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Activity of descending contralateral movement detector neurons and collision avoidance behaviour in response to head-on visual stimuli in locusts

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Abstract We recorded the activity of the right and left descending contralateral movement detectors responding to 10-cm (small) or 20-cm (large) computer-generated spheres approaching along different trajectories in the locust's frontal field of view. In separate experiments we examined the steering responses of tethered flying locusts to identical stimuli. The descending contralateral movement detectors were more sensitive to variations in target trajectory in the horizontal plane than in the vertical plane. Descending contralateral movement detector activity was related to target trajectory and to target size and was most sensitive to small objects converging on a direct collision course from above and to one side. Small objects failed to induce collision avoidance manoeuvres whereas large objects produced reliable collision avoidance responses. Large targets approaching along a converging trajectory produced steering responses that were either away from or toward the side of approach of the object, whereas targets approaching along trajectories that were offset from the locust's mid-longitudinal body axis primarily evoked responses away from the target. We detected no differences in the discharge properties of the descending contralateral movement detector pair that could account for the different collision avoidance behaviours evoked by varying the target size and trajectories. We suggest that descending contralateral movement detector properties are better suited to predator evasion than collision avoidance.

Key words Insect · Flight · Steering · Vision · Looming

Introduction

Avoiding a head-on collision and evading the lunge of a predator both require the rapid detection of looming stimuli and the execution of appropriate locomotor responses. Visual detection can be performed by neurons that respond maximally to objects on a collision course with an animal and collision-sensitive neurons have been described in locusts (Judge and Rind 1997; Gabbiani et al. 1999a) and pigeons (Wang and Frost 1992; Sun and Frost 1998). In locusts, two pairs of identified neurons, the lobula giant movement detectors (LGMDs) and the descending contralateral movement detectors (DCMDs) are arguably the best described collision-sensitive visual neurons (reviewed in Rind and Simmons 1999a) despite current disagreement over the properties of, and mechanisms underlying, their discharge patterns (Hatsopoulos et al. 1995; Rind and Simmons 1997, 1999b; Gabbiani et al. 1999b). The same neuron could be involved in generating different behaviours depending on internal or external context. Notwithstanding this, there has been much speculation over the years as to the behavioural role of the LGMD/DCMDs yet there is little definitive evidence supporting hypotheses that their role is in predator evasion (e.g. Rind and Simmons 1992) or in steering around obstacles in the flight path (e.g. Robertson and Reye 1992), or both. These hypotheses differ fundamentally in whether the similar visual stimuli are generated by object motion or by self motion and thus they differ in the behavioural and ecological relevance of the DCMD activity (Gibson 1979).

A looming stimulus results in an image that expands symmetrically and exponentially on the retina. The acceleration of an increasing extent of image edge travelling over the eye is the characteristic of a looming stimulus that is encoded by the LGMD (Rind and

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Bramwell 1996) and transferred to the ipsilateral DCMD by a spike-transmitting chemical synapse (Rind 1984; Rind and Simmons 1992; Simmons and Rind 1992). Computer-generated simulations of looming objects presented to one eye from the side of the animal are sufficient to evoke a looming response in the DCMD (e.g. Rind and Simmons 1997; Gabianni et al. 1999a). The intensity of this response decreases as the trajectory of the object is offset from the midpoint of the eye (Judge and Rind 1997) indicating that the DCMD is tuned to objects approaching on a direct collision course. Simultaneous recordings from both DCMDs, using real objects, suggest that the relative activity of the DCMDs varies predictably as the target trajectory is displaced across the animal's frontal field of view (D.N. Reye, unpublished observations). The main axon of each DCMD crosses the midline of the brain, descends into the thoracic ganglia (O'Shea et al. 1974) and makes connections to flight interneurons and motoneurons (Burrows and Rowell 1973; Simmons 1980). Thus, the DCMDs are good candidates for mediating visually guided steering during flight.

Visual stimuli approaching in the flight path induce characteristic modifications of the movements and positions of the wings and abdomen during flight that produce steering torques to move the locust away from an impending head-on collision (Robertson and Reye 1992; Robertson and Johnson 1993b). Detection of both the angle that the object subtends at the eye and the location of the closest edge of the object are important cues for evoking an appropriately directed collision avoidance response (Robertson and Johnson 1993a). The discharge of the pair of DCMDs contains information about the side of object approach (Robertson and Gray 1997; Mo et al. 1999) and, according to the model of Gabbiani et al. (1999a), each peaks at specific angular thresholds.

We examined the putative role of the DCMDs in collision avoidance during flight by comparing paired DCMD firing patterns in response to computer-generated looming stimuli that induce different locomotor consequences. First we characterized the simultaneous activity of both DCMDs to the approach of a 10-cm computer-generated sphere along various frontal trajectories at 3 m s^{-1} . We discovered that, although capable of evoking startle reactions, such stimuli did not evoke collision avoidance steering. Next we characterized the steering behaviour in response to the approach of a 20-cm computer-generated sphere along a subset of the original trajectories. Finally, we recorded paired DCMD responses to the 20-cm stimuli that evoked steering. The complete dataset permitted comparisons between DCMD responses to stimuli that evoked steering primarily to one side, with those that evoked steering to either side and with those that did not evoke steering. We found that the discharge characteristics of the DCMDs were not obviously related to collision avoidance steering and suggest that they may be better suited for a role in predator evasion.

Materials and methods

Animals

Adult *Locusta migratoria* were obtained from a crowded colony maintained in the Department of Biology at Queen's University (average temperature -25°C ; light:dark cycle 18:6). Animals that were at least 3 weeks past the adult moult were selected for experiments.

Computer-generated simulations

The visual stimuli were animation sequences created using 3D Studio Max animation software (Autodesk, San Francisco, Calif.) and rendered in AVI format at 80 frames s^{-1} . This refresh rate is approximately equal to the flicker fusion frequency of the locust compound eye (Miall 1978). Moreover, DCMD is equally well activated by stimuli presented at 67, 100 and 200 frames s^{-1} (Gabbiani et al. 1999a). Animations were run on a PC Pentium 166 equipped with 48 Mb of RAM, a 2-Mb ATI Mach 64 video card, and a DayTek model DT-1730 17-inch Multi-Scan Color Monitor set to a vertical refresh of 80 Hz. Animations were presented using the ATI video player aligned to the centre of the screen. The objects were black and white checkerboard spheres presented against a white background. The checkerboard pattern was used to provide 3D texture and to maintain the average luminosity constant within the object during stimulus presentation. The overall spike numbers in response to presentation of these patterned objects were generally quite low. One reason for this may have been the antagonism between light and dark edges noted by Simmons and Rind (1992). Nevertheless textured stimuli are effective at evoking behavioural reactions (Robertson and Reye 1992, and below) and we attribute the low spike frequencies to stimulation in the frontal region of the eye (see Discussion). Brightness, contrast and luminosity of the objects although not measured were kept consistent throughout the study. Animation sequences were created such that the objects approached at 3 m s^{-1} , which was the fastest approach speed that produced smooth playback using the specified computer hardware. The objects remained on the screen after the end of the presentation. We used two different sized objects with virtual diameters of 10 cm and 20 cm, respectively. The texture elements of the objects, i.e. the checkerboard patterns, were scaled linearly with the diameter of the target. Unique looming stimuli depend on the ratio of object size and approach speed such that the same monocular visual stimulation will be generated by an object doubled in size if its speed is also doubled (e.g. Gabbiani et al. 1999a). Thus, the 10-cm object at 3 m s^{-1} is equivalent to a 20-cm object at 6 m s^{-1} . The parameter $l/|v|$, (where l is half size and $|v|$ is speed) used by Gabbiani et al. (1999a) to specify approach conditions, was 16.7 ms and 33.3 ms for our stimuli. Each animal was presented with targets that approached along 17 different trajectories (see below). Trajectory presentation was randomised by assigning a value to each trajectory and randomising these values using a random sort transform in SigmaPlot 3.0 scientific graphing software (Jandel Scientific, San Rafael, Calif.). The interval between trial presentations was at least 60 s for DCMD experiments or 5 min for behavioural experiments to reduce adaptation of the DCMD response or behaviour respectively. The end of trial presentation was determined by rendering each AVI file with a 1-ms pulse that was generated from a Grass S88 stimulator and inserted into the AVI file such that it was time-aligned with the last frame of the simulation. The pulse was played through a Sound Blaster 16 audio card and monitored as a d.c. offset during data acquisition. The object images in the last frame had final diameters of 7 cm and 11 cm on the screen for the 10-cm and 20-cm spheres, respectively, indicating projected times to collision of 47.6 ms for the 10-cm sphere and 121.2 ms for the 20-cm sphere. These conditions were constrained by the desire to keep the initial and final images of the objects completely on the screen of the monitor for all trajectories.

Targets approached from a virtual distance of 5 m along one of three trajectory types (Fig. 1A); a direct collision course (converging), a course parallel to, but offset from, the straight ahead axis (offset), and a course that started directly in front of the animal and diverged away in a straight line (diverging). For converging and offset trajectories the target approached from one of eight starting positions (Fig. 1B): above (a) or below (b) in a plane parallel to the mid-vertical body axis, to the left (L) or right (R) in a plane parallel to the mid-horizontal axis, above and either from the left (aL) or the right (aR), and below from either the left (bL) or the right (bR). 0° represents a point that is directly in front of the intersection of the mid-vertical and mid-horizontal body axes. Converging targets approached along trajectories that were displaced 7° or 14° from the central 0° axis (equivalent to 60 cm and 122 cm displaced from the central position at the start). Offset targets approached along trajectories that were displaced 7 cm and 14 cm from the central 0° axis (equivalent to stopping positions on the screen subtending 35° and 54.5° at the animal). Diverging targets approached along trajectories such that the final position of the target on the screen at the end of the trial was displaced 7 cm and 14 cm from the central 0° axis (i.e. stopping at the same position as the offset targets).

DCMD experiments

For electrophysiological recording of DCMD activity during stimulus presentation all experiments were performed in a Faraday

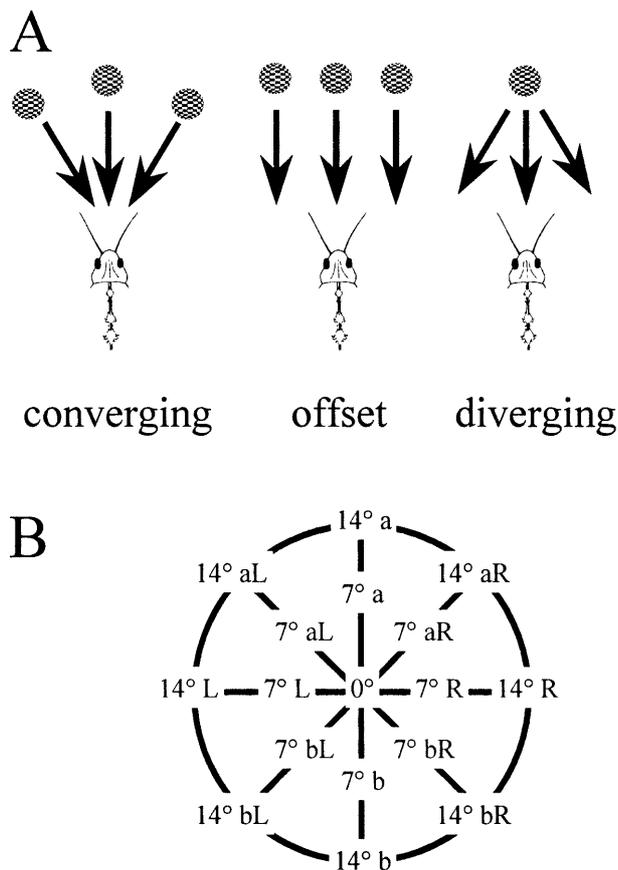


Fig. 1 A Dorsal aspect of the three main trajectory types: converging, offset and diverging. B Frontal aspect, from the locust's perspective, showing the starting and/or ending points of approaching targets in relation to the vertical and horizontal centre of the head of the locust (0°). a above; b below; L left; R right. See Materials and methods for further explanation

cage. The legs and wings of the locust were removed and a dorsal midline incision was made. The animal was pinned dorsal side up onto a corkboard and the thoracic cavity was exposed. The preparation was oriented such that the longitudinal body axis was perpendicular to and facing a computer monitor placed 10 cm or 20 cm away (Fig. 2A). Initial experiments had the screen placed at 10 cm but we found this distance disturbed air flow into the wind tunnel during the behavioural experiments (see below) so later experiments had the screen placed at 20 cm. No difference was found between results obtained with the screen at 10 cm and those with the screen at 20 cm and the results were pooled. The screen of the monitor was shielded with a grounded, electrostatic anti-glare screen. After removing the gut, overlying fat body and salivary gland, the cervical connectives were exposed. Extracellular silver wire hook electrodes were placed on each cervical connective such that they contacted the connectives along the dorsal medial margin and were insulated with a mixture of Vaseline and mineral oil. A silver wire was inserted into the abdomen of the locust and connected to ground. The activity of each DCMD was amplified using a differential, high gain, a.c.-coupled preamplifier (Grass P-15, Grass Instrument, Quincy, Mass.), monitored on a Gould digital oscilloscope (DSO 630) and time aligned to the output of the stimulus monitor. The entire Faraday cage was covered with black felt cloth to block out extraneous visual stimuli. Each DCMD, right and left, was named according to the position of the cell body in the brain relative to the longitudinal midline. Thus, the left DCMD (DCMDL) receives information from the left eye and its axon crosses over in the brain and projects posteriorly along the right side of the nerve cord and vice versa. In most cases described in this study the position of the DCMD is given relative to the side of stimulus presentation, i.e. with the cell body and primary input sites ipsilateral (DCMDi) and contralateral (DCMDc) to the side of target approach.

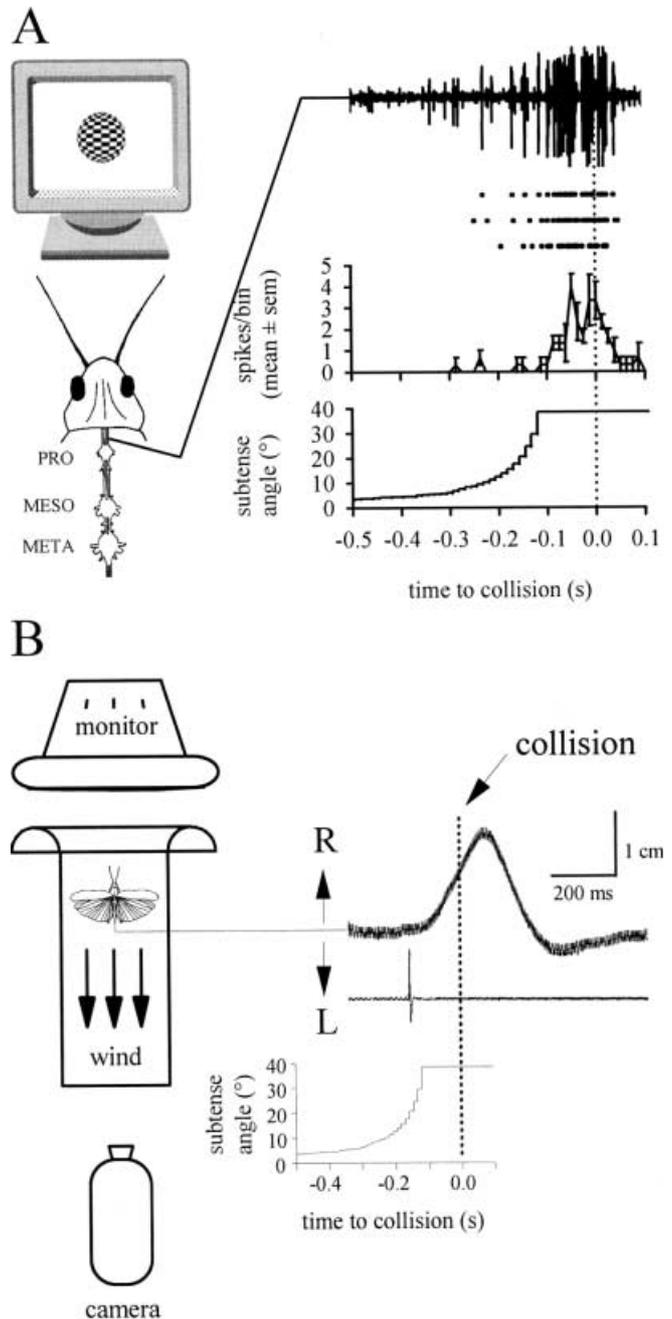
Two groups of ten locusts each were presented with either 10-cm or 20-cm targets. The specific trajectories used for each group are described in the text of the results section. Signals from the extracellular electrodes and the soundcard output, were digitised and acquired on-line using Datawave Technologies (Longmont, Co.) acquisition system. DCMD spikes were identified according to their characteristic discharge properties and extracellularly recorded spike amplitudes. Only similarly shaped action potentials in a particular amplitude window were counted. DCMD spike occurrence times were measured off-line, imported into a SigmaPlot 3.0 worksheet and divided into 12.5-ms bins, which was the interval between frames of the simulations, and aligned with the end of target approach (Fig. 2A). The data were plotted as the number of spikes/bin versus time to collision which was extrapolated from the end of target movement. To examine the dynamic properties of the DCMD responses the mean of three replicates for a given target trajectory for each animal was plotted as the mean number of spikes/bin (\pm SEM). The data were fit with a line of best fit as determined by CurveExpert V1.23 for Windows 95 curve-fitting software. The line that best fit the data was a rational function of the form:

$$y = \frac{a + bx}{1 + cx + dx^2} \quad (1)$$

where y is the number of spikes/bin, x is the time to collision and $a-d$ are the coefficients. This equation consistently fitted the data well (r^2 ranging between 0.80 and 0.95) but is not considered to have any biological significance. It was used solely to obtain objective measures of the start of the discharge and the rate of increase of the discharge.

We characterized the DCMD discharge to different targets and trajectories in terms of (1) the time to collision at the start of DCMD activity (the time when the line of best fit rose above 0.3 spikes, which represents a minimum of one spike from three replicates within a time bin); (2) the total number of DCMD spikes from the start of the discharge to the time of collision (obtained by summing values in the relevant bins); (3) the timing of the peak discharge (equivalent to the time value of the bin containing the most DCMD spikes); and (4) the spike frequency at peak discharge (calculated from the number of spikes in the 12.5-ms bin).

Fig. 2 **A** Experimental setup to measure descending contralateral movement detector (DCMD) activity during computer-generated target presentation. The location of the cell body relative to the longitudinal midline designates the right or left DCMD (see text). A recording from the left DCMD during presentation of a 10 cm target approaching at 3 m s^{-1} from directly in front of the locust is shown *top right*. Beneath the trace is a raster of three trials of the same trajectory with the average ($\pm \text{SEM}$) of the data organized into 12.5-ms bins and plotted below with the angle that the target subtends at the locust's head during approach. The time at which the target would collide with the locust is indicated by the dotted line. **B** Setup for behavioural experiments. Locusts were tethered and placed in a wind tunnel (wind speed = 3 m s^{-1}). Simulated approaching targets were displayed on a computer monitor placed 20 cm from the head of the locust. Wing kinematics and abdomen position were monitored by a video camera placed behind the tunnel. Abdomen position was also monitored with a Sandeman position transducer (Sandeman 1968) whose output is illustrated on the *right*. The traces shown are the output of the transducer (*top trace*) and the output of the stimulus monitor (*bottom trace*). A graph of target subtense over time is aligned in register with the transducer and stimulus traces. The *dotted line* shows the time of "collision" of the virtual target. In this example a target that approached from the locust's left elicited abdominal ruddering to the right. *PRO* prothoracic ganglion; *MESO* mesothoracic ganglion; *META* metathoracic ganglion



We were also interested in the characteristics of the discharge prior to a time 214 ms before collision. This time point ($t = -214 \text{ ms}$) is an estimate of the time that the DCMD discharge would have had to have occurred by to be responsible for the avoidance behaviours. It is derived from the average time of the behavioural reactions (176 ms before collision, see Results) plus a conduction delay and processing time which was calculated by subtracting a processing delay from visual input to peak DCMD discharge ($\sim 27 \text{ ms}$, Gabbiani et al. 1999a) from the latency between visual input and behavioural reaction ($\sim 65 \text{ ms}$, Robert and Rowell 1992). We characterized the DCMD discharge to this point in terms of (1) the spike frequency at $t = -214 \text{ ms}$ (calculated from the number of spikes in the 12.5-ms bin at that time); (2) the rate of increase of DCMD discharge at $t = -214 \text{ ms}$ (obtained from the slope of the tangent to the line of best fit at that time); and (3) the number of spikes from the start of discharge to $t = -214 \text{ ms}$ (obtained by summing the number of spikes in the relevant bins).

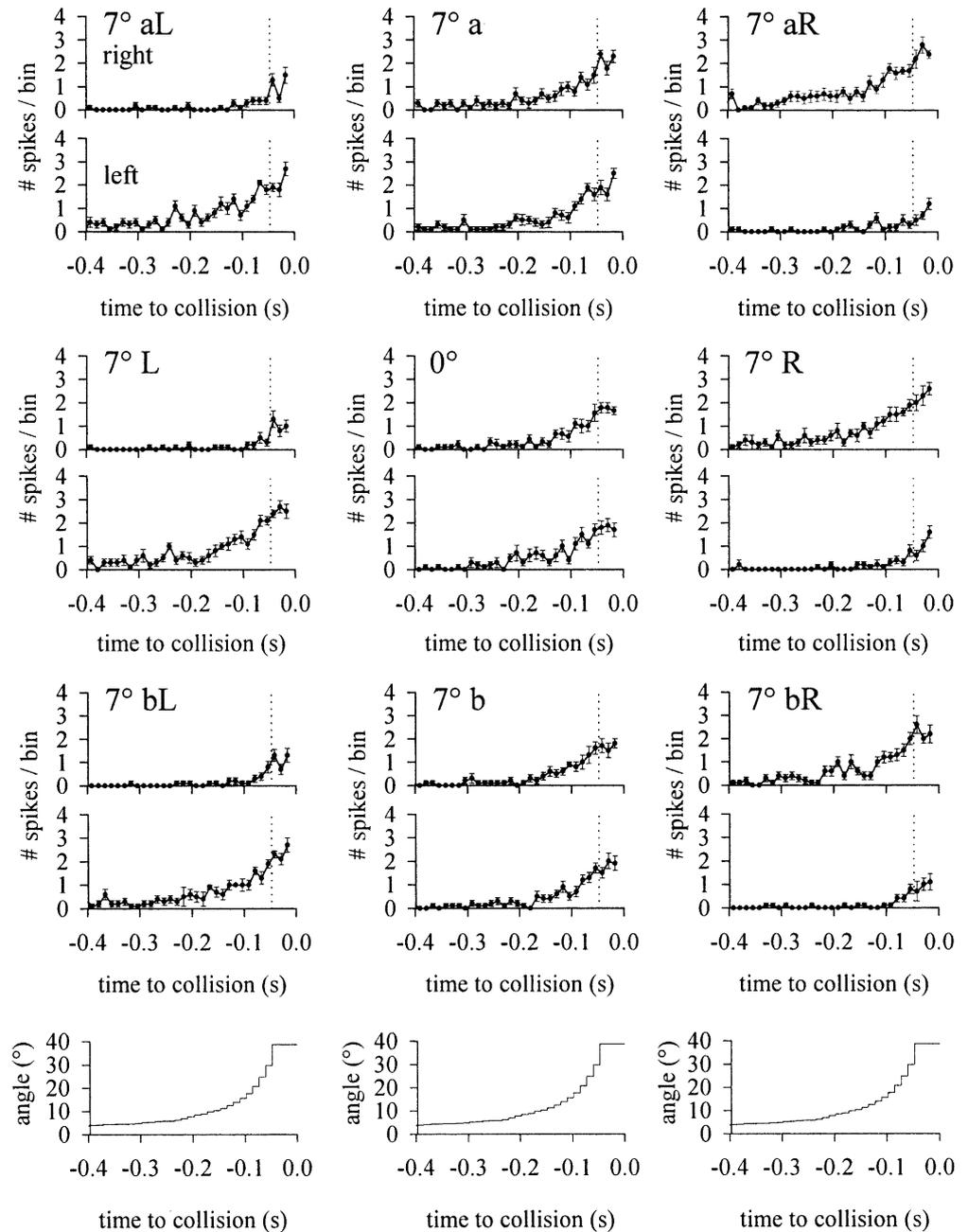
Behavioural experiments

Locusts were attached at the pronotum to a rigid copper rod with a mixture of beeswax and resin and suspended in a wind tunnel (windspeed 3 m s^{-1} , see Robertson and Johnson 1993a for a description of the tunnel) 20 cm from a computer monitor covered with an anti-glare screen. The sides, bottom and top of the wind tunnel were covered with white construction paper and a white cardboard cowling was placed from the edges of the computer monitor and flared out to extend over the front of the wind tunnel to block out external visual stimuli. This setup was optimal for providing an adequate stimulus without disrupting the airflow into the mouth of the wind tunnel. Locusts were flown at room temperature (approximately 22°C) for at least 10 min before the start of an experiment. If a locust did not fly continuously for 10 min in a typical level flight posture (see Robertson and Reye 1992) then it was not used for an experiment.

A total of 24 locusts were presented with 278 trials representing 3 replicates each of up to 9 unique target trajectories. The specific trajectories used are described in the text of the results section. Locusts were videotaped from behind using a Hitachi 5200A video camera (shutter speed = $1/250 \text{ s}$). The resulting videos were played

back on a Panasonic (model no. PV 4770 K) VCR at 60 fields s^{-1} to measure wing and abdomen kinematics during stimulus presentations. This allowed a resolution of only three frames per wingbeat cycle but was sufficient to detect changes in wing asymmetry during the downstroke and the position of the abdomen (see Robertson and Johnson 1993a). Some trials were videotaped using a Motion Scope 500 High Speed Digital Video System at $500 \text{ frames s}^{-1}$ (OPTIKON, shutter speed = $1/1000 \text{ s}$). The recordings were triggered by the computer animation in order to record 5 s of data for analysis. This gave a much higher resolution of 25 frames per wingbeat cycle for these trials. The responses were time aligned to the stimulus using the last frame of the animation as determined from the video playback. The abdomen position was also measured via a Sandeman position transducer (Sandeman 1968). The output of the transducer was filtered with a Krohn-Hite low pass filter (model 3750) to remove 60-cycle noise and time aligned to the stimulus monitor.

Fig. 3 Responses of DCMDR (top graph in each pair) and DCMDL (bottom graph in each pair) to 10-cm targets approaching along converging trajectories in which the target starts on centre or 7° off the centre in a given direction. Note that the start of the response of one DCMD is similar when the targets approach from the same vertical plane (e.g. 7° aL, 7° L and 7° bL). Targets approaching in the same horizontal plane (e.g. 7° aL, 7° a and 7° aR) elicit responses in DCMDs that are dependent on the trajectory. For example, the start of the response of DCMDR begins sooner as target trajectories are shifted to the right and vice versa for DCMDL. The dotted line in each graph indicates the time of the last frame in the simulation. Details in text



The digital video recording from the Motion Scope 500 was transferred to VHS videotape at one frame per second. The videotapes of both low-speed (Hitachi 5200A) and high-speed (Motion Scope 500) footage were analyzed to determine the wing angles and confirm the direction of shifts in abdomen position. This was done with a frame by frame analysis, of approximately 90 frames (Hitachi 5200A) or 500 frames (Motion Scope 500) around the time of collision, using hardware and software by PEAK Performance Technologies (Englewood, USA). The analysis involved digitising seven points on each frame of videotape: the top of the tether, the bottom of the tether, each wing tip and the tip of the abdomen. The coordinates of each digitised point were used to calculate the angle between each wing and the tether (the long axis of the tether was set to 0°) and the abdomen position relative to the end of the tether. Angles were measured with an accuracy of $\pm 2.5^\circ$ and abdomen positions with an accuracy of ± 0.5 mm; the accuracy depended on the ability to resolve the tip of the wings and abdomen in different

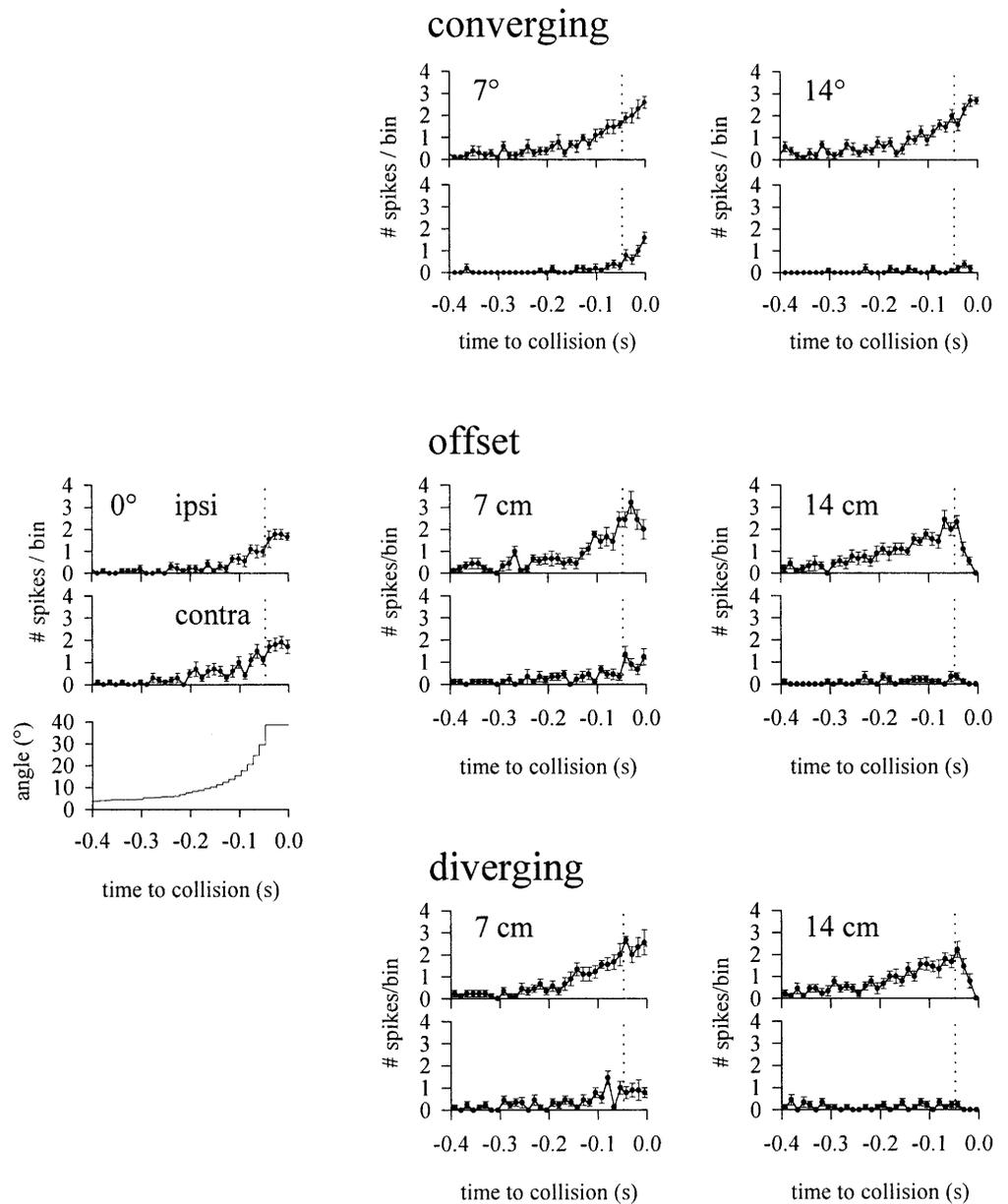
frames. Forewing angles were used to determine forewing asymmetry (FWA), which is the difference in measured forewing angles relative to the tether during the downstroke (right wing angle minus left wing angle). A positive FWA indicates that the angle between the right wing and the tether is greater than between the left wing and the tether and thus suggests that the locust is attempting to steer to the right (see Robertson and Reye 1992). Note that for convenience, although measured relative to the tether, wing elevations are presented in figures as angles relative to a 0° position vertically below the animal. Most data for wing kinematics were obtained using the low-speed Hitachi 5200A and these data were filtered such that data points were collected only during the downstroke of each wingbeat (see Robertson and Johnson 1993a). Measurements of abdomen position were obtained from every frame of video. Data from each trial was scored based on the presence and direction of a steering response as follows: steering away from the side of the approaching target was assigned a value

of +1, steering toward the side of the approaching target was assigned a value of -1, and no steering response was assigned a value of 0. For trials in which a value of +1 or -1 was obtained, the latency from the start of the response to the projected time of collision was calculated.

Statistical analysis

The data were tested for normality and equal variance but usually did not satisfy the requirements for parametric statistical comparison. Dynamic properties of the DCMD responses were compared using a Kruskal-Wallis ANOVA on ranks followed by a Dunn's multiple comparison procedure or, when possible, using a parametric ANOVA followed by Student-Newman-Keuls multiple comparison test using SigmaStat 2.0 statistical software (Jandel Scientific, San Rafael, Calif.). Values were considered to be significantly different at $P < 0.05$. Data from all experiments were plotted using SigmaPlot 4.0 graphing software (Jandel Scientific, San Rafael, Calif.).

Fig. 4 Response of ipsilateral DCMD (*top graph in each pair*) and contralateral DCMD (*bottom graph in each pair*) to 10-cm targets approaching along the centre line or along converging (*top*), offset (*middle*) or diverging (*bottom*) trajectories that are displaced 7° or cm and 14° or cm) from the centre line. The *dotted line* in each graph indicates the time of the last frame in the simulation. Details in text



Results

Response of both DCMDs to the approach of 10-cm spheres along different trajectories

Sample mean responses from both DCMDs in ten animals presented with 10-cm targets approaching along each of the 49 trajectories are displayed in Figs. 3 and 4. Figure 3 shows the mean responses for right and left DCMDs responding to targets converging along the midline or 7° from the midline trajectory. Responses were mirror symmetrical for right and left DCMDs and subsequent treatment of the data ignores the distinction of right and left by considering DCMDs as ipsilateral or contralateral to the side of target approach. Figure 4 shows the mean responses for ipsilateral and contralateral

eral DCMDs responding to converging, offset and diverging targets closer to (7° cm and 7 cm) and further away from (14° cm and 14 cm) from the longitudinal midline. There were no significant differences between the data obtained for offset and those for diverging targets and subsequent comparisons are only for offset and converging targets. Quantitative and statistical treatment of the data is summarized in Fig. 5 (for converging and offset targets in the vertical meridian) and Fig. 6 (for converging and offset targets in the horizontal meridian).

For converging targets in the vertical meridian (Fig. 5A) we found that the DCMD discharge started 30–50 ms earlier when the target approached from above compared to targets approaching on the midline or from below the horizon. Also the discharge was significantly greater by having about five (36%) more spikes from the start of the discharge to projected collision for targets coming from above the horizon. There were no significant differences in the timing or magnitude of the peak discharge frequency which was at or after the time of collision. A similar trend in a preference for targets

above the horizon was evident in the timing of the start of the discharge to offset targets (Fig. 5B). A significant difference between converging and offset targets for these trajectories was that targets offset 14 cm above or below the midline achieved a peak frequency about 40 ms earlier than for any other target. However this peak frequency was reduced compared with direct and equivalent converging targets.

There was considerably more disparity in discharge characteristics in the horizontal meridian (Fig. 6). Converging targets approaching from the ipsilateral side fired earliest (around 300 ms before collision), with the highest discharge frequencies (around 300 spikes s^{-1}) and greatest total number of spikes (around 30; Fig. 6A). Targets approaching contralaterally were poor at eliciting DCMD firing and targets on the midline were intermediate. For most measures there was no significant difference between equivalent converging and offset targets (Fig. 6B). The exception was for the timing of the peak frequency which for converging targets occurred close to the time of collision and for offset targets occurred as much as 80 ms prior to collision (offset 7 cm

Fig. 5A, B Quantitative comparison of DCMD activity in response to presentation of 10-cm targets varying in approach in a vertical meridian. In this and subsequent graphs the DCMD discharge is characterised in terms of the time to collision (*ttc* top graph) at which the discharge starts, the timing of the peak discharge (*time of peak* second graph from top), the spike frequency at the peak (*peak frequency* third graph from top) and the total number of spikes from the start of discharge (specified in the top graph) and projected collision at $t = 0$ (*number of spikes* bottom graph). The data were not distributed normally and are plotted as box plots indicating the median and 5th, 25th, 75th and 95th percentiles. A bar above the box plots indicates that each box is not significantly different from all others under the bar at that level, even although the bar may be interrupted. Boxes that are not linked by any bar, continuous or interrupted, above the box plots are significantly different at $P < 0.05$.

A Responses to targets on the centre line and converging from above or below the centre line. **B** Responses to targets on the centre line and offset above or below the centre line. The size of the displacement is indicated on the abscissa and was 7° (or cm) and 14° (or cm)

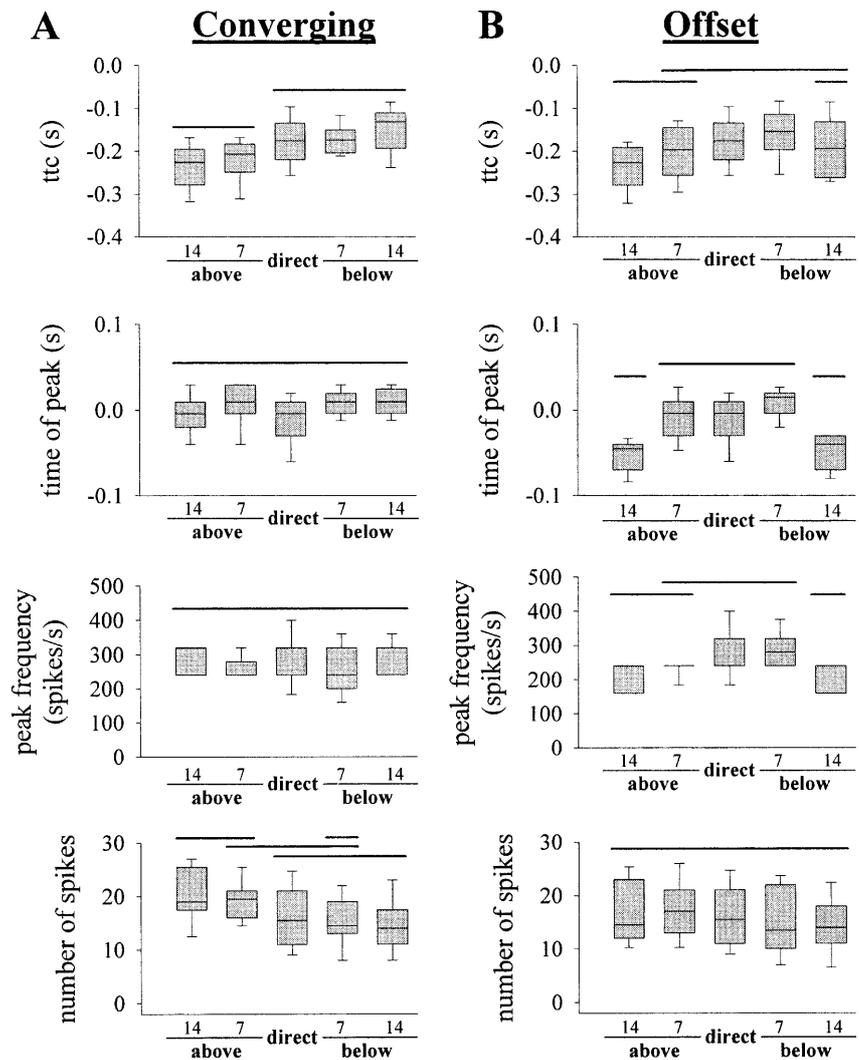
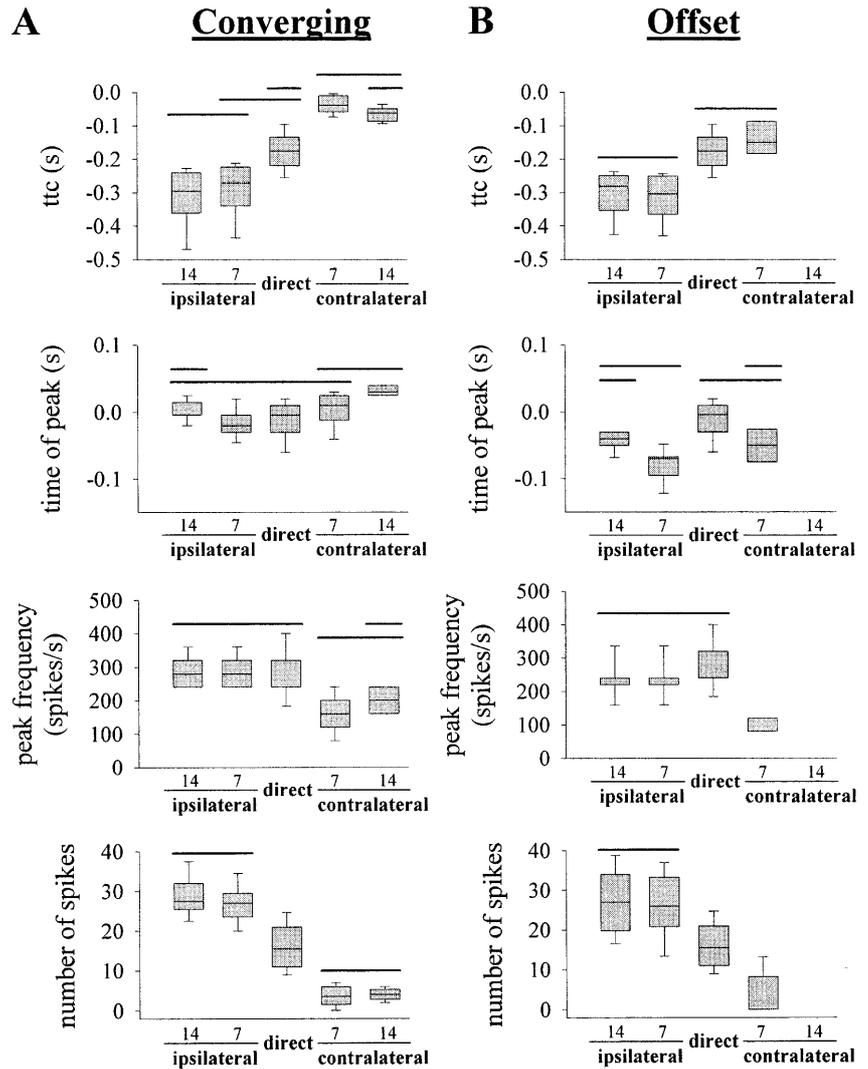


Fig. 6A, B Quantitative comparison of DCMD activity in response to presentation of 10-cm targets varying in approach in a horizontal meridian. **A** Responses to targets on the centre line and converging from the side ipsilateral or contralateral to the DCMD. **B** Responses to targets on the centre line and offset to the side ipsilateral or contralateral to the DCMD. The size of the displacement is indicated on the abscissa and was 7° or cm and 14° or cm). Targets offset by 14 cm failed to elicit activity of the contralateral DCMD (fewer than three trials with measurable activity) and an empty column is illustrated to indicate this



ipsilateral). Targets offset 14 cm from the midline were unable to elicit measurable discharges from the contralateral DCMD. To summarize: for small targets the most effective trajectories to elicit DCMD discharge were those that approached from above the horizon and from the ipsilateral side. Targets approaching head-on were inferior at exciting the DCMDs. There were observable trends for converging targets to be more effective than equivalent offset targets (e.g. higher peak frequencies) but these were not significant.

Behaviour

Initial experiments with 10-cm targets approaching along any trajectory produced either no response or a startle response within 30 ms of collision. A startle response was characterized by the extension of the front and hind legs and typically included the cessation of flight. We observed no definitive steering responses (see below). Subsequent experiments with 20-cm targets produced either no response, a startle response, steering

toward targets converging or offset to the right or left, or steering away from targets converging or offset to right or left. There were no discernible responses to diverging targets (data not shown).

For the large targets 24 locusts were used for a total of 278 trials. Targets approached from trajectories that were set 14° or 14 cm off the midline in either direction. These were, including straight on (0°), converging from the right (cR) or left (cL), offset to the right (oR) or left (oL), converging from above (ca) or below (cb) and offset from above (oa) and below (ob).

Figure 7 shows an example of a steering response of a locust to a 20-cm target converging from the left. The changes in forewing asymmetry and lateral shift of the abdomen indicate an attempted turn to the right, away from the target (see Robertson and Reye 1992, and Robertson and Johnson 1993a for an explanation of the aerodynamic consequences of body posture). In this example the latency of the change in forewing asymmetry was approximately 100 ms before collision, whereas the latency of the shift in abdomen position was approximately 120 ms before collision.

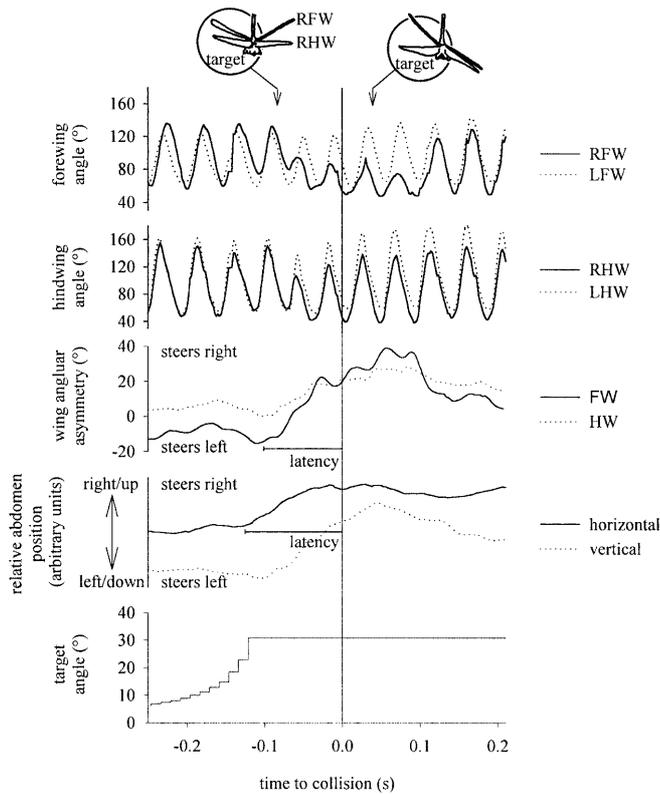


Fig. 7 Sample trial showing steering behaviour of a locust in response to a 20-cm target approaching from the left (converging). The *top two graphs* show the angles of elevation of the forewings and hindwings relative to the tether. The *third graph from the top* shows the asymmetry of the forewings and hindwings as calculated from the angle of the right wing minus the angle of the left wing for each pair. The fourth graph shows the horizontal and vertical position of the tip of the abdomen. The bottom graph shows the angle that the target subtends at the locusts head during approach. All data are time aligned to “collision” of the target (indicated by the line extending from 0). Just before collision there is a marked shift in the angle of the right forewing (RFW) and a similar, although less pronounced, shift in the angle of the right hindwing (RHW). The changes in wing angle are reflected in the graph of asymmetry that indicates an attempted turn to the right (see text). This behaviour is also reflected in the ruddering of the abdomen to the right before collision. The drawings of the locusts show the images obtained before and after collision which were obtained at the times indicated by the arrows on the upper graph. The circles represent the final position of the approaching spheres in which the checkerboard pattern has been omitted to show more clearly the position of the wings. The RFW and RHW are indicated. The latencies between the establishment of wing asymmetry and abdominal ruddering (horizontal shift) relative to collision are indicated in the third and fourth graph, respectively

Of the 24 animals that were presented with 20-cm targets, 8 showed steering to the right and to the left whereas 3 animals steered only to the right, 9 animals steered only to the left regardless of target trajectory, and 2 animals showed no directed steering response. Two were not included because only one trial was completed for each.

Steering behaviour in response to 20 cm targets approaching along various trajectories is summarized in Table 1. A comparison between converging and offset

Table 1 Summary of steering responses to large targets. Numbers in columns indicate percentages of trials (total in parentheses). *Other* indicates a disagreement between wing kinematics and abdominal ruddering directions; *a* above; *b* below; *R* right; *L* left

	Directed steering			None
	Away	Toward	Other	
All (278)	50.4			49.6
0°, a, b (81)	50.6			49.4
R, L (197)	59.4			40.6
Directed (117)	60.6	36.8	2.6	
Converging (58)	50.0	50.0		
Offset (56)	75.0	25.0		

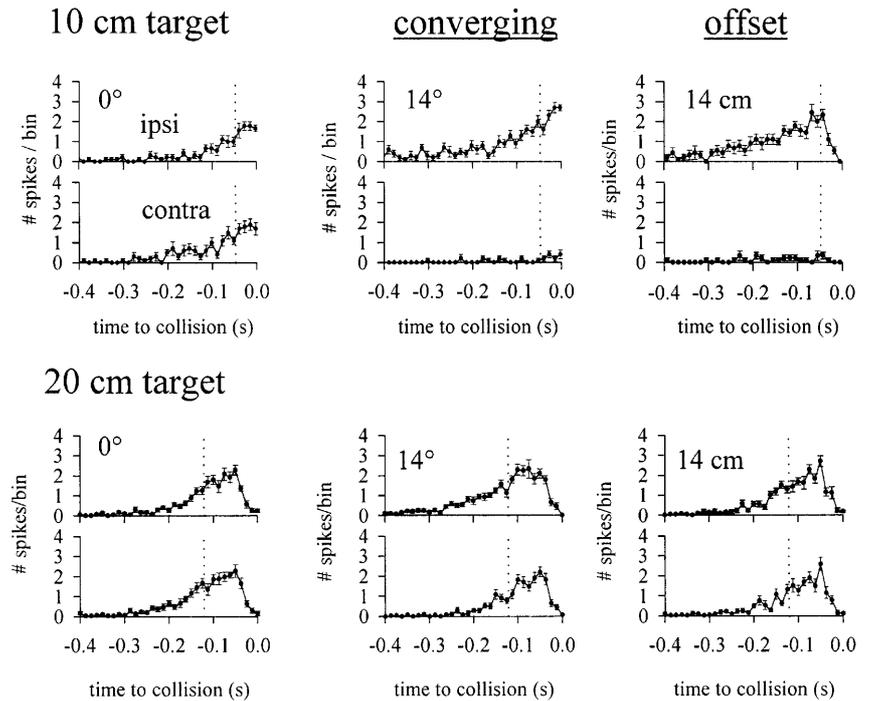
targets approaching from the right or left suggests that a target approaching along an offset trajectory was more capable of generating a steering response away from the target (75% of locusts steered away from offset targets whereas locusts were equally likely to steer in either direction for converging targets). Moreover, the data also suggest that targets approaching from straight on (0°), from above (a) or below (b) are less effective at generating a steering response than are targets approaching from the right or left of the animal’s longitudinal axis. The mean latency for all trials that showed a directed steering response (either away from or toward the target) was 176.6 ± 3.0 ms before “collision”. This value was consistent when measured from individual trajectories. These data demonstrate that the computer simulations used here are capable of producing directed steering responses with a latency that is similar to that of the responses produced by real objects (120 ms, see Robertson and Johnson 1993a, 1993b).

DCMD responses to converging large and small targets

Given that locusts did not respond to small objects approaching in their flight path we re-examined the response properties of the DCMDs, in particular to determine the responses to targets capable of eliciting steering. We compared these new results with those we had obtained previously using small targets. We specifically examined the responses of each DCMD to 20-cm targets approaching along trajectories that were converging 14° or offset 14 cm from the right or left (i.e. 14° R and 14° L) as well to targets approaching head-on (0°). The mean responses of both DCMDs to targets converging or offset were qualitatively similar to those observed in response to 10 cm targets approaching along the same trajectories (Fig. 8). In both cases the DCMD ipsilateral to the target responded more strongly than did the contralateral DCMD. The difference in the time of target stop here compared to that in Figs. 3 and 4 is due to the size of the target on the screen when the simulation ceased (see Materials and methods).

The responses to large targets were less disparate than those to small targets (i.e. there was less of a difference between the responses to ipsilateral and contralateral

Fig. 8 Response of ipsilateral DCMD (*top graph in each pair*) and contralateral DCMD (*bottom graph in each pair*) to small (10 cm) and large (20 cm) targets approaching along the centre line (0°) or along converging or offset trajectories that are displaced 14° or cm) from the centre line in a horizontal meridian. The *dotted line* in each graph indicates the time of the last frame in the simulation. Note that the last frame of the simulations occurred earlier before collision for large targets. Details in text



targets). The comparison for small and large offset targets is essentially identical to that for small and large converging targets and in the interests of economy is not presented here. Statistical comparison between the discharge properties of equivalent small and large converging targets (Fig. 9A) showed only one significant difference; the timing of the peak discharge which was around collision for small targets but was around 71 ms earlier before collision for large targets. It is worth noting at this point that the last frame of the simulations occurred 73.6 ms earlier before collision for large targets compared to small targets. We also examined the nature of the discharge to small and large targets at 214 ms before collision which is an estimated time by which neural events causing the steering reactions would have to have occurred to avoid collision (see Materials and methods). There was no difference between the responses of small and large targets at this time (Fig. 9B). Moreover, only ipsilateral converging targets (small or large) elicited DCMD activity before this time (Fig. 9A) and in most cases there was only time for one to three spikes to have occurred before $t = -214$ ms (Fig. 9B). To summarize: in terms of start of the discharge, peak frequency and total number of spikes small, ipsilateral converging targets were equally effective as equivalent large targets at eliciting DCMD activity and this did not appear to be early enough to account for the timing of steering manoeuvres in tethered flying animals.

DCMD responses to converging and offset large targets

To determine whether there were any differences in the DCMD response to converging and offset large targets

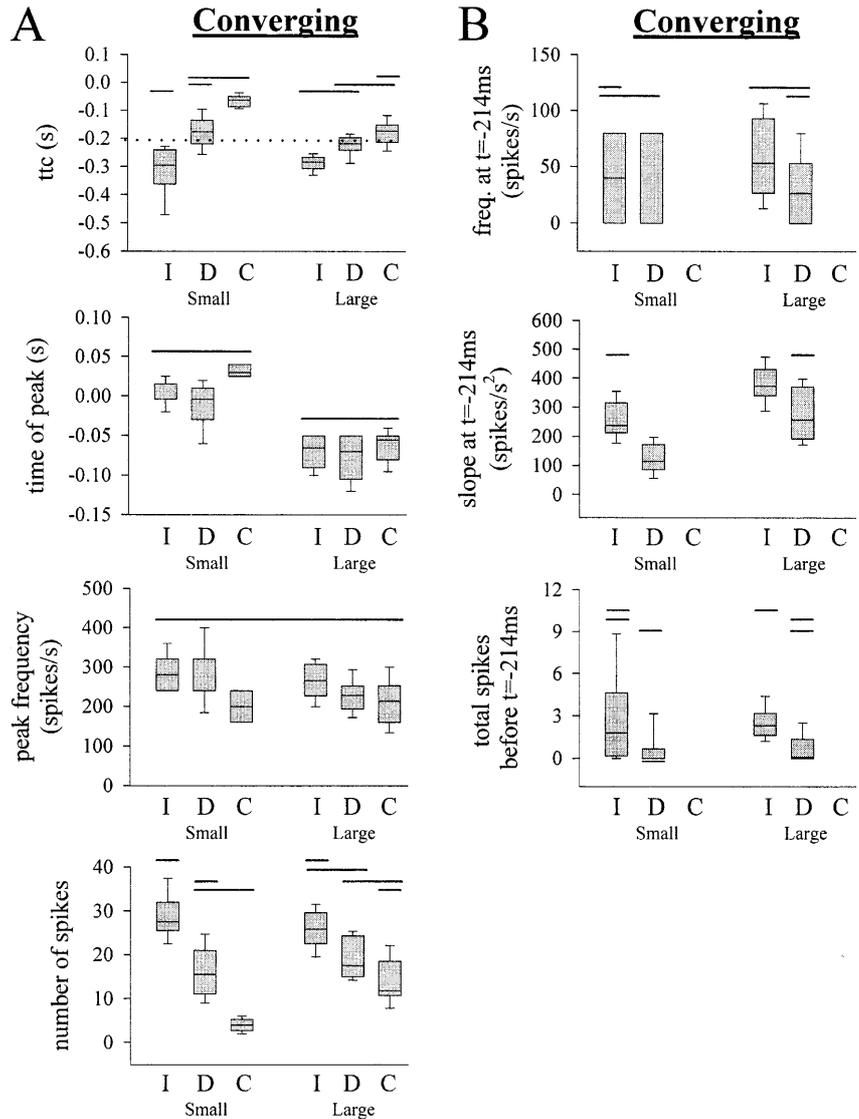
that might account for the behavioural differences we compared the discharge properties for these trajectories (Fig. 10). Ipsilateral targets were more effective stimuli than contralateral targets in terms of start of discharge, peak frequency and the total number of spikes but there was no statistical difference between the responses to converging and offset targets. To summarize: converging, offset and diverging large targets had different behavioural consequences but we could not detect any difference in the discharge of the DCMDs to identical stimuli that might account for this.

Discussion

One purpose of the experiments described here was to determine if the combined activity of a bilateral pair of known looming detectors in the locust visual system, the DCMDs, can encode information about the nature of behaviourally relevant looming objects approaching in the flight path. To this end, we have demonstrated that computer-generated looming stimuli are sufficient to (1) stimulate the DCMDs in a manner that is similar to real looming objects, and (2) produce stereotypical collision avoidance behaviours in tethered flying locusts. Moreover, the relative activity of the right and left DCMD and the steering response are superficially related to the trajectory of an approaching object. Specifically, paired DCMD activity and flight steering are more sensitive to target trajectories that vary in the horizontal plane than in the vertical plane. This is the first detailed description of the activity of both DCMDs during presentation of stimuli that produce a typical flight steering behaviour.

A second purpose of the experiments described here was to relate variations in the discharge of the DCMDs

Fig. 9A, B Quantitative comparison of DCMD activity in response to presentation of small and large converging targets approaching along the centre line (*D*) or displaced 14° in a horizontal meridian either ipsilaterally (*I*) or contralaterally (*C*) to the DCMD. **A** Characterisation of total DCMD discharge. **B** Characteristics of the discharge at a time $t = -214$ ms that is appropriate for generating behaviours that occur 176 ms prior to collision. See text for details. Empty columns indicate fewer than three trials with measurable activity



produced by different target trajectories and sizes to variations in the steering behaviour produced by identical stimulation. We found that the most effective stimuli for the DCMD were targets converging from above and to one side. Statistically, small targets were no less effective than large targets and indeed there were trends indicating a preference for small targets. However, small targets were ineffective stimuli for evoking steering reactions during tethered flight. We recognize that a future goal should be to record from the DCMDs during presentation of these stimuli during tethered flight. We cannot rule out the possibility that flight activity alters in some subtle way the sensitivity of the DCMDs such that they would show a pronounced preference for large stimuli. Nevertheless our data demonstrate a discordance between effective stimuli for DCMD and effective stimuli for collision-avoidance steering. Similarly, large offset stimuli evoked steering that was predominantly directed away from the side of approach of the target whereas large

converging stimuli evoked steering to either side; yet there was no difference in the DCMD discharge to these two types of stimuli. These observations suggest to us that the DCMDs are unlikely candidates for an involvement in avoiding head-on collisions during flight but are more suitable for detecting the looming approach of a predator such as a swooping bird (Rind and Simmons 1992). It should be noted that the DCMDs alone are unlikely to be responsible for driving any particular behaviour but are more likely to be part of a cohort of descending neurons whose combined activity orchestrate flight manoeuvres.

Technical considerations

It has been shown that the response of the DCMDs declines dramatically when a digitized object expands more than 3° in a given step (Rind and Simmons 1997). Moreover, if the refresh rate of the simulation is below

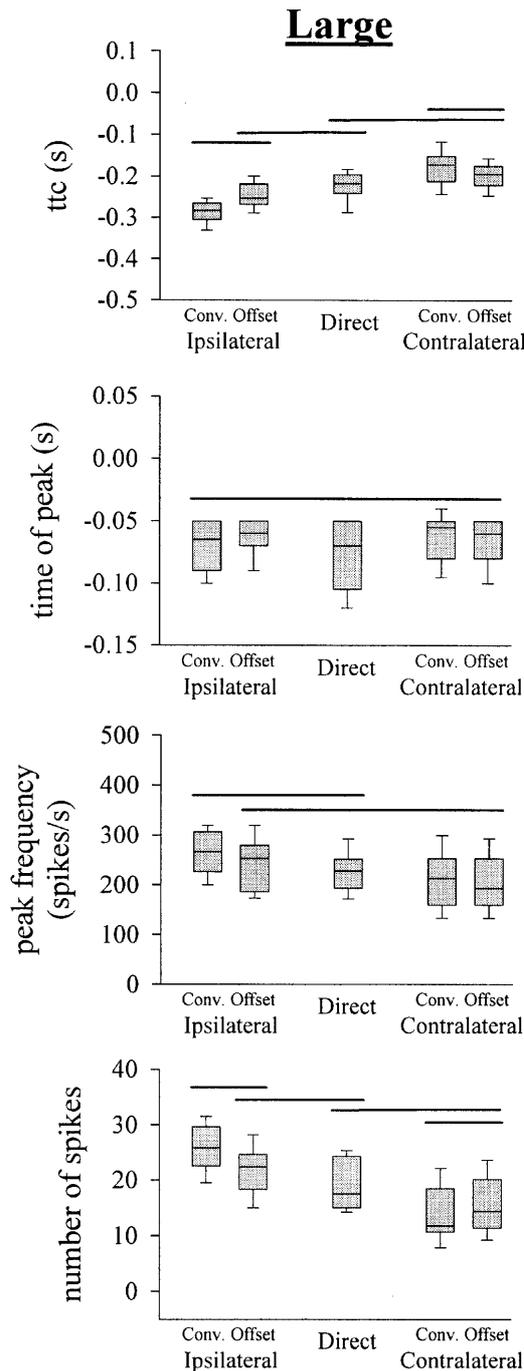


Fig. 10 Quantitative comparison of DCMD activity in response to presentation of converging and offset large targets approaching along the centre line (*D*) or displaced 14° or cm in a horizontal meridian. See text for details

the flicker-fusion frequency of the locust's eye, the DCMDs will not respond as strongly as they would to a real looming object. Therefore, it is crucial to be able to create a computer-generated object that approaches with a sufficiently high refresh rate. In our studies the refresh of the animations and the vertical refresh of the monitor were set at 80 Hz, which is comparable to the flicker fusion frequency of the locust eye (Miall 1978). Al-

though we were not able to measure directly the refresh of the animation during playback, the response of the DCMDs was similar to that described for real objects (Schlotterer 1977) and for computer-generated objects in which the refresh rate was set well above the flicker fusion frequency of the locust eye (Rind and Simmons 1997), i.e. DCMD firing continued to increase after the object stopped. Also, recent experiments have demonstrated that the DCMD is equally well stimulated by looming objects presented at 67, 100 and 200 frames s^{-1} (Gabbiani et al. 1999a). Combined with the fact that the locusts initiated directed steering in response to our simulations, this strongly suggests that the simulations used in this study were sufficient to stimulate the visual system including the DCMDs. Moreover, the spheres used in this study would expand uniformly as the target "approached", whereas the corners of a square target, as used in other studies, would expand more rapidly than the sides and thus would stimulate the primary photoreceptors at an unequal rate, which could affect the activity of the DCMDs. However, the potential differences resulting from different target shapes remains to be tested.

A second consideration involves the set up for the behavioural experiments. Locusts tethered in a wind tunnel or in an electrophysiology setup remain stationary relative to their surround and thus the visual system is not presented with a flow field that would occur during unrestrained flight. Thus the steering response may be affected by artefacts of tethering. However, this is unlikely since the same response has been observed in other investigations (Robertson and Reye 1992; Robertson and Johnson 1993a, 1993b) and occurs approximately 120 ms before collision, which would provide sufficient time for the resulting aerodynamic forces to move the animal out of the flight path. Moreover, these responses have been observed in response to stimuli of other sensory modalities (Robertson et al. 1996; Dawson et al. 1997), suggesting that intentional steering, such as collision avoidance, may take precedence over corrective steering, such as that produced by variations in the flow field. Results from the behavioural experiments suggest that there may have been a bias towards steering to the right. There is currently no reason to believe that locusts have an inherent preference to steer to the right though other studies have shown similar results (Möhl 1985, 1988; Robertson and Reye 1992; Robertson and Johnson 1993a). When the responses were measured in relation to targets approaching on an offset trajectory, however, 75% of the time the locusts attempted to steer away from the target, regardless of the side from which it approached.

Other potential components of collision-avoidance circuitry

The DCMDs are not the only motion-sensitive neurons in the locust's visual system that project to the thoracic

ganglia. The descending ipsilateral movement detectors (DIMDs) are also motion-sensitive and make connections to flight neurons (Burrows and Rowell 1973), and thus may be involved in evoking a collision avoidance behaviour. Thus, an understanding of the circuitry used to produce collision avoidance may require recordings from neurons such as DIMD, and/or other, as yet undescribed, neurons that are used to detect the approaching objects and provide important cues to the rest of the flight motor.

Other descending input can also provide information on the locust's flight path, most notably the wind detectors and ocelli (Arbas 1986; Griss and Rowell 1986; Rowell 1988, 1989; Hensler 1989, 1992; Wolf 1990; Burrows and Pflüger 1992; Preiss and Spork 1993). However, it is established that these detectors are involved in corrective steering and part of the autopilot. During collision avoidance it is imperative that the locust change course quickly and these inputs are likely overridden and not directly involved in intentional steering. Moreover, steering responses were observed in these experiments in which the wind direction and surrounding visual environment were constant.

DCMD responses

The firing of the DCMDs in response to looming objects is similar to that reported in previous studies (Schlotterer 1977; Rind and Simmons 1992; Simmons and Rind 1992; Hatsopoulos et al. 1995; Judge and Rind 1997; Rind and Simmons 1997; Gabbiani et al. 1999a) and thus confirms that they are effective looming detectors. The relative insensitivity of DCMD to stimuli in the forward-looking region of the eye has been consistently described (Rowell 1971; Schlotterer 1977) and may be related to the existence of an acute zone in the arrangement of ommatidia in that region (Horridge 1978). We observed that the DCMDs are more sensitive to horizontal changes in target trajectory than to vertical changes though there was a significant increase in sensitivity to stimuli from above the horizon. This was seen for all three trajectory types used here (converging, offset and diverging). For targets converging from the right or left, DCMD_i fired more strongly, whereas DCMD_c firing was weaker. The initiation of DCMD activity to contralateral stimuli likely reflects the time in which a converging target enters the contralateral eye's field of view. The binocular overlap of the two eyes is approximately 20° as measured from the angle at which the pseudopupil of each eye disappeared as the head was rotated around the midfrontal axis (data not shown, see also Horridge 1978). Thus, each eye will receive visual input from as much as 10° of the contralateral side. Given the architecture of the eyes and head, the point of overlap of the fields of view of the two eyes begins approximately 8.5 mm from the head. Therefore for small targets converging from 14° this means that the closest edge will enter the contra-

lateral eye's field of view 166 ms before collision, whereas for large targets converging from 14° this will be 266 ms before collision. The fact that discharge of contralateral DCMDs began after these times, i.e. after the targets entered the binocular range of the contralateral eye, suggests that there is a minimum number of ommatidia in the frontal region of the eye that must be stimulated to drive the DCMD.

For 10-cm targets approaching along offset and diverging trajectories, the firing of both DCMDs decreased between the time of target stopping and projected collision. For these trajectories, as the targets approached the locust the movement relative to the eye would have changed from looming to translatory and it is now well established that the DCMDs are most sensitive to looming stimuli. Thus it would be expected that the point of nearest approach for these trajectories would result in a decrease in the firing rate of the DCMDs. Moreover, it is likely that contralateral DCMD received little, if any, information about targets offset 14 cm or diverging 14° to the right because the targets would quickly move out of the contralateral eye's field of view. Thus, their firing would increase only marginally above the basal rate.

Behavioural responses

The wing kinematics and abdominal ruddering data presented here suggest that the locusts attempted to steer in response to a simulated approaching object. The lack of response to a 10-cm object suggests that the object is either not perceived as being important or that the locust detects it too late to make an effective in-flight response. The former is unlikely since flying locusts in a swarm are as small if not smaller than the 10-cm-diameter targets used here. It is likely that a flying locust would attempt to avoid such an object in an effort to maintain flight. Thus, it is most likely that the collision avoidance system did not detect the 10-cm targets used here in time to initiate an escape response. The fact that DCMD did detect these targets suggests that they are not involved in avoiding head-on collisions during flight.

The response to a 20-cm target involved steering toward or away from the target. Converging targets evoked steering responses equally away from and toward the side of the target. Either strategy will be effective in moving the locust out of the way of the target that is, by definition, on a collision course. Thus, converging targets may provide the locust with a choice for steering direction. The response to offset targets is primarily in the direction opposite to the side of target approach. In this case steering toward the side of target approach would move the locust directly into the path of the target whereas moving in the opposite direction would move it away from the target. Consequently, moving away from the closest edge, as described by Robertson and Reye (1992), may be the preferred response to offset targets.

Comparison of DCMD responses with previous work

It has been demonstrated that the firing rate of the DCMD increases with object approach and is related to angular acceleration of the target edges. For comparable target sizes and speeds, however, the number of spikes at a given time is generally lower in our experiments. As noted above this is likely due to the fact that here targets are approaching within 14° of the longitudinal midline whereas previous studies examined the activity of a single DCMD to objects approaching in a trajectory aligned with the horizontal and vertical midpoint of a single eye. Moreover, it has been shown that DCMD activity is most sensitive to trajectory changes in the horizontal plane (Judge and Rind 1997; and this study). Thus the trajectories used here would be expected to produce DCMD activity that was attenuated relative to those of previous studies.

The activity of the DCMD has been described as being tuned to collision trajectories such that offset deviations from collision of 3° result in attenuated firing (Judge and Rind 1997). Similarly neurons in the pigeon nucleus rotundus are described as tuned such that response drops to half maximal with a 3.3° divergence from a collision trajectory (angle measured at the midpoint of the object's trajectory; Wang and Frost 1992). In both cases the value of the tuning is not an absolute and has meaning only with reference to the particulars of each experiment (i.e. the distance of the object when it starts its approach). Moreover the consequences of the deviation to the viewer will also depend on the size of the object. We suggest that one possible measure of collision detection tuning that would be independent of the start position and size of the object is the half angle subtended at the viewer (subtense of half the object width). Targets that are offset or diverge by one-half angle from the direct collision track will just skim by the viewer. Collision will result if the trajectory is offset or diverges less than one-half angle. It would be interesting to determine if there is any similarity between the safety factors of collision detection neurons as defined by half angles of deviation to reduce firing to half maximal.

There is currently some debate in the literature regarding the nature of the DCMD discharge: accelerating past collision (Rind and Simmons 1999a, 1999b) or peaking before collision according to the eta function (Gabbiani et al. 1999a, 1999b; see also Sun and Frost 1998 for such neurons in the pigeon). Our data cannot directly address this issue because the experiments were carried out before it became an issue and were not designed to test either of these ideas. Moreover, our stimuli were presented to the frontal regions of the eye and included offset as well as converging approaches. Nevertheless, several of our observations are consistent with the interpretation of Rind and Simmons. The most effective stimuli in our experiments all peaked around or after the projected time of collision. Any peak prior to collision could be interpreted as either due to an offset stimulus becoming translatory, particularly for larger

offsets, or due to the termination of the simulation. In the latter case, large converging targets peaked about 70 ms prior to collision but this was about 50 ms after the final frame of the simulated target approach. Any decrease in firing, such as would define a peak, that occurs more than 30 ms after the visual stimulation ceases cannot be attributed to anything other than a normal consequence of the end of the stimulus. Interestingly the discharge to small converging targets peaked (started to decrease) about 50 ms after the final frame of the simulation also but the latter was 47 ms before the time of collision resulting in an accelerating discharge past collision.

We re-analysed of the results of Robertson and Johnson (1993b) to test the prediction that the time before collision at the time of a steering reaction is linearly related to $l/|v|$ (Fig. 11). This analysis suggests, in the model of Hatsopoulos et al. (1995) and Gabbiani et al. (1999a), that steering reactions to real objects occur 72.6 ms after an angular threshold of 8.7° has been surpassed. The timing of the start of DCMD discharge we describe here, however, does not fit with an interpretation of surpassing an angular threshold. Small targets, both offset and converging, elicited discharge that coincided with the target subtending 6° (ipsilateral), 8° (above) or 10° (direct). The discharge to large targets started at around the same time before collision whereas for crossing the same angular threshold it should have started around 630 ms before collision. According to the Gabbiani model our large target ($l/|v| = 33.3$ ms) would be a more effective stimulus than our small target ($l/|v| = 16.7$ ms) and would elicit firing earlier, yet we saw no significant difference and there was a trend for the smaller target to be more effective. This can be explained by considering that our small target at 3 m s^{-1} is

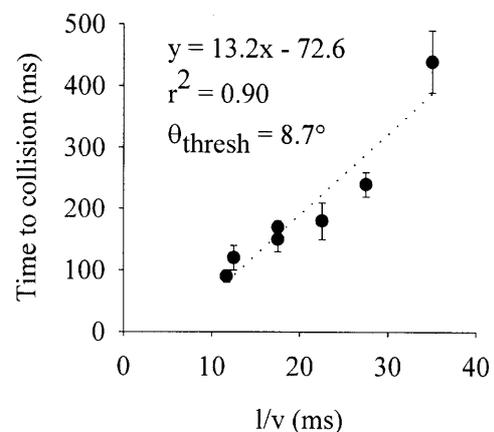


Fig. 11 Relationship between target approach parameter $l/|v|$ and the timing of avoidance steering to real objects relative to the time of collision. The *dotted line* indicates the best least squares fit through the points ($r^2 = 0.90$, $P < 0.005$). The intercept and slope suggest that the steering reaction occurred 72.6 ms after the targets subtended 8.7° [angular threshold = $2 \tan^{-1}(1/\text{slope})$; Gabbiani et al. 1999a]. Data re-analysed from Robertson and Johnson (1993a) for 720 trials in 20 animals with 4 size conditions and 3 speed conditions

equivalent to the large target approaching at 6 m s^{-1} . The model of Rind and Simmons specifically predicts an earlier, increased discharge as the speed of approach is increased independent of size (see, for example, Rind and Simmons 1999a, Fig. 4B) and hence predicts that the large target at 3 m s^{-1} would be less effective than the small target at 3 m s^{-1} (\equiv large target at 6 m s^{-1}). We anticipate that as research progresses, interneurons other than the DCMD with the appropriate sensitivity to approaching stimuli will be found to be responsible for generating the manoeuvres to avoid head-on collisions during flight.

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