Sublinear processing of compound and multiple object motion

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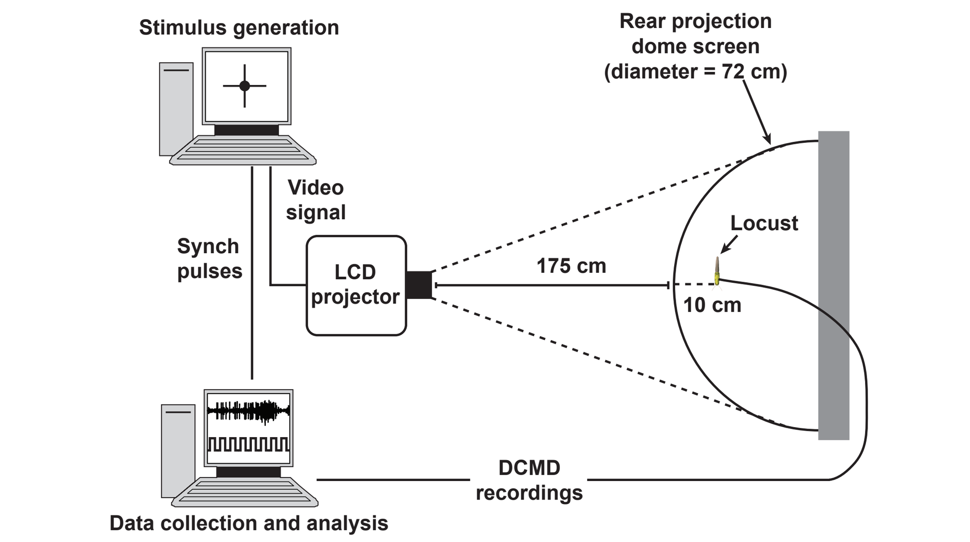
Introduction

To produce effective collision avoidance behaviours, the nervous system must be able to extract salient sensory cues related to looming stimuli (objects approaching on a direct collision course). Characterization of looming sensitive neurons in insects [1-3] and birds [4] have led to studies that provide insights into biophysical mechanisms underlying responses to single approaches of basic shapes [5,6] or multiple local motion stimuli [7]. In the natural environment, however, animals are often confronted with complex spatiotemporal patterns of visual information. For example, recent studies based on responses to simplified stimuli have shown that saliency of visual cues is often influenced by emergent properties of complex visual scenes [8]. However, little is known of how responses of looming sensitive neurons are influenced by visual complexity.

The locust visual system contains a well defined neural pathway composed of the lobula giant movement detector (LGMD) and its postsynaptic target, the descending contralateral movement detector (DCMD), that is highly responsive to looming stimuli [2,3,9,10]. Postsynaptic nonlinear integration of excitatory and feed-forward inhibitory inputs [5-7] likely underlie the biophysical mechanisms of looming responses in the LGMD, which is characterized by a firing rate that peaks after a certain retinal threshold angle is exceeded [5,11-13]. The time of peak firing is related to the ratio of the half size of the object (l) and its approach velocity (v) ($l/|v|$). LGMD spikes are transferred to the DCMD in a 1:1 manner [14] via mixed electrical and chemical synapses [15,16]. Subsequently, the DCMD connects to flight interneurons and motorneurons within the thoracic ganglia [17-19]. Therefore, looming responses in this pathway may have consequences for collision avoidance behaviours that are influenced by the angular threshold size of an approaching object [2,20]. Recent recordings of DCMD responses to looming stimuli in tethered flying locusts [21] notwithstanding, the role of the LGMD/DCMD pathway in collision avoidance has not yet been explored directly.

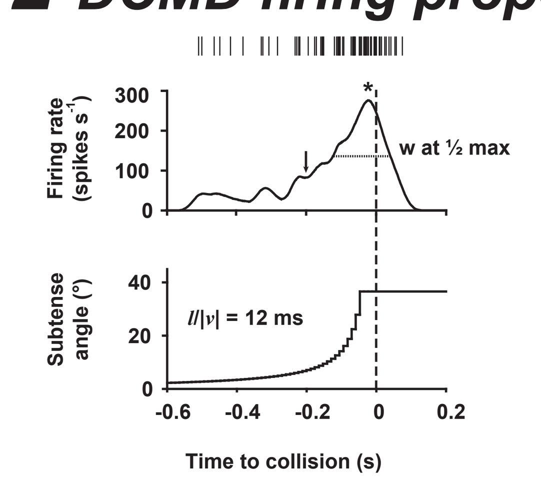
Results from habituation experiments [22] predict that the LGMD should be able to respond to approaches of multiple objects approaching from different trajectories. Therefore, we designed experiments to examine the effects of object number and complexity on looming responses in this pathway by recording activity in the DCMD. Some of the data presented (Figs. 2-9, n=25) have been published previously [23]. Data in Fig.10 are from different animals (n=25).

1 Experimental setup



Locusts were mounted on a rigid tether such that the right eye was centred on the apex of the rear projection dome screen. A bipolar extracellular hook electrode was used to record DCMD activity from the ventral nerve cord during stimulus presentation. Synchronization pulses from the stimulus generation computer were used to align DCMD activity with the looming stimuli.

2 DCMD firing properties



Rasters of DCMD spike times (top) were smoothed with a 50 ms Gaussian filter to estimate the instantaneous firing rate middle) during approach (bottom). To quantify the DCMD response profile we measured the amplitude and time of peak firing (*), the peak width at ½ the peak firing rate (w at ½ max), the firing rate 200 ms before collision (arrow) and the total number of DCMD spikes. This figure shows the response to one approach of a 7 cm disc at 3 m s^{-1} from 90°.

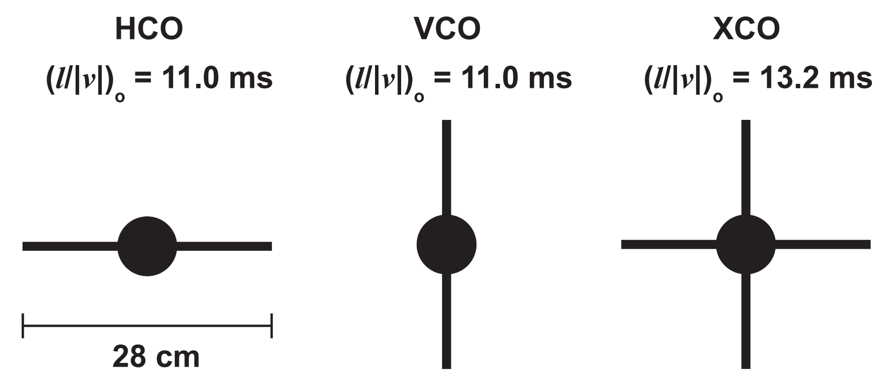
Compound objects

The relationship between the half size and approach velocity of compound objects $(l/|v|)_o$, can be described by the formula:

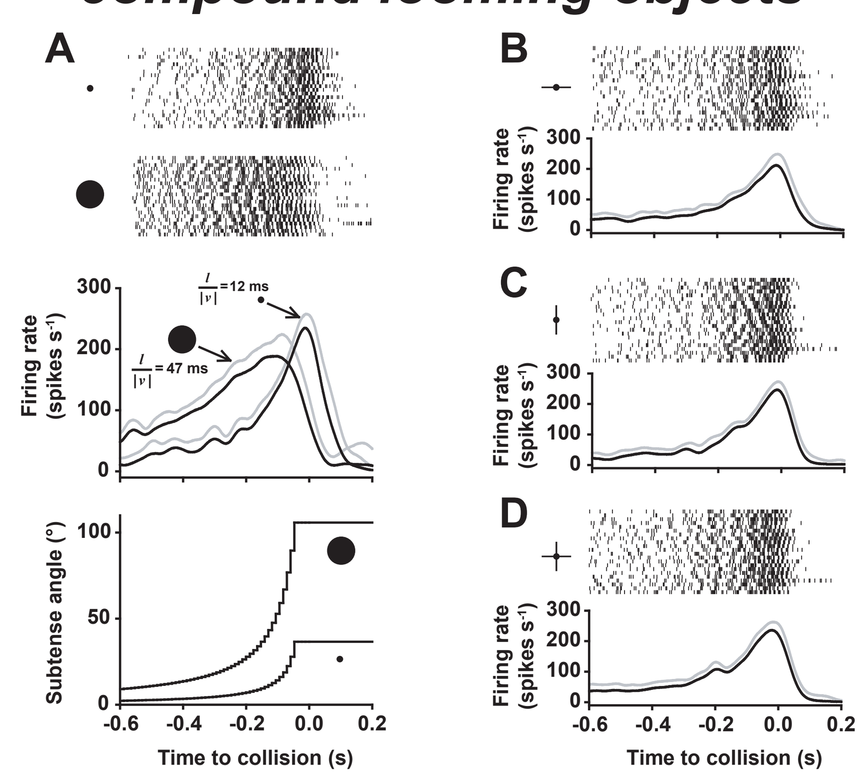
$$\left(\frac{l}{|v|}\right)_O = \sum_{i=1}^{n}\left(\frac{l}{|v|}\right)_i P_i$$

where n is the number of unique edges (n=3) and P_i is the proportion of the object perimeter occupied by each unique edge type.

3 Compound object shape

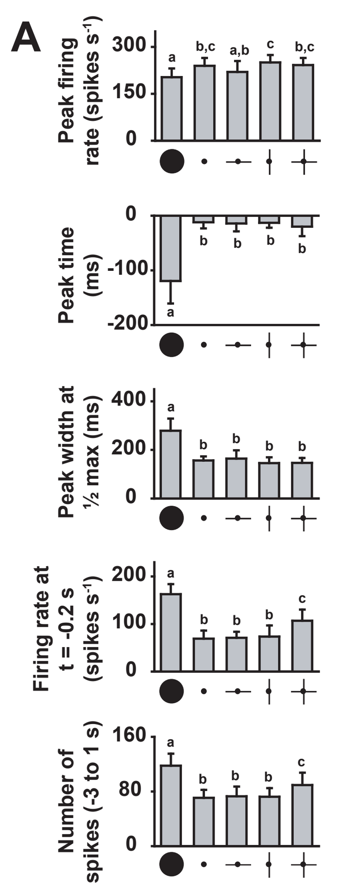


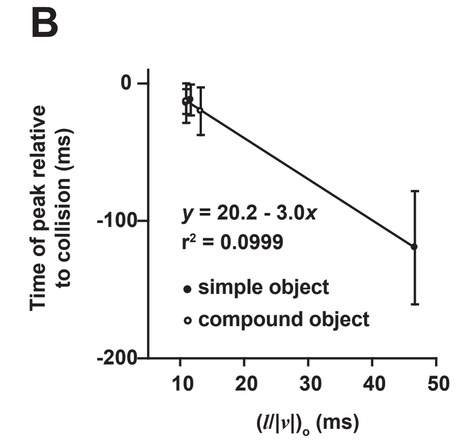
4 DCMD responses to simple and compound looming objects



Response profiles are similar for compound objects ($(l/|v|)_o$ = 11 - 13.2 ms) and simple objects with similar approach parameters ($l/|v|$ = 12 ms). (mean (black line) + SD (grey line)).

5 Invariance to object shape

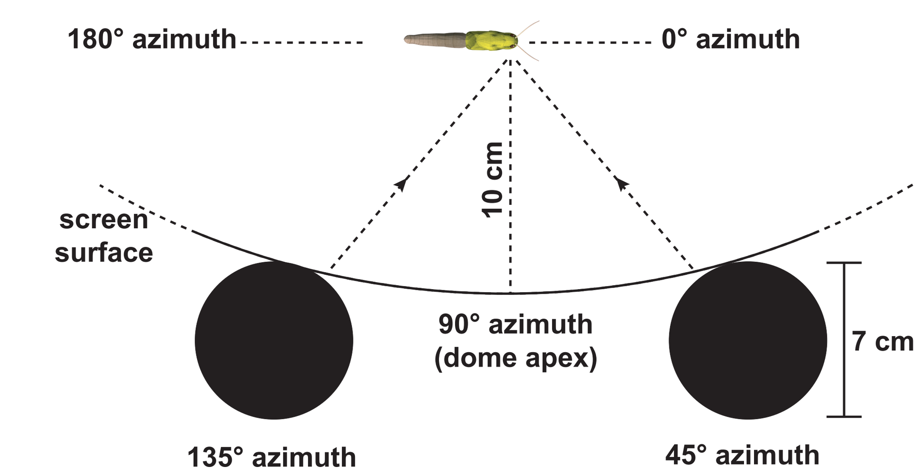




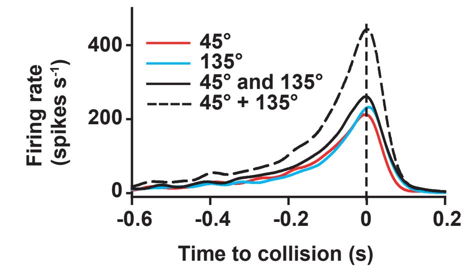
DCMD firing parameters were similar during approaches of simple small discs and compound objects with similar approach parameters. A) There were no significant differences in the time of peak firing or the peak width at ½ peak amplitude. There were significant, though small, differences in the peak firing rate, the firing rate 200 ms before collision and the total number of spikes. Bars with the same letters were not significantly different at $\alpha = 0.05$ (one way ANOVA). B) The linear relationship between $(l/|v|)_o$ and the peak firing time during approach [11] was maintained for simple and compound objects.

Paired objects

6 Approach parameters

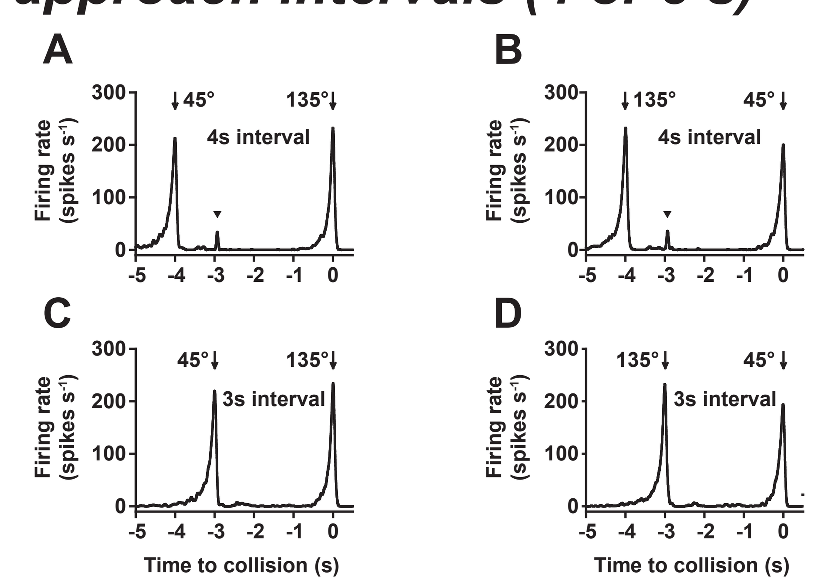


7 Sublinear response to simultaneous approaches



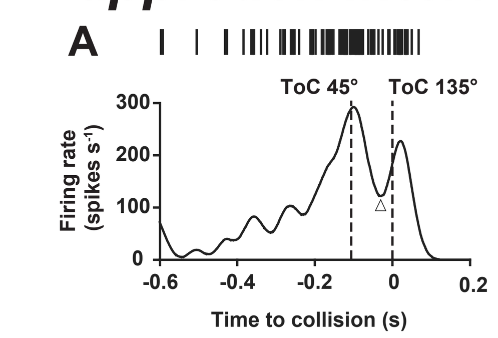
Mean plots of smoothed histograms for single approaches from 45° (red line) and 135° (blue line are overlaid with plots of the response to simultaneous approaches (black line) and the predicted linear sum of individual approaches (dashed line).

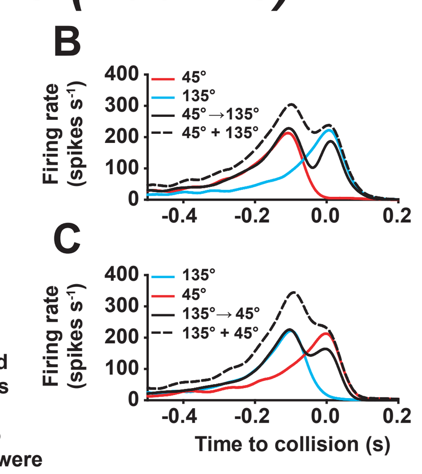
8 No effect of non-overlapping approach intervals (4 or 3 s)



Responses were not affected by previous approaches from a different region of the visual field either 4 seconds (A, B) or 3 seconds (C, D) earlier. Initial approaches were from 45° (A, C) or 135° (B, D). Approaches from 135° did, however, evoke larger responses than did approaches from 45°. The arrowhead indicates the time of the DCMD off response when the initial object disappeared (4 s interval). For 3 s intervals the first object remained on the screen.

9 Sublinear response during short approach intervals (106 ms)

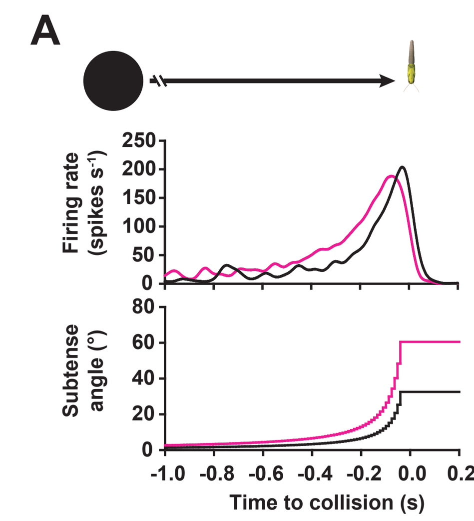




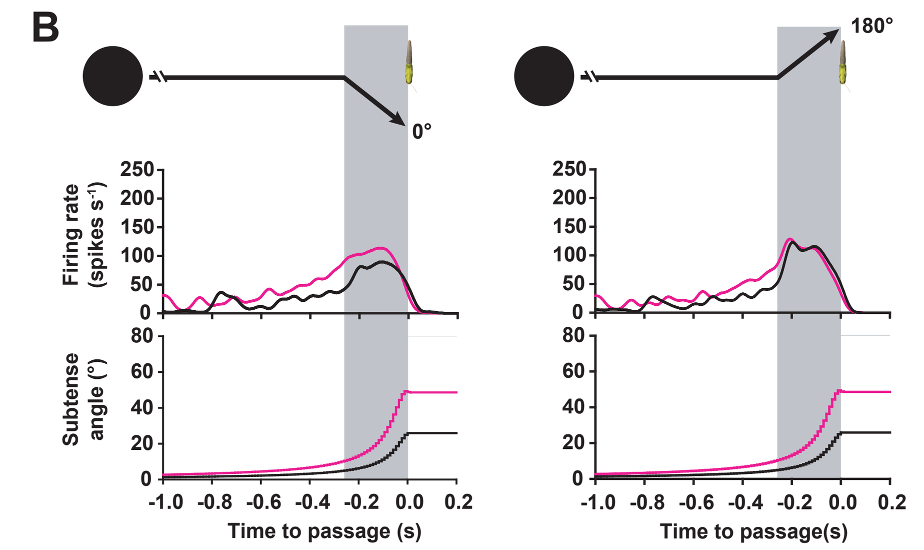
A) Histogram from a single trial showing that paired approaches 106 ms apart evoked two distinct peaks delimited by a decreased firing rate (valley, Δ).
B) As with simultaneous approaches, responses to paired approaches (black line) were sublinear and were effected by the direction of the initial approach. Data represented as in Fig. 7.

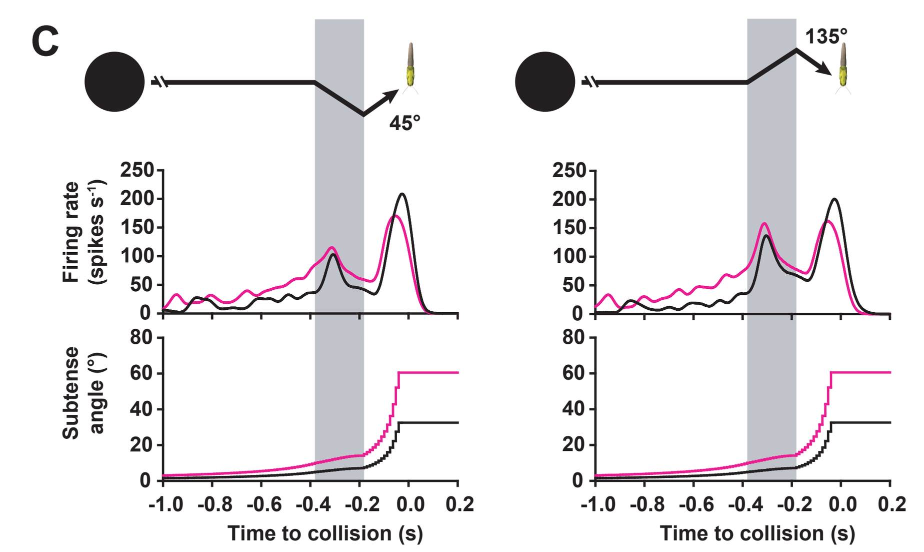
Compound trajectories

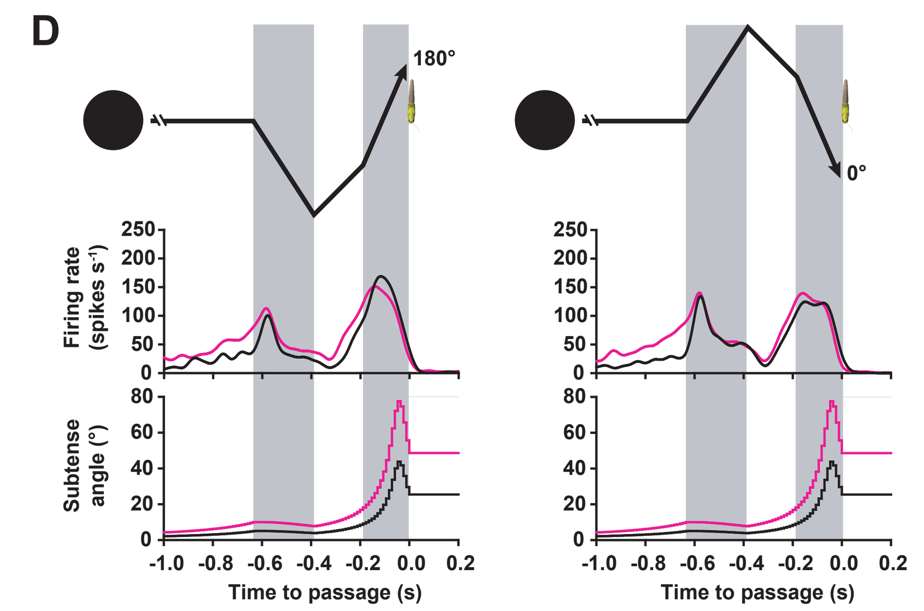
10 Response modulation induced by changing trajectory



Approaches of simple spheres ($l/|v|$ = 12 ms (black) or 23 ms (pink)) started 90° from the center of the right eye and ended either on a direct collision course (A, C) or in a plane parallel to the long axis of the animal (B, D). Final direct approaches were from 90° (A), 45° or 135° (C). Non direct final approaches ended 15 cm rostral (0° in B,D) or 15 cm caudal (180° in B, D) to the right eye. Grey bars represent times of non-direct approaches and the boundaries indicate the timing of a trajectory change. Discs and locust images not to spatial scale. Modulations of the DCMD firing rate clearly follow changes in the approach trajectory.







Summary

Compound objects

- Looming compound objects evoke characteristic DCMD responses.
- Similar $l/|v|$ values evoke similar response profiles, irrespective of object complexity.

Paired objects

- Previous approaches from different regions of the visual field 3 or 4 seconds earlier do not affect responses to later approaches.
- Simultaneous or closely timed approaches evoke sublinear responses.
- Looming responses are affected by the direction of approach.

Compound trajectories

- Changes to non-looming trajectories during an approach evoke transient, delayed increases in the firing rate.

Conclusions

- Encoding of object approach properties is relatively insensitive to object shape.
- Responses to individual looming objects during simultaneous or closely timed paired approaches are strongly sublinear.
- DCMD activity is affected by the timing and direction of trajectory changes during an approach.

Future studies

- Test for DCMD habituation during repeated approaches of objects traveling along varying paths.
- Test effects trajectory changes from initial non-looming to looming.
- Examine effects of compound trajectories on behavioural responses of loosely tethered flying locusts.
- Record DCMD activity of flying animals presented with the same stimuli used here.

References

1 Wicklein M. and N. J. Strausfeld J. Comp. Neurol. 424(2), 356 (2000); **2** Hatsopoulos N. *et al.* Science 270, 1000 (1995); **3** Simmons P.J. and F. C. Rind J. Neurophysiol. 68(5), 1667 (1992); **4** Sun H. and B. J. Frost Nat. Neurosci. 1(4), 296 (1998); **5** Gabbiani F. *et al.* Nature 420, 320 (2002); **6** Gabbiani F. *et al.* J. Neurophysiol. 94(3), 2150 (2005); **7** Krapp H.G. and F. Gabbiani J. Neurophysiol. 93, 2240 (2005); **8** Kayser C. *et al.* Curr. Opin. Neurobiol. 14(4), 468 (2004); **9** Judge S.J. and F. C. Rind J. Exp. Biol. 200, 2209 (1997); **10** Schlotterer G.R. Can. J. Zool. 55(8), 1372 (1977); **11** Gabbiani F. *et al.* J. Neurosci. 19(3), 1122 (1999); **12** Gabbiani F. *et al.* J. Neurosci. 21(1), 314 (2001); **13** Matheson T. *et al.* J. Neurophysiol. 91(1), 1 (2004); **14** Rind F.C. J. Exp. Biol. 110, 143 (1984); **15** Killman F. *et al.* Cell Tissue Res. 296, 645 (1999); **16** O'Shea M. and J. L. D. Williams J. Comp. Physiol. 91, 257 (1974); **17** Burrows M. and C. H. F. Rowell J. Comp. Physiol. [A] 85, 221 (1973); **18** Simmons P.J. J. Exp. Biol. 86, 87 (1980); **19** Robertson R.M. and K. G. Pearson J. Comp. Neurol. 215, 33 (1983); **20** Robertson R.M. and A. G. Johnson Naturwiss. 80, 176 (1993); **21** Santer R.D. *et al.* J. Comp. Physiol. [A] 191(1), 61 (2005); **22** Gray J.R. J. Exp. Biol. 208(13), 2515 (2005); **23** Guest B.B. and J.R. Gray J. Neurophysiol. 95, 1428-1441 (2006)

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