Local habituation maintains sensitivity of visual neurons to multiple looming objects

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Objectives:

To determine if looming-sensitive neurons in the locust are able to respond to repeated approaches of multiple visual stimuli that vary in trajectory or size.

Background:

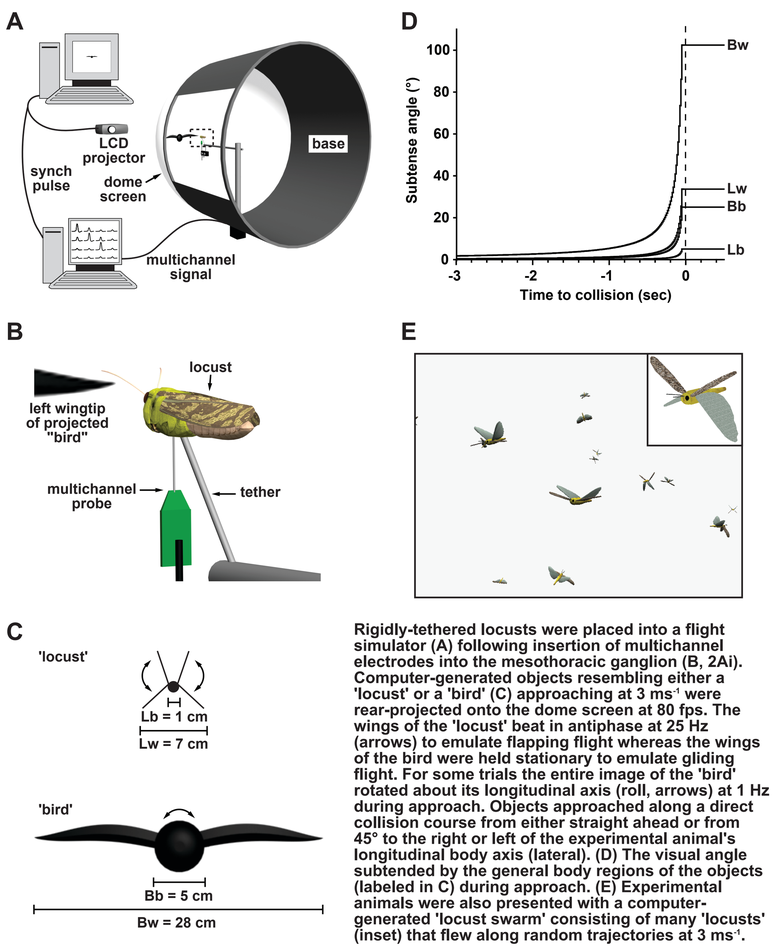
To produce adaptive behaviours animals must be able to remain vigilant to multiple objects in their environment that produce a range of spatiotemporal properties. For example, survival depends on the ability to distinguish between conspecifics and potential predators.

In the locust the Lateral Giant Movement Detector (LGMD) integrates visual input from the compound eyes and transfers information about looming stimuli[1,2,3] in a 1:1 spike ratio, to the Descending Contralateral Movement Detector (DCMD)[4]. The DCMD descends to the thoracic ganglia to make synaptic connections to interneurons and motorneurons that control the legs and wings[5,6,7,8]. Thus the LGMD/DCMD complex is an excellent model system to study mechanisms of how an animal is able to extract information about ecologically-relevant visual stimuli.

The DCMDs of gregarious locusts are resistant to habituation of repeated presentations of a looming object[9] which could permit effective flight within a swarm. However, there is little information on how the DCMDs respond to visual stimuli that emulate objects that the locust may encounter in the real world.

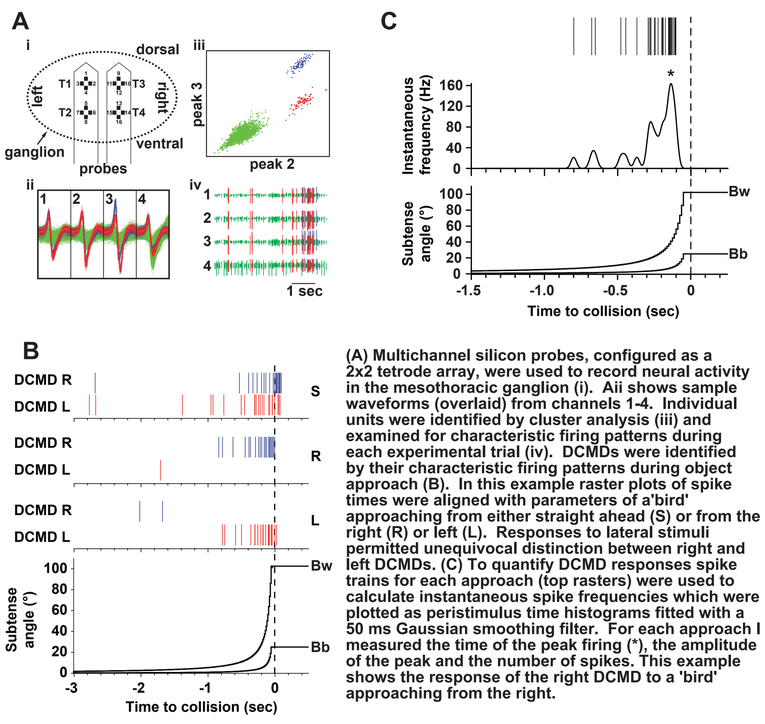
The experiments described here were designed to describe the responses of the DCMDs to objects that emulate the approach of a conspecific and a potential predator (a 'bird'). Moreover, the experiments address 2 main questions: 1) how do habituated DCMDs respond to objects approaching along a new trajectory or to a new object size? 2) how do the DCMDs respond to multiple objects on random trajectories, as might be expected in a locust swarm?

1 Experimental setup



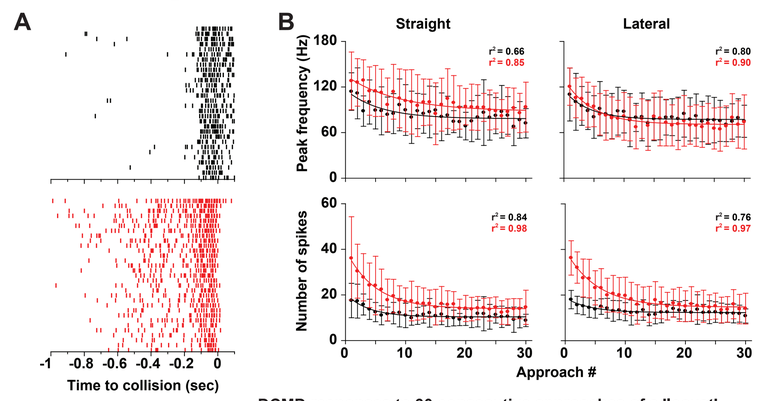
Rigidly-tethered locusts were placed into a flight simulator (A) following insertion of multichannel electrodes into the mesothoracic ganglion (B, 2Ai). Computer-generated objects resembling either a 'locust' or a 'bird' (C) approaching at 3 ms^{-1} were rear-projected onto the dome screen at 80 fps. The wings of the 'locust' beat in antiphase at 25 Hz (arrows) to emulate flapping flight whereas the wings of the bird were held stationary to emulate gliding flight. For some trials the entire image of the 'bird' rotated about its longitudinal axis (roll, arrows) at 1 Hz during approach. Objects approached along a direct collision course from either straight ahead or from 45° to the right or left of the experimental animal's longitudinal body axis (lateral). (D) The visual angle subtended by the general body regions of the objects (labeled in C) during approach. (E) Experimental animals were also presented with a computer-generated 'locust swarm' consisting of many 'locusts' (inset) that flew along random trajectories at 3 ms^{-1}.

2 DCMD recordings



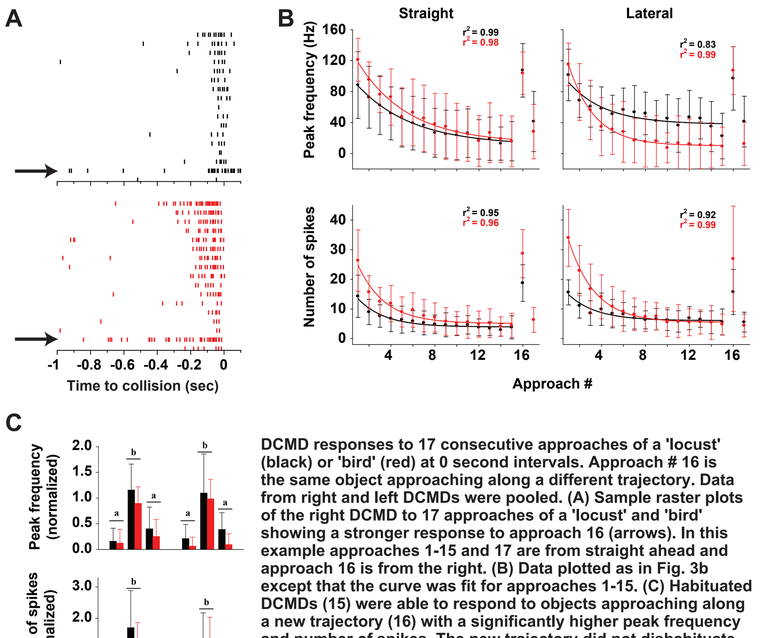
(A) Multichannel silicon probes, configured as a 2x2 tetrode array, were used to record neural activity in the mesothoracic ganglion (i). Aii shows sample waveforms (overlaid) from channels 1-4. Individual units were identified by cluster analysis (iii) and examined for characteristic firing patterns during each experimental trial (iv). DCMDs were identified by their characteristic firing patterns during object approach (B). In this example raster plots of spike times were aligned with parameters of a'bird' approaching from either straight ahead (S) or from the right (R) or left (L). Responses to lateral stimuli permitted unequivocal distinction between right and left DCMDs. (C) To quantify DCMD responses spike trains for each approach (top rasters) were used to calculate instantaneous spike frequencies which were plotted as peristimulus time histograms fitted with a 50 ms Gaussian smoothing filter. For each approach I measured the time of the peak firing (*), the amplitude of the peak and the number of spikes. This example shows the response of the right DCMD to a 'bird' approaching from the right.

3 Habituation of DCMD responses



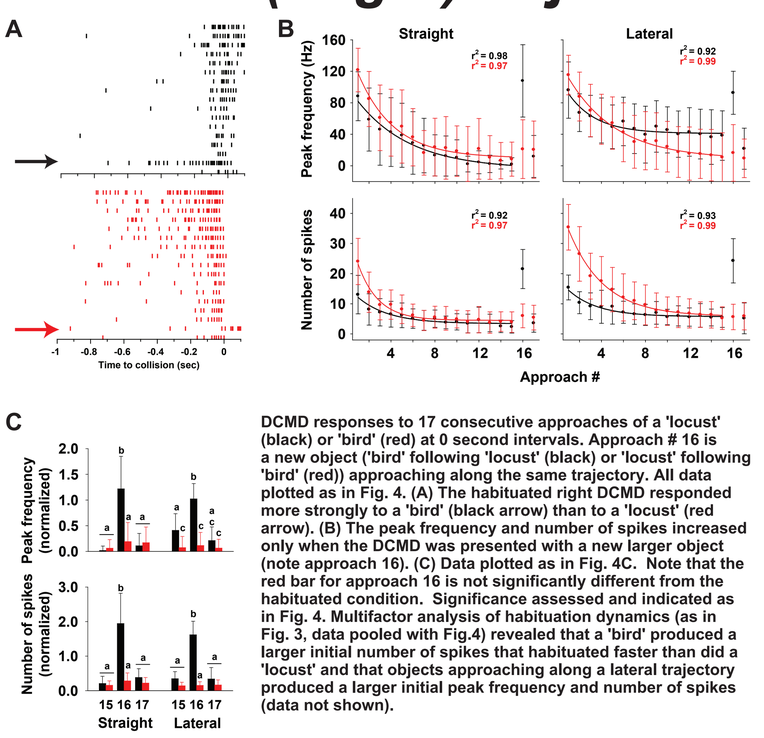
DCMD responses to 30 consecutive approaches of a 'locust' or 'bird' at 30 second intervals. (A) Sample raster plots from one sequence of 30 approaches showing responses of the right DCMD to a 'locust' (black) and a 'bird' (red) approaching from the right. (B) The peak frequency and number of spikes decreased following the first approach of either a 'locust' or 'bird' and plateaued after 10 or 15 approaches. Data plotted (mean ± S.D) are from 9 animals. Each plot was well fit by a single exponential decay of the form $y = y_0 + ae^{-bx}$ where y_0 is related to the asymptote, a is a scaling factor, b describes the rate of decay and x is the approach number. Data from straight trajectories are pooled from the right and left DCMDs. Data from lateral trajectories were pooled from responses of the right DCMD to objects approaching from the right and the left DCMD to objects approaching from the left. To assess whether DCMD habituation was the same for repeated presentations of a 'locust' and 'bird' I normalized the value of the 30th (habituated) approach to the 1st approach (C). The only significant difference (*) was an increased habituation of the number of spikes to laterally approaching objects (Kruskal-allis One Way ANOVA on ranks, $H_3 = 11.945$, $p=0.008$ followed by Dunn's multiple comparison, $p<0.05$). A multifactor ANOVA of natural log-transfomed regressions of data from each run (data not shown) revealed that the initial peak frequency, the number of spikes and the habituation rate of these 2 parameters was lower for responses to a 'locust' than to a 'bird'.

4 Maintained sensitivity to a new object trajectory



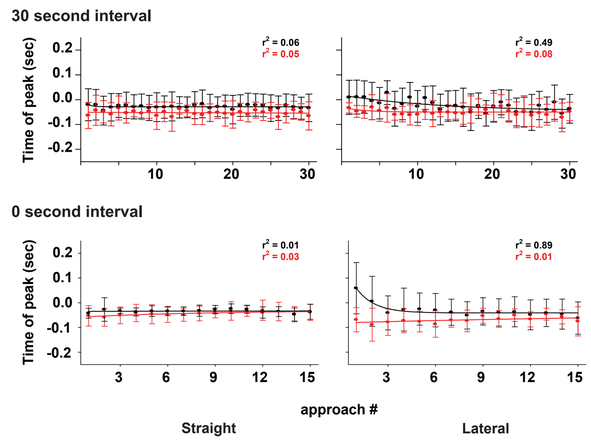
DCMD responses to 17 consecutive approaches of a 'locust' (black) or 'bird' (red) at 0 second intervals. Approach # 16 is the same object approaching along a different trajectory. Data from right and left DCMDs were pooled. (A) Sample raster plots of the right DCMD to 17 approaches of a 'locust' and 'bird' showing a stronger response to approach 16 (arrows). In this example approaches 1-15 and 17 are from straight ahead and approach 16 is from the right. (B) Data plotted as in Fig. 3b except that the curve was fit for approaches 1-15. (C) Habituated DCMDs (15) were able to respond to objects approaching along a new trajectory (16) with a significantly higher peak frequency and number of spikes. The new trajectory did not dishabituate the response to the original trajectory (17). Data labeled with different letters are significantly different (One Way ANOVA). ANOVA PARAMETERS

5 Maintained sensitivity to a new (larger) object



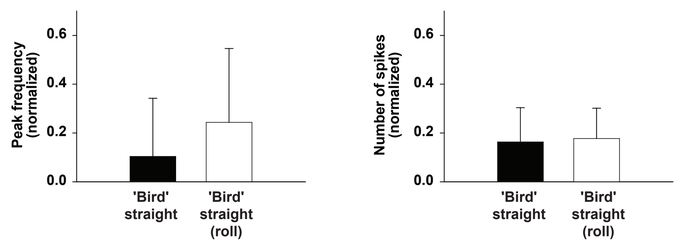
DCMD responses to 17 consecutive approaches of a 'locust' (black) or 'bird' (red) at 0 second intervals. Approach # 16 is a new object ('bird' following 'locust' (black) or 'locust' following 'bird' (red)) approaching along the same trajectory. All data plotted as in Fig. 4. (A) The habituated right DCMD responded more strongly to a 'bird' (black arrow) than to a 'locust' (red arrow). (B) The peak frequency and number of spikes increased only when the DCMD was presented with a new larger object (note approach 16). (C) Data plotted as in Fig. 4C. Note that the red bar for approach 16 is not significantly different from the habituated condition. Significance assessed and indicated as in Fig. 4. Multifactor analysis of habituation dynamics (as in Fig. 3, data pooled with Fig.4) revealed that a 'bird' produced a larger initial number of spikes that habituated faster than did a 'locust' and that objects approaching along a lateral trajectory produced a larger initial peak frequency and number of spikes (data not shown).

6 Peak time habituates to small lateral objects



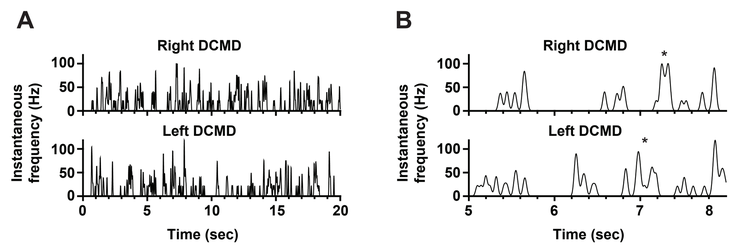
The time of peak DCMD firing was invariant for objects approaching from straight ahead, regardless of the interval between approaches. The peak occurred 28 ± 27 ms before collision of a 'locust' and 50 ± 40 ms before collision of a 'bird'. The peak time decreased (i.e. occurred earlier) during repeated lateral approaches of a 'locust', especially when presented at 0 second intervals. The peak time was invariant for a laterally approaching 'bird'.

7 Internal motion does not affect habituation



One series of runs for each animal included a 'bird' approaching from straight ahead which rotated about its roll axis (see Fig. 1 C). Each roll series consisted of 15 approaches at 0 second intervals. The normalized peak frequency and number of spikes of the pooled right and left DCMDs during approach 15 ('Bird' straight (roll)) were compared to the same parameters measured during a gliding approach of a 'bird' from straight ahead with no roll ('Bird' straight). There was no significant difference in either parameter, suggesting that internal motion of an approaching object does not influence habituation of the DCMD response. Data plotted are the mean ± SD. The peak times were invariant and did not differ significantly between rolling and non-rolling 'birds' (data not shown).

8 Responses to multiple objects



DCMD activity does not habituate to multiple 'locusts' moving along random trajectories. (A) Instantaneous frequencies of the right and left DCMD, smoothed with a 50 ms Gaussian filter show multiple peaks throughout the 20 second stimulus period. (B) Expanded view of A showing multiple peaks and partial overlap of peaks (asterisks) during a 3.25 second stimulus period.

Summary/Conclusions:

- Locust DCMDs were able to maintain 80% of the intial response to repeated approaches of a 'locust' or 'bird' presented at 30 second intervals.
- DCMD activity habituated to approximately 20% of the the initial response during repeated approaches of a 'locust' or 'bird' at 0 second intervals.
- Habituated DCMDs were able to respond to an object approaching along a new trajectory or to a new, larger object.
- The time of DCMD peak firing habituates (occurs earlier) to small objects approaching along a lateral trajectory
- Internal motion of an approaching object does not affect habituation of the DCMDs.
- DCMDs do not habituate to multiple objects approaching along random trajectories.

These findings suggest that habituation to repeated looming stimuli may occur at specific synapses between upstream visual neurons and the LGMD. This localized habituation may function to allow locusts to remain vigilant to multiple objects in the natural environment.

References

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