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

Accepted: 6 January 2001 / Published online: 23 February 2001
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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
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; Gabbianni 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 Gabbianni 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 startled 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 moults 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 (Gabbianni 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 checkerboards 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. Gabbianni 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 Gabbianni 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.