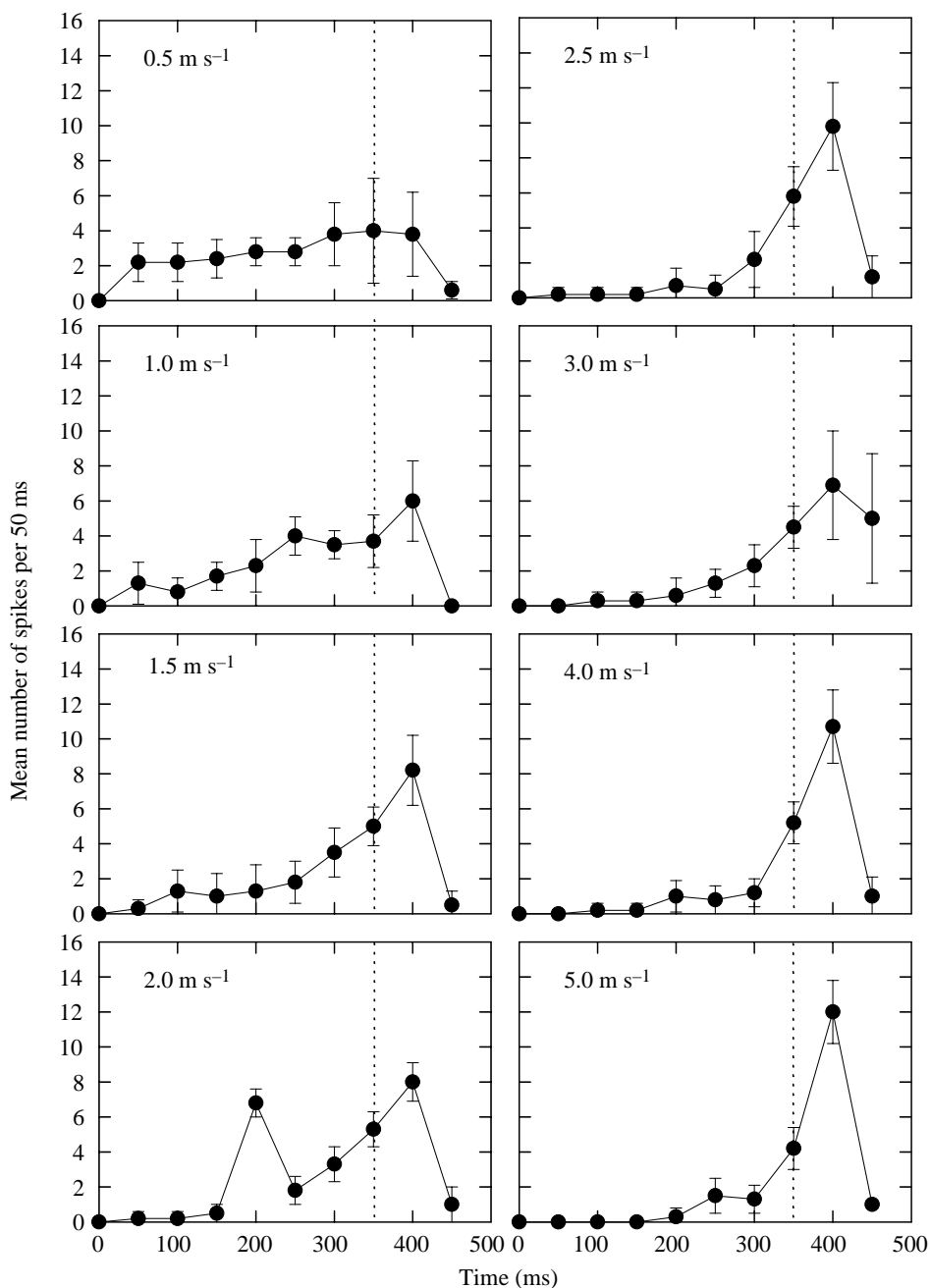


Fig. 3. Changes in the mean spike rate of the DCMD neurone during the direct approach of a 50 mm×50 mm object at different velocities. The end of movement is indicated by a vertical dotted line on each graph. Values are means ± s.e.m., N=6.

collision course over the range of contrasts used (0.06 to -0.35), preferring objects that moved towards the eye. The DCMD response did not saturate over this range; the greater the contrast between the object and the background, the greater was the response (Fig. 2). The response was clearly above baseline at the lowest contrast used (-0.06). The DCMD was tested with objects darker than the background because the DCMD is more sensitive to negative contrast (Rind and Simmons, 1992). All subsequent experiments were performed with an object contrast of -0.35 .

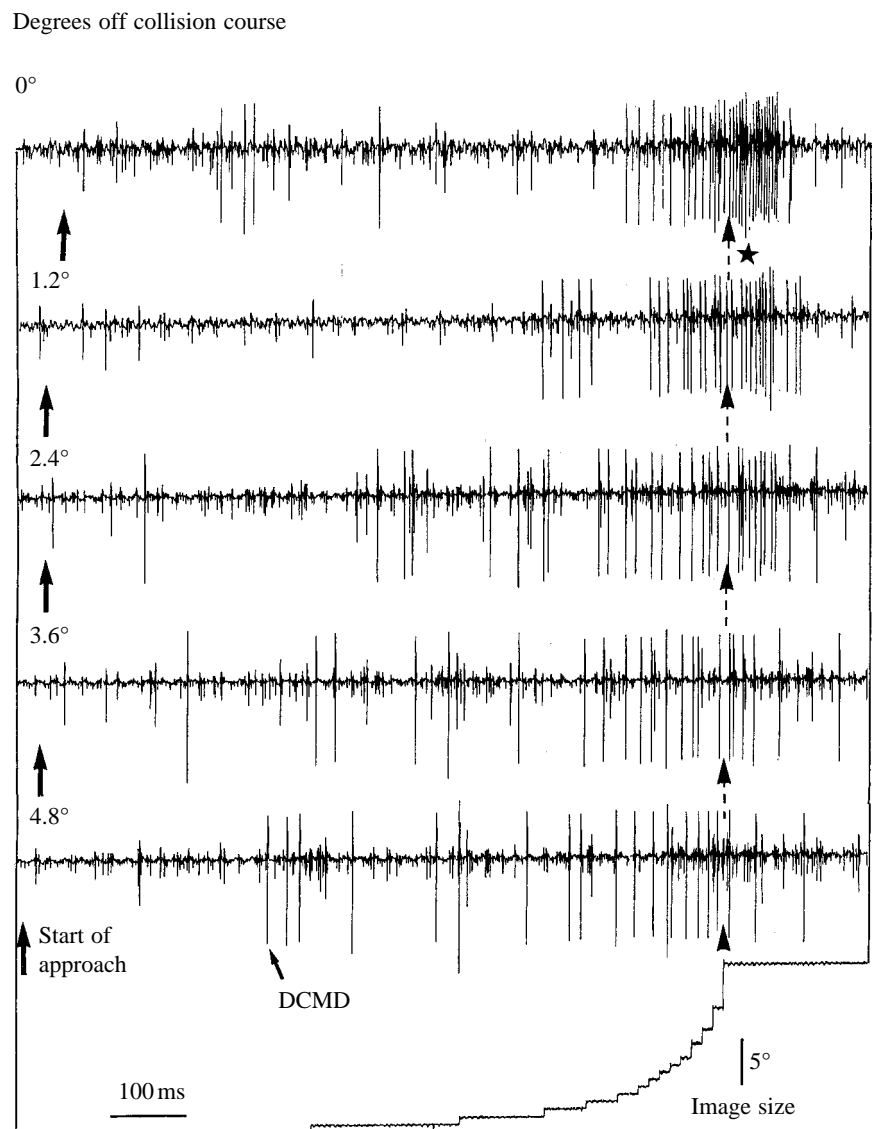
We next simulated a wide range of approach velocities from 0.5 to 5 m s^{-1} , with an object $50 \text{ mm} \times 50 \text{ mm}$ in size (Fig. 3). All the approaches were made with the object on a collision trajectory, and over this range the DCMD responded with an increased spike rate as the simulated object approached the eye. The response peaked after the approach had ceased, usually within 50 ms of the end of motion (dotted line, Fig. 3). The simulated object approached to within 100 mm of the eye and stopped, so that the time taken before it would have reached the eye depended on the speed of approach. For approach velocities

slower than 2 m s^{-1} , the peak occurred before the time of contact. The form of the response was very similar to that described in Fig. 6B of Rind and Simmons (1992) over a similar range of velocities ($0.5\text{--}10 \text{ m s}^{-1}$). These preliminary experiments demonstrate the adequacy of the Silicon Graphics system for stimulating the LGMD/DCMD neurones.

Responses to objects approaching on near-miss trajectories

Small objects, $30 \text{ mm} \times 30 \text{ mm}$ in size, were simulated approaching the locust eye at a constant velocity of 2.5 m s^{-1} . A different approach trajectory was simulated on each trial with horizontal deviations from a direct collision path, in steps of 0.6° . Typical DCMD responses to such stimuli are shown in Fig. 4. The most vigorous response was given to an object on a direct collision path (0° off collision course). The main response occurs after the approach is over (dotted line and arrowheads, Fig. 4) and after the projected time to collision, where this would have occurred (star on top trace in Fig. 4). The relationship between DCMD response and trajectory was

Fig. 4. Extracellularly recorded DCMD spikes in response to objects approaching on collision or near-miss trajectories. Horizontal displacements from a collision trajectory are shown in steps of 1.2° . The bottom trace monitors image size throughout the approach. The monitor had a maximum range of 256 levels; only integer changes in level were monitored. The computer screen was refreshed every 13.9 ms . A star under the top trace indicates when collision would have occurred and the arrowheads indicate when the approach ended. The simulated object ($30 \text{ mm} \times 30 \text{ mm}$) approached at a velocity of 2.5 m s^{-1} ; further stimulus details are given in the Materials and methods section.



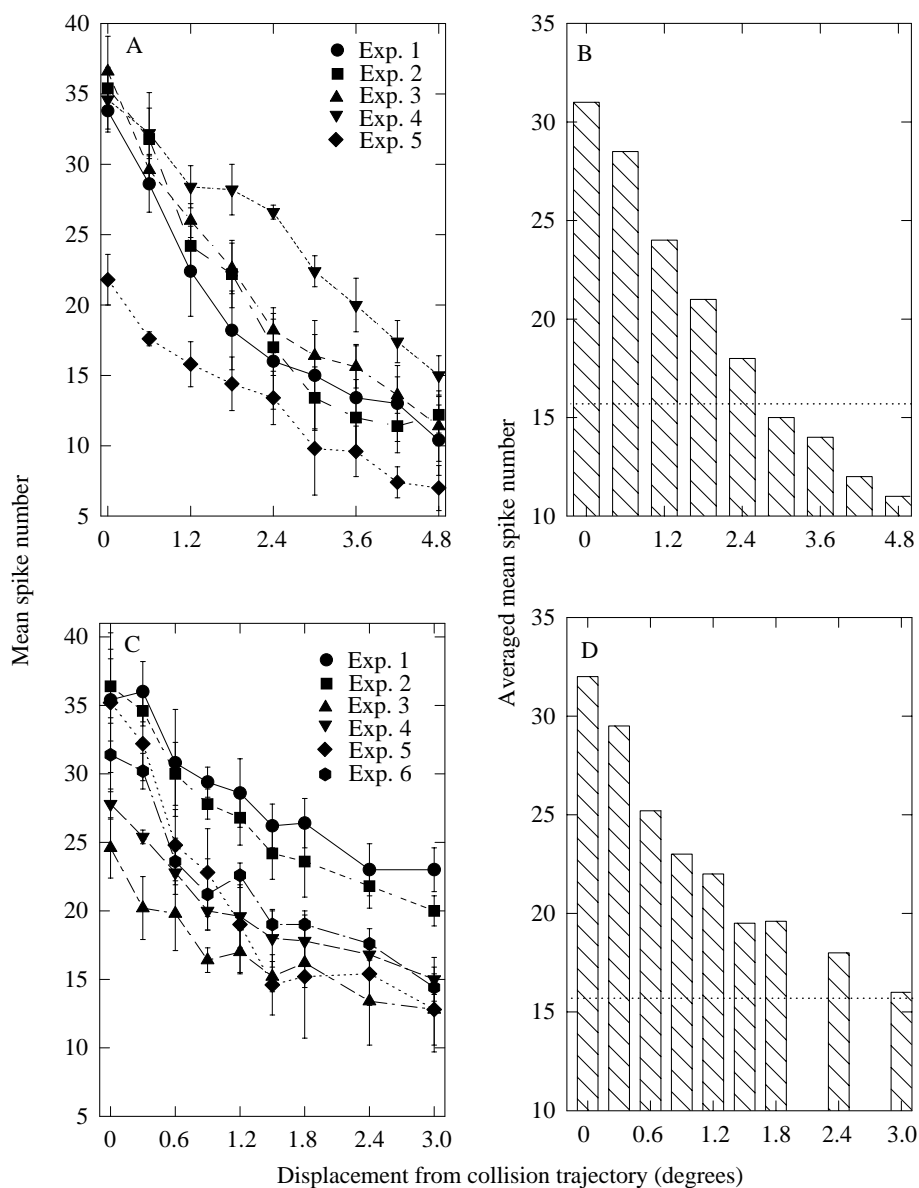


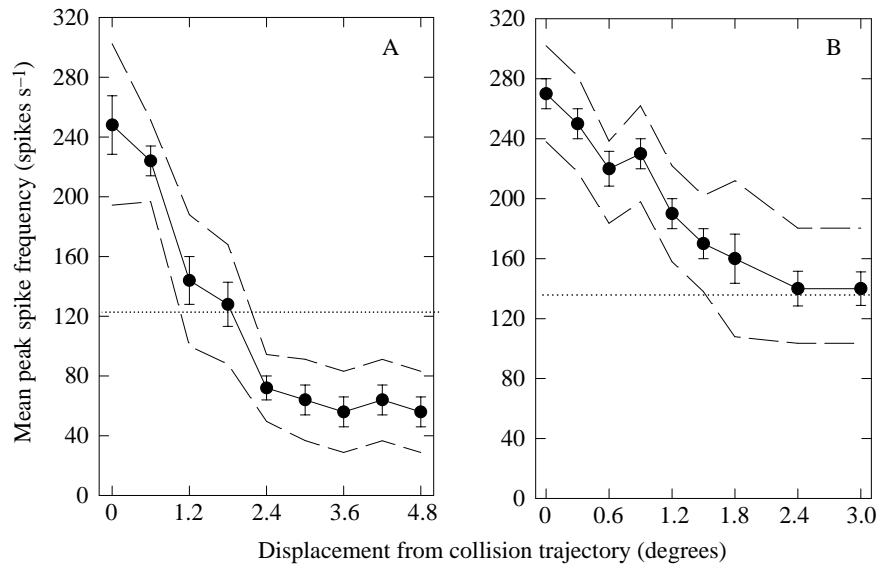
Fig. 5. Mean total DCMD spike numbers in response to objects approaching on a collision or near-miss trajectory. Spike numbers per approach were calculated as in Rind and Simmons (1992) and Wang and Frost (1992). A 30 mm \times 30 mm object approached at a velocity of 2.5 ms $^{-1}$. (A) Horizontal displacement from a collision trajectory is shown in steps of 0.6 $^{\circ}$. (B) Responses for all five experiments shown in A have been averaged to give a better indication of the overall trend. The dotted line shows the half-maximum level of this response. (C) Mean total DCMD spike numbers in response to vertical displacement from a collision trajectory is shown in steps of 0.3 $^{\circ}$. (D) Mean responses for the six experiments shown in C have been averaged. The dotted line shows the half-maximum level of this response. Other stimulus details were as in Fig. 4. In A and C, values are means \pm S.E.M., $N=6$.

examined quantitatively for both horizontal and vertical deviations from a collision trajectory (Figs 5–7). For horizontal deviations, mean total DCMD spikes were counted for each trajectory in five experiments (Fig. 5A). All experiments showed similar trends, with response declining as object trajectories moved away from a collision course. Individual experiments revealed a tuning spread in the DCMD response with a half-width at half peak value ranging from just below 2.4 $^{\circ}$ (experiment 1) to 4.2 $^{\circ}$ (experiment 4). When the mean spike numbers from the five experiments were averaged (Fig. 5B), the sensitivity profile of the DCMD to stimuli displaced horizontally from a collision trajectory had a half-width at half peak between 2.4 and 3.0 $^{\circ}$ (dotted line Fig. 5B). When these experiments were repeated with deviations in the vertical direction, a similar response profile was revealed (Fig. 5C,D), although the DCMD was found to be less tightly tuned to a direct collision trajectory. When the mean spike

numbers from the six experiments were averaged, the sensitivity profile of the DCMD to stimuli displaced horizontally from a collision trajectory had a half-width at half peak of approximately 3.0 $^{\circ}$ (dotted line Fig. 5D).

An even tighter tuning was revealed when either peak rate (spikes s $^{-1}$ measured over 25 ms; Fig. 6A,B) or spike discharge rate (spikes per 25 ms; Figs 4 and 7A,B) was used as the index to tuning. The peak rate had a half-width at half response peak of 1.8 $^{\circ}$ for horizontal deviations (Fig. 6A) and 3.0 $^{\circ}$ for vertical deviations (Fig. 6B). When the 95% confidence limits of the mean peak rates were plotted for each deviation, they clearly showed that significant differences occur in DCMD activity with a deviation from a collision course of as little as 1.2 $^{\circ}$ in either the horizontal or vertical directions (Fig. 6A,B). The sharp increase in the rate of spiking during object approach was no longer present with approaches more than 1.8 $^{\circ}$ off axis in the horizontal direction (Figs 4, 7A), but it was still present (at

Fig. 6. Response of the DCMD neurone to objects approaching on collision or near-miss trajectories. (A) Horizontal displacements away from a collision trajectory occurred in steps of 0.6° , with a maximum displacement of 4.8° . (B) Vertical displacements away from a collision trajectory occurred in steps of 0.3° or 0.6° , with a maximum displacement of 3.0° . Each displacement was presented six times, movement ceased at 350 ms. Mean peak spike frequency (dark line on plot) is shown (\pm S.E.M.) calculated over 25 ms intervals. The dashed lines on either side of the curve show the 95% confidence limits of the mean. The dotted horizontal line indicates the level of half-maximum peak frequency. Objects were $30\text{ mm}\times 30\text{ mm}$ in size and approached at a velocity of 2.5 m s^{-1} . Other stimulus details were as in Fig. 4.



99% confidence limits) for approach trajectories 1.8° off axis in the vertical direction (Fig. 7B).

In all these experiments, any peak in spike rate occurred after the end of simulated movement (arrowheads in Fig. 4; magenta line in Fig. 7A,B). With an approach speed of 2.5 m s^{-1} , any collision would have occurred a minimum of 35 ms after the end of simulated movement.

Discussion

We have shown that the LGMD/DCMD neurones in the locust visual system respond preferentially to objects approaching on a collision course compared with a near-miss course. The tuning in the LGMD/DCMD neurones was particularly tight when deviations occurred away from a collision trajectory in the horizontal direction. The degree of tuning depended on the index used. The tightest tuning was shown by peak firing frequency, where the response half-width at half height was 1.8° . The build-up to the final peak response level was much steeper when an object approached on a collision course compared with a near-miss trajectory. This would mean that if an escape or evasive response were triggered by the DCMD at a criterion number of impulses per second, the tuning to directly approaching objects would be further sharpened. In the vertical plane, the same indices of tuning were coarser. For example, for vertical deviations away from a collision trajectory, peak firing frequency had a half-width at half height of between 2.4 and 3.0° . One reason for the difference in tuning in the horizontal *versus* the vertical directions may be anatomical: in the lobula, the main branches of the LGMD project horizontally, with a mesh of fine projections extending both horizontally and vertically (Rind, 1984). The consequence of this may be that motion in the horizontal direction is better represented over the dendrites of the LGMD. O'Shea and Rowell (1976) have already noted that there is a hole in the receptive field of the LGMD corresponding to the position of its main dendritic process in the lobula. The

retina itself is not likely to be the source of this difference since the photoreceptor acceptance angles in the horizontal ($1.5\pm 0.2^\circ$) and vertical ($1.4\pm 0.1^\circ$) (mean \pm s.d., $N=6$) directions are very similar (Wilson, 1975). The interommatidial angles in the horizontal and vertical directions vary with eye position and, at the side of the eye, where these stimuli were presented, they are approximately equal (Horridge, 1978).

In the pigeon, Wang and Frost (1992) recorded from neurones in the nucleus rotundus that were maximally excited by objects approaching the animal. Some of the neurones showed extremely tight tuning centred on a 0° azimuth straight in front of the animal, with a mean response half-width at half height of 3.3° and a mean above-baseline width of 16° . When we used the same response index (total spike number per stimulus), we found comparable, or better, performance in the locust LGMD/DCMD neurones to horizontal deflections away from a collision trajectory.

The LGMD/DCMD neurones are thought to have a role in coordinating the escape behaviour of the locust in response to approaching objects (Rind and Simmons, 1992; Robertson and Reye, 1992). The output connections made by the DCMD in the thorax are consistent with this role (Simmons, 1980; Pearson *et al.* 1980; Pearson and Goodman, 1981; Gynther and Pearson, 1989). It has also been shown that these outputs are subject to presynaptic inhibition from a variety of sources, which ensures that action potentials and therefore escape reactions are only produced in an appropriate behavioural context (Pearson and Goodman, 1981; Steeves and Pearson, 1982). The presynaptic inhibition comes from the DCMD neurone itself, from its contralateral homologue and from mechanosensory interneurons. Where it has been measured, the presynaptic inhibition reaches a peak 5 ms after the spike that evoked it (Pearson and Goodman, 1981). The high and rapidly rising spiking output of the DCMD in response to a directly approaching object may be particularly effective in evoking an escape reaction since, at this time, spikes arrive

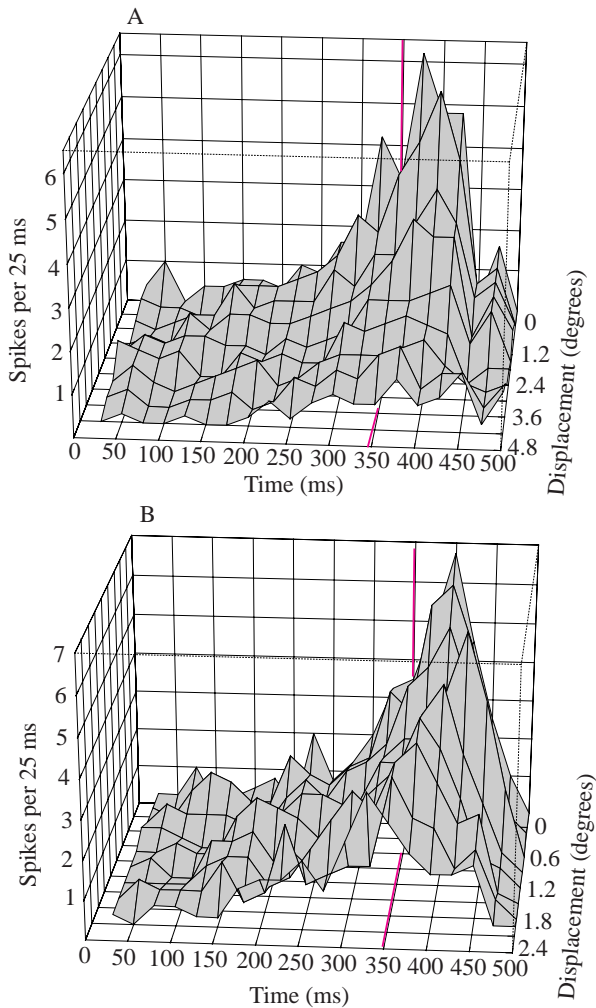


Fig. 7. Response of the DCMD neurone to objects approaching on collision or near-miss trajectories. Objects were 30 mm \times 30 mm in size and approached at a velocity of 2.5 m s $^{-1}$. (A) Horizontal displacements away from a collision trajectory occurred in steps of 0.6 $^{\circ}$, with a maximum displacement of 4.8 $^{\circ}$. (B) Vertical displacements away from a collision trajectory occurred in steps of 0.3 $^{\circ}$ or 0.6 $^{\circ}$, with a maximum displacement of 3.0 $^{\circ}$. Each displacement was presented six times, movement ceased at 350 ms (magenta line on plot). Mean spike numbers are shown throughout object approach, calculated over 25 ms intervals. Other stimulus details were as in Fig. 4.

within 2 or 3 ms of one another and may escape the suppressive effect of the lateral inhibition and be able to trigger an action potential in a postsynaptic neurone. Consistent with this was the observation that one of the variables most tightly tuned to a direct collision trajectory was the peak spike frequency.

In each locust, there is a pair of LGMD/DCMD neurones on each side of the animal, so that the approach of an object may be registered differentially by both the left and right LGMD/DCMD neurones and translated to differential activation of flight motoneurones on the two sides of the locust (Simmons, 1980; Robertson and Reye, 1992; Robertson and Johnson, 1993).

A model incorporating the input organization of the LGMD neurone has recently been described (Rind and Bramwell,

1996). The model was challenged with a range of moving visual stimuli, including objects approaching on a collision course. The model predicted that, when an object moves over the retina, a critical race develops between excitation, generated in the input elements of the LGMD when an edge of the object passes over them, and inhibition spreading either laterally between the input elements or forwards (Rind and Bramwell, 1996). For a strong LGMD/DCMD response, the excitation must overtake the inhibition. This occurs when an object approaches on a collision course with the eye, in which case image edges move with increasing velocity over the eye and expand rapidly so that inhibition arrives at each input unit after excitation has caused the unit to reach threshold and so generate a response in the output element of the model, the 'LGMD'. When non-collision trajectories were simulated using this model, lateral inhibition was found to sharpen the tuning of the network 'LGMD' for direct approaches in two ways (Rind and Bramwell, 1996; F. C. Rind, unpublished observations). First, when an image edge moves rapidly and expands over the retina, as it does in the final stage of object approach, excitation arrives at the inputs to the 'LGMD' before lateral inhibition and, as the amount of edge increases, so the excitation builds up rapidly. For the same object on a horizontal near-miss trajectory, all edges do not move or expand in the same way; rather, the farther edge moves rapidly over the eye, but the nearer edge moves more slowly and, overall, the expansion in the amount of edge is reduced because the object does not come as close to the eye. Lateral inhibition is then able to suppress more of any excitatory response generated. The second way that lateral inhibition was found to increase the tuning of the network 'LGMD' for direct approaches was that, for larger deviations, the edge of the object nearest the eye moves over the same part of the retina over which the farther edge has already passed and stimulated. The large pool of lateral inhibition that persists after motion of the farther edge causes excitation to be cut back when the near edge then moves into the same area. With an object approaching on a direct collision course, its image edges continually move out over unstimulated areas of retina.

A third effect that would increase the response of the LGMD/DCMD neurones to directly approaching objects was noted in experiments on the neurones themselves. The response to nearby light/dark and dark/light edges was much reduced compared with each edge presented separately. This was not due to response saturation because it occurred over the range of edge lengths where adding more edge of the same polarity increased the LGMD/DCMD response (Simmons and Rind, 1992). This property would sharpen the LGMD/DCMD response for collision trajectories where edges of opposite contrast polarity move over the retina away from one another as the object approaches. With increasing deviation away from a collision trajectory, edges of opposite contrast polarity move over the retina towards one another as the object approaches, and then passes, the eye.

In the locust visual system, the LGMD/DCMD neurones are not unique in their response properties. Investigations have revealed that a second motion-sensitive neurone in the locust

lobula, the LGMD2, responds directionally when challenged with motion of objects towards the eye (Rind, 1996; Simmons and Rind, 1997). The LGMD2 shares the same critical image cues as the LGMD/DCMD neurones, although its input organisation shows differences. The LGMD2, for instance, receives only excitation at light-off, whereas the LGMD is excited at both light-on and light-off (Rind, 1987; Simmons and Rind, 1997). Before the selective response of the LGMD neurones to motion in depth was known, Rind (1987) identified a whole class of motion-sensitive visual neurones that share with the LGMD/DCMD and LGMD2 neurones the same nondirectional response to horizontal motion in the x,y -plane. The relative importance of this pathway in the locust was highlighted by the study of Gewecke and Hou (1993), who identified 23 types of visual neurone in the locust lobula, three of which gave directional responses and 18 gave nondirectional responses when presented with motion in the x,y -plane. The presence of this system of optic lobe neurones suggests that the input organisation, exemplified by the LGMD/DCMD pathway, subserves a more fundamental analysis than was previously appreciated, possibly conferring sensitivity to object range.

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