problems raised by the initial formulation of τ and suggested that looming could provide a first-order approximation of ttc for use in fast interceptive actions, although τ alone could not possibly account for many of the accurate ttc judgements made by humans.

If looming is not sufficient to account for the temporal precision of some human behaviour, what other data are available? One useful source of information is available from binocular vision: it is possible for binocular cues to provide ttc information in the same way as looming (via their rate of change)[9]. Rushton and Wann[10] explored the use of looming and binocular information in catching in humans by perturbing either or both of these cues inside a virtual-reality display. They demonstrated that the human nervous system used both cues and that interfering with either cue causes timing errors. These data could be accounted for using a simple scheme called the 'dipole' model. This model copes with 'cue drop out' (for example, losing a binocular view of the ball) by implicitly switching to the remaining cue and returning to dual weighting if both cues become available. If a conflict arises between the looming and the binocular information then the model simply increases the weight of the most-immediate cue (that is, the one that specifies the shortest ttc).

In summary, Rind and Simmons[1] have provided an admirable description of how neurones respond to looming stimuli and they thus provide an excellent review of one of the neural systems subserving ttc judgements. In humans, looming can provide useful information on ttc but it cannot explain the precision of many timing judgements. The weight of evidence suggests that looming is combined with binocular cues for fast interceptive actions in humans. Furthermore, analysis of extant studies suggests that the perceptual information used for timing action is both task and situation specific[11]. Tresilian argued that there can be no general theory of ttc perception because of the dynamic nature of the visual system: a noisy adaptive neural system that converges on complicated and task-specific solutions to 'get the job done'[11]. Timing judgements might involve looming and binocular information, but the use of these cues is neither necessary nor sufficient for a range of tasks. Future studies will hopefully elucidate the other neural mechanisms involved in providing the requisite perceptual information for such precise behaviour.

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The many ways of building collision-sensitive neurons

In their article, Rind and Simmons[1] convey some of the recent excitement and progress in the study of collision-detecting neurons. Their account, however, is incomplete and inexact with respect to several recent developments.

One recent paper[2], briefly and partially described by Rind and Simmons, shows that the pigeon nucleus rotundus contains, besides the one Rind and Simmons described in Fig. 2B of their article[1], two additional classes of looming-sensitive neurons. One class appears to be most sensitive to thresholds in angular velocity. The second class of neuron signals, through its peak firing-time, the moment when the approaching object reaches a specific angular size (4–7°). Most remarkably, the latter class has response profiles that match exactly those reported previously for the locust lobula giant-movement detector (LGMD) by us[3,4], though the angular threshold size detected by LGMD is larger than that in pigeons (15–35°). Several behavioral experiments[3,5,6] have shown that a threshold in angular size is the variable that is most closely related to the initiation of escape responses in the locust. Therefore, the peak firing rate of the LGMD, or some other variable similarly correlated with it, might well trigger these responses.

Our original report[3] was criticized on technical grounds by Rind and Simmons[7–9] and again in their article[1]. In response to their original criticism[7] we repeated our experiments with a 200 Hz refresh rate monitor[4], at a variety of contrast values[4], body temperatures[4] and with several locust species[10], which confirmed our original results. This work[4] was not mentioned by Rind and Simons[1] despite the fact that it addressed their original criticism.

We would also like to clarify an important point. Our original observation[3,4] is that the time of peak LGMD firing rate relative to collision in response to approaching objects is linearly related to l/v, where l is the object half-size and v is its approach velocity (see Ref. 2 for a similar observation in the pigeon). Contrary to what Rind and Simmons have written[1], this does not imply that peak firing rate will always occur prior to collision. A theoretical argument[4] built upon this experimental observation predicts that the firing rate of the LGMD can be described by a product of two terms related to the angular size of the object and its angular velocity of expansion during approach. This relationship has been verified experimentally[3,4]. Rejecting this description on the basis that peak LGMD firing can occur after presumed collision[1] shows a misunderstanding of both these data and the theoretical prediction. In addition, we observe that peak LGMD firing follows presumed collision if $l/v \leqslant 5$ ms (Ref. 4). This would correspond to a 75 cm-wide object, such as a predatory bird[11], approaching at 75 m/s or 270 km/h. It is likely that most insect brains are ill-prepared to cope with such moving threats.

In the last part of their article[1], Rind and Simmons present a model for the response of the LGMD to looming objects. This model is based on a 'critical race' between feedforward excitation and lateral inhibition[12] that is presynaptic to the LGMD (Ref. 8). They conclude from this model that lateral inhibition has a predominant role in shaping the response of LGMD to looming stimuli. Another source of inhibition, however, is known to impinge directly onto the dendrites of the LGMD (Ref. 12) and could, therefore, also have an important role in shaping its responses. Given that the model is only weakly constrained by experimental data, we believe their conclusion is unwarranted; only experimental evidence can clarify the relative activation of these two inhibitory pathways during object approach.

Finally, Rind and Simmons suggest that this lateral inhibitory network[12] might be implemented between afferents to the LGMD via cholinergic synapses that were described recently in electron micrographs (Fig. 5 in their article[1]). While muscarinic receptors have been shown to have a presynaptic inhibitory effect on transmitter release, postsynaptic responses mediated by fast nicotinic and slow muscarinic receptors in insect neurons are, however, excitatory[13,14]. Furthermore, the modulatory effect mediated by presynaptic M_2-like receptors[15] has a slow activation time-course that is incompatible with fast inhibition, as postulated by Rind and Simmons[1] (2–4 ms; Fig. 4 of Ref. 1). Current morphological and pharmacological evidence, therefore, seems to point to lateral excitatory, rather than inhibitory, networks.

In summary, recent work has revealed many possible ways to 'build' collision-sensitive neurons. The LGMD offers a unique opportunity to elucidate the biophysical mechanisms underlying responses to looming objects in one such class of cells.

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Reply

We thank Mon-Williams[1] for his interest in our article[2], but doubt that he is correct to over-emphasize the role of binocular cues in the way that humans judge time to collision (ttc) with rapidly approaching objects. When the relative contribution of monocular looming cues and binocular disparity cues for humans who are judging ttc have been measured[3,4], both are found to have a role: when the object subtends an angle of around 0.7°, the monocular system predominates, whereas when the subtending angle is around 0.03°, binocular cues predominate. The binocular system operates optimally with objects that are less than 2 m from the eye. In cricket, a ball 70 mm in diameter approaches the batsman, from a distance of 22 yd (20.13 m) and, if bowled by the Australian cricketer Glen McGrath, the ball could be travelling at 90 miles/h (40.2 m/s). The approach takes around 405 ms and at the time the ball leaves the bowler's hand it will subtend an angle of around 0.43° on the eye. Relatively speaking, this is not a small stimulus and monocular cues are important for this ttc discrimination[3,4]. In another situation where humans make precise judgements about rapidly approaching objects, playing table-tennis[4], the ball subtends an angle of 0.86° at the level of the net, so it too is a large object and, therefore, suitable for processing by the monocular system. Land and Furneaux[5] have tracked eye movements of table-tennis players and found they did not keep their eyes on the ball all the time, an anticipatory eye movement is made, after the opponent hits the ball, which is directed to where the ball is expected to bounce. From there, the ball is tracked before being hit with the bat.

Both these approaching objects are moving fast, 40.5 m/s for the cricket ball and 4 m/s for the table-tennis ball[4]. It is doubtful that the stereoscopic system has the temporal resolution to track objects approaching at such speeds[6,7] and studies that have found the use of binocular cues to be advantageous in ttc have used approach speeds of around 2 m/s (Ref. 3) or less[4]. The study of Rushton and Wann[3], which was published after our article[2] had gone to press, shows not that looming cues are unimportant in timing human interceptive actions but rather that, under certain conditions, binocular cues might also be important. As we mention in our article[2], many animals, including gannets, pigeons and locusts, do not have well-developed binocular vision and use monocular cues for timing their reactions to rapidly approaching objects.

In their letter[8], Gabbiani *et al.* explain that there might be several ways to build a collision detector. Unfortunately, the two papers they mention[9,10] were published while our article was in press and we could add little new material. Gabbiani and co-workers have produced a scheme[11], involving the multiplication of different inputs, in which the collision detector peaks before collision and, thus, allows a neurone to anticipate collision. We are not aware of any reason why some neurones might not use such a multiplicative strategy, but for the locust lobula giant-movement detector (LGMD)–descending contralateral-movement detector (DCMD) system the weight of evidence (outlined in our article[2]) is firmly behind the critical race between lateral inhibition and excitation over the dendrites of the LGMD coupled with strong feed-forward inhibition that causes the LGMD response to build up throughout object approach. Despite their use, in a second paper[10], of higher frame refresh rates for their visual display, in order to dispel one of our criticisms of the earlier paper, they fail to explain discrepancies between our previously published results[12–15] and their own. We would now also add that their latest results[10] show strong evidence of habituation, particularly under the conditions (Fig. 3; $l/v \geqslant 20$ ms) that best support their claim of a peak in the response of the DCMD before collision. In reponse to their belief that a peak in firing always occurs before collision, we should like to add that it was Gabbiani and co-workers[11] who stated that 'because this product peaks before the image reaches its maximum size…this neuron can anticipate collision'. As for their statement that insect brains are not equipped to deal with stimuli that would delay peak firing until after collision[8], a ratio of $l/v \leqslant 5$ ms could be generated by an 8 cm-wide object moving at 8 m/s (28.8 km/h), or a 4 cm-wide object travelling at 4 m/s (14.4 km/h); the object does not have to be unreasonably large and fast. Although the synapses in the input network that is connected to the LGMD might be different from any characterized to date, there is good, longstanding evidence, which is outlined in our article[2], for lateral inhibition between the afferent neurones. There is no physiological evidence for a lateral excitatory effect of neighbouring afferents on one another, as suggested by Gabbiani *et al.* in their letter[8].

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