Collision avoidance and a looming sensitive neuron: size matters but biggest is not necessarily best

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Locusts possess visual neurons that can be uniquely identified in each locust and that respond selectively to looming stimuli, giving the animal a warning of impending collision. It has been suggested that one such neuron, the lobula giant movement detector (LGMD), issues this warning by generating a peak in its response that occurs *ca.* 25 ms after a looming object reaches a subtense of 17° on the eye. This peak is proposed to be a trigger for escape behaviour. We use both modelling and electrophysiological techniques to show that this early peak in LGMD response is not the 'essential functional variable' used naturally by the locust to trigger escape, but rather results from the unnaturally large stimulus used in the previous experimental work. The natural predators of *Locusta* in Africa, where the locust evolved, are small birds such as the fiscal shrike *Lanius collaris humeralis* and the carmine bee-eater *Merops nubicus*, with pectoral diameters of 40–45 mm (measurements from museum specimens). *Locusta* in flight are less than 100 mm wing tip to wing tip. When a locust views small approaching objects, the response of the LGMD continues to increase throughout the object's approach and the locust is able to trigger escape behaviours without the LGMD response peaking prior to collision.

Keywords: locust; looming; insect; collision-avoidance; lobula giant movement detector; descending contralateral movement detector

1. INTRODUCTION

Locusts possess uniquely identified visual neurons that respond selectively to looming stimuli, giving a warning of impending collision (Rind & Simmons 1992, 1997, 1998, 1999; Rind 1996; Judge & Rind 1997; Simmons & Rind 1997; Gabbiani *et al.* 1999, 2001, 2002; Gray *et al.* 2001). A recent report by Gabbiani *et al.* (2002) suggests that one such neuron, the lobula giant movement detector (LGMD), issues this warning by generating a peak in its response that occurs *ca.* 25 ms after a looming object reaches a subtense of 17° on the eye. This peak is proposed to be a trigger for escape behaviour (Gabbiani *et al.* 1999, 2001, 2002; Graham 2002). We suggest that this peak in LGMD response is not the 'essential functional variable' used naturally by the locust to trigger escape, but

is the result of a mismatch between the stimulus size used and the neuronal response.

2. MATERIAL AND METHODS

Locusts were bred in our crowded culture facilities and used 10 days after their final moult. Recordings were made extracellularly from the axon of the descending contralateral movement detector (DCMD) neuron in the cervical connectives using silver wire hook electrodes. Data were stored and analysed using a 1400plus data acquisition unit with SPIKE2 software. Locusts viewed visual stimuli generated using a Cambridge Research Systems board and displayed on a Kikusui electrostatic monitor with a frame refresh rate of 200 Hz. Details of the stimuli are given in the figure legends. The computational model of the LGMD neuron (Rind & Bramwell 1996) was written in C++ and run on a Dell computer.

3. RESULTS

The visual stimuli used by Gabbiani *et al.* (1999, 2001, 2002) to excite the LGMD neuron were large looming squares, 120–280 mm wide. When we show the locust a small looming object, 80 mm in diameter, or less, the LGMD response does not peak at the time proposed by Gabbiani *et al.* (2002) (arrows and asterisks in figure 1*a–d*), but continues to increase until after the loom ends, generating instantaneous spike frequencies in excess of 400 Hz (dots in figure 1*a–c*). Because locusts initiate escape jumps in response to this 80 mm diameter stimulus, this suggests that such behaviour does not require a peak in LGMD response (Childs 1999).

In Gabbiani *et al.* (2002), the LGMD's maximum instantaneous spike frequency was 100 Hz to a stimulus functionally equivalent to that in figure 1*b* ($l/v = 40$ ms, where l is half object size and v is approach velocity, which in this example means a 160 mm × 160 mm square approaching at 2 m s⁻¹). In their study, the maximum spike frequency to even the fastest looms, was never more than 260 Hz. When we analysed their earlier recordings made extracellularly from the LGMD (via the DCMD axon (Gabbiani *et al.* 2001)), we found that the instantaneous spike frequencies were also consistently lower (figure 1*d*) than in our experiments (figure 1*a–c*), with a single interval above 200 Hz in one presentation and only three in another.

We can explain the discrepancy in the LGMD responses and peak timing using an existing LGMD model with the original parameter values (Rind & Bramwell 1996) and using large looming stimuli as inputs to the model (figure 2*a*). These stimuli cause the model-LGMD response (black dots in figure 2*b*) to end prematurely, as a result of postsynaptic feed-forward inhibition. This inhibitory pathway is triggered when a threshold number of photoreceptors are activated within a short time (asterisks in figure 2*b*), and its activity occurs increasingly early within a loom as stimulus size increases from 75 mm × 75 mm. Excitation in the model-LGMD (expressed as membrane potential with a maximum value of 400 corresponding to simultaneous activation of all inputs units) is affected in a similar way, peaking at a value of 200 in response to a 75 mm × 75 mm stimulus but reaching only 112 to the largest object simulated (100 mm × 100 mm, figure 2*b*).

Feed-forward inhibition onto the locust LGMD is very powerful and is γ -amino-butyric-acid-mediated (Rind 1996; Gabbiani *et al.* 2002). When inactivated using picrotoxin (Gabbiani *et al.* 2002), excitation in the LGMD increases and the apparent peak in its activity shifts beyond the end of the loom. We are able to predict this

Figure 1. LGMD responses to the image of a looming object. Approach occurred with a velocity of (a) 0.5 m s^{-1} and ceased at 2 s, 140 ms before collision; (b) 1 m s^{-1} and ceased at 2 s, 70 ms before collision; and (c) 10 m s^{-1} and ceased 7 ms before collision. In each section, the upper trace indicates the angular subtense of the image seen by the locust as the computer-generated object approached on a collision course. The image was displayed with a 200 Hz refresh rate, on a screen placed 7 cm from the locust's eye. As the object neared collision, its image size changed rapidly. In the middle trace, the response of the LGMD was monitored extracellularly via the DCMD, which spikes following each spike in the LGMD (Rind 1984). In the lower trace the LGMD instantaneous (black dots) and mean (calculated over 50 ms, red curve) spike rates followed the expansion of the object's angular size from 1 – 59° , with a minimum latency of 25 ms (Rind 1996). An asterisk and arrow indicate the time, 25 ms after the looming object subtended 17° on the eye, when the LGMD response should have reached its peak (Gabbiani *et al.* 2002). (d) An analysis of the instantaneous frequency of LGMD spikes from Gabbiani *et al.* (2001), plotted against their timing during the approach. The approach began at 0 s and ended at 0.6 s. An asterisk indicates the time at which the image subtended 17° at the eye and an arrow indicates the timing of the peak response identified by averaging 10 stimulus presentations. The two approaches shown are the first, (black dots) and last, (red dots) of 10 stimulus presentations.

effect by removing feed-forward inhibition from our model-LGMD (triangles in figure 2b). Activation of this inhibitory pathway (asterisks) coincides with the peak in LGMD response (red dots). In response to smaller stimuli, both our model-LGMD and the locust DCMD track object approach throughout the loom and excitation is cut back by feed-forward inhibition, but only after stimulus movement ceases.

4. DISCUSSION

The peak in the LGMD response seen by Gabbiani *et al.* (1999, 2001, 2002) and in fig. 8 in Gray *et al.* (2001) is not the essential functional variable that allows the locust to time its avoidance reactions, but is the result of the unnaturally large stimuli that they used. Instead, the essential functional variable is a steady increase in spike rate, triggering a jump at a threshold value. A locust has a single opportunity to avoid collision with an approaching object or escape predation. However, Gabbiani *et al.* (1999, 2001, 2002) averaged their data over successive

stimulus presentations to identify the peak response. This may not reflect the normal LGMD response. For example, in figure 1d, taken from their work, the peak in LGMD activity does not appear to be where either the asterisk (peak identified by averaging) or the arrow (time when the image subtense exceeds 17° at the eye) are located in the first approach (black dots) of the 10 that they delivered.

We believe that the LGMD has evolved to detect objects with diameters in the range of 50–90 mm. Locusts flying in a swarm, for example—likely objects to trigger collision avoidance—have a 80–100 mm wing-tip to wing-tip length, and two common African locust predators, the fiscal shrike *Lanius collaris humeralis* and the carmine bee-eater *Merops nubicus*, both have carpal-to-carpal pectoral widths (shoulder to shoulder) of only 40–46 mm (40 mm for the shrike, measurement courtesy of British Museum of Natural History, and 45–46 mm for the carmine bee-eater measurement courtesy of Bob McGowan, National Museums of Scotland). These predators swoop on locusts with their wings stationary or held into their bodies so that

Figure 2. (a) Schematic illustration of the input organization of the model-LGMD (Rind & Bramwell 1996). Layers 1–3 consisted of retinotopic arrays, each with 250 processing units. These converge onto a single 'LGMD' unit in the fourth layer. The response of the model-LGMD can be recorded as the image of a looming object is mapped onto the photoreceptor units, which provide the input to the model. Layer 1, photoreceptor units; layer 2, laterally projecting inhibitory units, excitatory units and single postsynaptic feed-forward inhibitory unit; layer 3, summing units; layer 4, single LGMD-unit. Black-filled circles and dotted lines, inhibitory connections; triangles, excitatory connections. (b) Responses of the model-LGMD to looming objects of different sizes. Approach occurred with a velocity of 10 m s^{-1} and ceased at 40 ms, 7 ms before collision. All graphs are plotted on the same time-scale. The locust LGMD signals object approach for approach velocities from 0.25 – 12 m s^{-1} (Rind & Simmons 1992, 1999). The trends continued with objects larger than $100 \text{ mm} \times 100 \text{ mm}$, but are not shown. Black dots, postsynaptic feed-forward inhibition onto the model-LGMD intact; triangles, postsynaptic feed-forward inhibition onto the model-LGMD switched off. Asterisks indicate the time at which the feed-forward inhibition onto LGMD becomes active during the loom and red dots indicate the timing of the peak in the model-LGMD's response to large looming objects.

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their image on the locust's retina as they approach will be close to their pectoral diameter. The ecological tuning of the locust collision-detecting neuron has been studied by using stimuli larger than those naturally eliciting escape or collision avoidance reactions. The collision avoidance strategy of any animal should be best at signalling the sizes of objects that the animal commonly encounters. Only a bird of the size of the wandering albatross *Diomedea exulans* would subtend as much as $280 \text{ mm} \times 280 \text{ mm}$ during their hunting dives (260 mm pectoral width, measurement from museum specimen, courtesy of Eric Morton, the Hancock Museum, Tyne and Wear) and yet this is the maximum stimulus size used by Gabbiani *et al.* (1999, 2001, 2002). These birds are not known to prey on locusts.