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Seeing what is coming: building collision-sensitive neurones

F. Claire Rind and Peter J. Simmons

The image of a rapidly approaching object has to elicit a quick response. An animal needs to know that the object is approaching on a collision course and how imminent a collision is. The relevant information can be computed from the way that the image of the object grows on the retina of one eye. Firm data about the types of neurones that react to such looming stimuli and trigger avoidance reactions come from recent studies on the pigeon and the locust. The neurones responsible are tightly tuned to detect objects that are approaching on a direct collision course. In the pigeon these neurones signal the time remaining before collision whereas in the locust they have a crucial role in the simple strategy this animal uses to detect an object approaching on a collision course.

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INFORMATION about approaching objects is highly significant to many animal species and can signal the approach of a predator, or imminent collision with another object as the animal moves around. Detecting imminent collision is challenging to the visual system because of the speed at which the information must be extracted from the changing image on the retina and used to guide behaviour. As an object moves directly towards the head, both the size of the image on the retina and the disparity between the images on the two retinas increase. In humans, both these features contribute to the perception that an object is moving towards the observer and psychophysical observations indicate that this depth perception involves combinations of inputs from separate neural mechanisms that detect changes in image size and changes in binocular disparity[1–3]. These findings are supported by single-unit studies in primates, which have reported neurones in the medial superior temporal cortex that respond both to a change in image size and to a change in binocular disparity[4]. However, the temporal resolution of the stereoscopic pathway in humans is low and it is, therefore, not well suited to the task of tracking objects moving rapidly towards the subject[1,5]. Similarly, cat binocular neurones in area 18 that signal motion in depth[6] are more responsive to low velocities of retinal motion, between 10° and 40° per second. In humans, vergence eye movements in response to the radial expansion of a pattern can be induced monocularly and can occur with a latency of 80 ms, shorter than expected for stereoscopic processing[7]. In invertebrates measurements of motion in depth that involve binocular interactions are extremely rare[8,9], mainly because there is little overlap between the visual fields of the left and right eyes and the absolute distances separating the two eyes are small[10].

Looming stimuli

In humans a compelling illusion of motion in depth is given by a retinal image that changes in size[11]. Images that grow in size trigger avoidance reactions in a number of species[12]. Gibson suggested that the crucial feature for determining whether an object is on a direct collision course with an observer, is the symmetrical expansion of the retinal image[13]. Consistent with this hypothesis, psychophysical investigations by Regan and Hamstra have revealed that the human visual system uses separate channels for tracking the leading and trailing edges in the image of an approaching object[14]. Regan and Hamstra argue that this, combined with specific information about the size or rate of change of an object's image, provides the basis for collision avoidance when driving on the motorway and during ball hitting. As these are important operations, knowing how a nervous system extracts such information would represent a significant step forward in this area of research.

Estimating time to collision

In order to time its reactions appropriately, an animal needs to gain an estimate of the time remaining before colliding with an approaching object. This could be derived from a knowledge of the distance and speed of movement of the object, neither of which would be readily available. An alternative strategy, suggested by Lee, is to determine the ratio between retinal image size at a given instant and the rate of expansion of the image[15] (Fig. 1A). Both of these measurements can be extracted from the pattern of image motion that flows over the retina of each eye, for example, during locomotion (flow field). This particular ratio, τ, gives an accurate measure of time to collision as long as the image is not too large and

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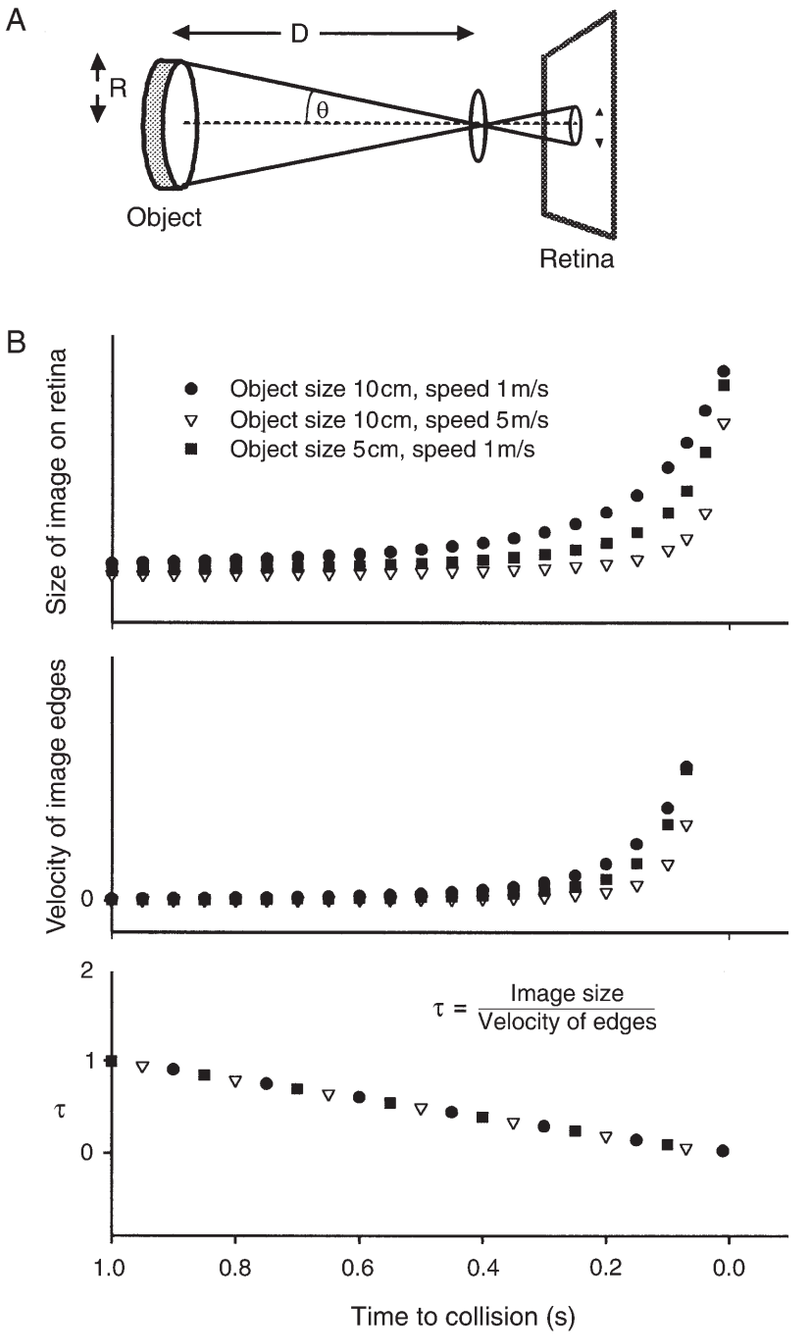

Fig. 1. ***Geometry of the image of an approaching object.*** **(A)** *As an object, radius R, approaches the eye, the image expands over the retina. When the object is a distance, D, from the lens of the eye, it subtends an angle of 2θ, where θ is given by tan θ = R/D.* **(B)** *When an object approaches the eye, the size of its image on the retina and the velocity with which the edges of the image travel over the retina both increase. The way in which these increases occur depends both on the size and the velocity of movement of the object* (top and middle panels). *The ratio of image size to velocity (τ), however, is directly related to the time remaining before collision and is independent of object size* (bottom panel).

provided that the velocity of the object relative to the observer is constant. Its value is independent of absolute speed or of the size of the object (Fig. 1B). In real situations, closing velocity is rarely constant, but there are a number of examples indicating that animals trigger specific reactions when τ reaches a particular value. This was first shown for gannets, which close their wings just before entering the water during a plunge dive[16]. The timing of wing closing correlates more closely with a particular value of τ than with other parameters, such as the distance to the water surface or the time elapsed during a dive. Subsequently, good evidence has been presented suggesting that humans use τ to estimate time to collision in psychophysical tests and when playing ball games or driving a car[14,15]. The timing of landing responses by flies and pigeons also correlate well with τ (Refs 17,18).

Neurones that signal the time to collision

Electrophysiological recordings from single neurones in the pigeon provide the best evidence for the existence of neuronal mechanisms for measuring the time to collision. Wang and Frost examined the spike responses of neurones in the dorsal posterior zone of the nucleus rotundus[19], a brain nucleus downstream from the optic tectum. An anaesthetized pigeon viewed images of a sphere that moved on a variety of straight trajectories towards or away from it (Fig. 2A). The sphere was covered with a black and white pattern, rather like that found on many soccer balls, so that the overall luminance of the image did not change when the sphere approached the eye. All of the 145 neurones from which recordings were made responded to movements in the visual field, but 24 were clearly selective for approaches made directly towards the pigeon. These neurones had very large receptive fields, which covered over 100° of the pigeon's field of view, and gave very small responses to the movement of the sphere in directions other than directly towards the pigeon. Detailed tuning curves were obtained for three of these neurones and showed a remarkably tight tuning for a direct collision course. The peak response, measured as mean spike-firing frequency during stimulation, was centred precisely on a collision course and the response fell to half of the maximum if the object's trajectory moved 3.3° away from a direct collision course (Fig. 2A). The neurones were tuned specifically to approaching objects rather than overall expansion of the flow field because they did not respond to an expanding wide-field chequer-board pattern. A stationary chequer-board pattern behind an approaching soccer ball did not significantly alter the response to the object's approach.

Each neurone signalled a particular time to collision because the profile of the response was independent of the absolute size or the speed of the approaching object (Fig. 2B). During approach, the response increased from background level to peak mean firing rate within about 100 ms. The time before collision at which different neurones became active varied between 800 and 1400 ms. Sensitivity to looming stimuli probably arises from connectivity within the rotundus because neurones with this specificity have not been found in the optic tectum. Recent analysis has shown that the looming-sensitive cells can be divided into different functional subgroups, each of which responds to different features of the expanding image[21].

Evidence that the looming-sensitive neurones have a role in controlling the pigeon's startle response is provided by the tight correlation found between the timing of the responses made by these neurones, electromyograms from a major flight muscle and the bird's heart rate. The electromyograms showed an increase in activity 20–100 ms after the onset of response by a looming-sensitive neurone and heart rate increased threefold when the pigeon saw the image of a rapidly approaching sphere. Neither the electromyogram nor the heart rate increased if the sphere receded from the

pigeon and all three responses declined markedly from their peak levels if the approach trajectory deviated by as little as 5° from collision.

Collision-sensitive neurones in an insect

A pair of synaptically linked, uniquely identifiable neurones in the locust CNS rival looming-sensitive neurones in the pigeon in their tightness of tuning for objects approaching on a direct-collision trajectory[22]. These neurones are known as the lobula giant-movement detector (LGMD) and the descending contralateral-movement detector (DCMD). In extracellular recordings from the thoracic ventral nerve cord, spikes from the DCMD are large and readily identifiable. The neurone responds briefly to any sudden movement within a large receptive field, a property that has made it popular for research and for teaching undergraduates for almost 50 years[24,25]. Spikes in the DCMD follow those seen in the LGMD at frequencies up to at least 400 Hz (Ref. 26). Sensitivity for approaching objects was suggested by Schlotterer[27], and it was confirmed subsequently that responses to approaching objects were greater than those to receding or translating objects[28]. The neurones generate a prolonged, accelerating burst of spikes that tracks object movement throughout the duration of its approach[22,23] and they would be capable of signalling the approach of a swooping bird[28]. Recently, Judge and Rind have measured the tuning of the DCMD to approaching object trajectories[22]. The DCMD spiking response declines to half the maximum level if the object's trajectory deviates from a direct collision course by 3°, with tuning slightly tighter in the azimuth than in the elevation (Fig. 2C).

Unlike the looming-sensitive neurones in the pigeon, the response produced by the LGMD increases during the approach of an object in a manner that depends on both the size and the approach speed of the object (Fig. 2D). It is unlikely, therefore, that this neurone could, on its own, signal the time remaining to collision. However, it has been proposed that information about time to collision could be gained by an exponential function, $f(t) = C.\dot{\theta}.e^{-\alpha\theta}$, where θ is the angular extent of the image, $\dot{\theta}$ is the instantaneous rate of change of θ, and C and α are constants[29]. This function would result in a rapid decline in LGMD excitation before the end of the simulated approach and the start of this decline could be used as a measure of the time before collision[29]. Although this mechanism could work theoretically, the LGMD does not behave in this way[23]. In particular the peak in the response of the LGMD can occur at, or after the projected time of collision, which allows no time for escape.

Consistent with a role for the LGMD–DCMD pathway in triggering avoidance reactions, postsynaptic targets for the DCMD include motoneurones and premotor interneurons that are involved in jumping and flying[30–32]. Observations of tethered, flying locusts indicate that the steering manoeuvres used to avoid an approaching object are triggered when the image of the object reaches a particular size (subtending 10° at the eye) rather than at a particular time before collision[33,34]. The timing of flexion of the locust hind leg, which is the first stage in escape jumping, is also related to the image size (Ref. 29; E. Childs, pers. commun.). In addition, leg cocking, which is the first stage in an escape jump, occurs in response to the trains of DCMD spikes that continue until after the looming stimulus has vanished (E. Childs, pers. commun.).

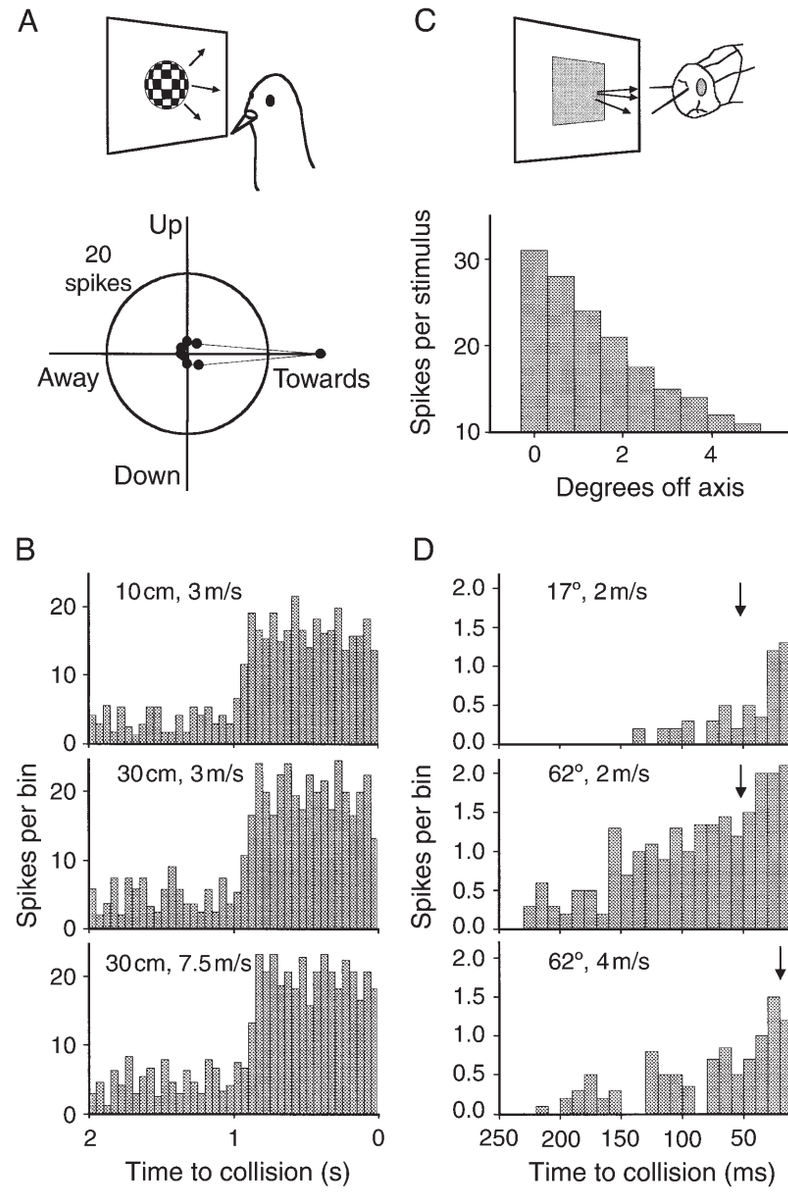

Fig. 2. ***Characteristics of neurones in the pigeon and the locust that signal an object approaching on a collision course.*** *Pigeons* **(A,B)** *or locusts* **(C,D)** *viewed computer-generated images of objects that were approaching at different angles relative to a direct collision course.* (A) *The tuning curve for a neurone in the dorsal-posterior part of the pigeon nucleus rotundus. Mean spike frequencies were recorded from five repetitions of approaches along a fixed vertical plane that varied in their angle of elevation.* (B) *Histograms of spike frequency during simulated approaches show a switch from background spike rate to about 20/bin at a fixed time before collision irrespective of the size or approach speed of the object. Histograms are the averages of five approach movements.* (C) *The tuning curve for the locust descending contralateral-movement detector (DCMD) for objects approaching at different trajectories along a fixed horizontal plane shows that this neurone is very sharply tuned to detect directly approaching objects. Responses were averaged from five repetitions.* (D) *The response by the locust DCMD starts to increase very soon before the time to collision and continues until after movement of the image stops (arrows). The form of the response depends on the size and the approach speed of the object. Results are the means from six repeated approach movements.* (A) drawn from data in Ref. 20; (B) reproduced, with permission, from Ref. 19; (C) redrawn, with permission, from Ref. 22; (D) redrawn, with permission, from Ref. 23.

The input organization of a collision-warning neurone

The LGMD distinguishes between approach and recession from the way in which edges of an object's image grow and move over the compound eye[35].

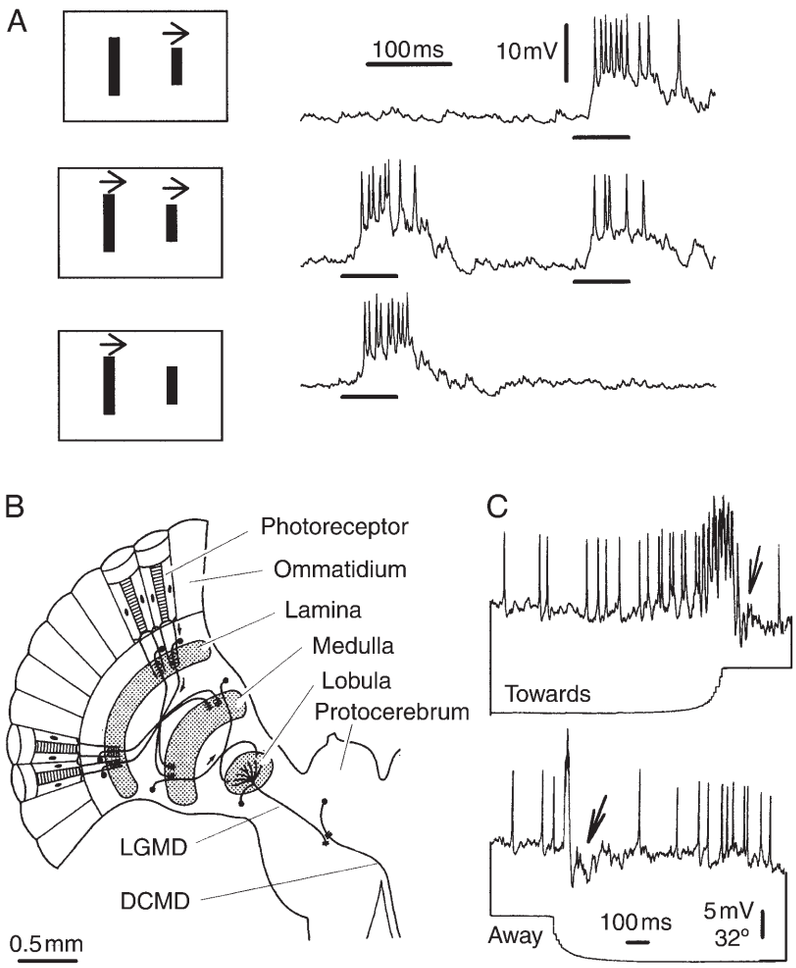

Fig. 3. ***Intracellular recordings from the locust lobula giant-movement detector (LGMD) that show two forms of inhibition.*** **(A)** *The locust viewed a screen on which two vertical bars moved laterally. Movement of the right bar alone caused vigorous excitation of the LGMD (top trace), which was reduced if the left bar moved before the right one (middle trace). Following movement of the left bar alone, no IPSPs were recorded in the LGMD (lower trace), indicating that the inhibitory effect occurred presynaptically to the LGMD.* **(B)** *Schematic illustration of the locust visual system viewed from behind.* **(C)** *The locust viewed the image of a rectangular object approaching and later retreating at 5 m/s. Following the end of approach and the start of retreat, which are times when large parts of the visual field are stimulated rapidly, a barrage of IPSPs was recorded (arrows).* (A) reproduced, with permission, from Ref. 38; (B) reproduced, with permission, from Ref. 25; (C) redrawn, with permission, from Ref. 39.

Changes in luminance, caused by object motion, generate little or no response and the neurones detect the approach of light or of dark objects. Their responses to diverging image edges are no greater than those to converging edges. The critical cues are increases in the amount of edge in the image and acceleration of those edges over the retina. This was demonstrated by stimulating the eye with moving lines that changed either in length or in speed when they moved. The two critical image cues are extracted locally without reference to global image patterns, which ensures they are recognized quickly. The use of two cues strengthens the DCMD response and when an object is on a collision course with the locust, both the cues will be maximized. The cues embody the rate of expansion of an object's retinal image. Detection of looming objects using these two cues is shared by other similar shaped neurones of the locust optic lobe[36].

Stimulation of one area of the retina suppresses the response of the LGMD to the stimulation of a second area without causing any accompanying inhibition of the LGMD itself (Fig. 3A)[37,38]. This indicates that there is inhibition directed laterally between the array of retinotopically arranged units that excite the LGMD through synapses onto the distal parts of its dendritic fan. These units originate in the second optic neuropile, the medulla (Fig. 3B), and have not yet been identified, although there are a number of candidate neurons[40,41]. The medullary units are excited transiently by changes in illumination and transmission from them to the LGMD decrements with their repeated activation[37,42]. Sudden or intense wide-field stimuli, such as rapid changes in light intensity, do directly cause IPSPs in the LGMD (Fig. 3C) and these must originate from a separate set of units because the IPSPs in the LGMD have longer latencies than EPSPs that follow these stimuli[39,42].

The specificity of the LGMD for images of objects that are approaching rather than receding is thought to be generated as a result of a critical 'race' over the dendrites of the LGMD in the optic lobe. The race is between the excitation, caused by movement of the edges of the expanding image, and the lateral inhibition that is mediated by synapses onto neurones from the medulla. Vigorous responses by the LGMD and DCMD occur when excitation arrives before inhibition and wins the race. Two separate investigations provide convincing evidence that this mechanism operates in the locust optic lobe. First, a computational model that incorporates features of the known input organization of LGMD (Fig. 4A) responds directionally to approaching objects with excitation that increases with a similar time course to that recorded from the living LGMD (Fig. 4B)[39,43]. The model shows a tight tuning for objects approaching on a direct collision trajectory, similar to that seen in the LGMD. Using the model, it is possible to track waves of inhibition across the network of medullary units when objects approach or recede from the virtual eye. It is also possible to manipulate different parameters, such as the strength and the latency of lateral inhibition, and to demonstrate their importance in the operation of the LGMD (Fig. 4C,D). The second investigation is an electron-microscope study of the arrangement of synaptic inputs onto the distal dendrites of the LGMD and provides evidence for the lateral interactions among units presynaptic to the LGMD (Ref. 38). There are many synapses on the dendrites of the LGMD and the synapses are arranged in a manner that suggests they participate in compact local circuits that compute impending collision (Fig. 5A–D). Each afferent profile that synapses with the LGMD is also presynaptic to the neighbouring afferent profile (Fig. 5C,D). This synaptic arrangement is eminently suitable for providing the anatomical substrate for lateral inhibition. Inhibition is directed from neighbouring afferents locally to the excitatory presynaptic terminals themselves. If this arrangement operates in the manner proposed, then the medulla neurones must release a neurotransmitter that excites the LGMD but inhibits neighbouring neurones in the medulla. Staining with antibodies against GABA revealed no evidence to suggest that this was the neurotransmitter of the afferent neurones. Staining for AChE, however, revealed dense deposits of this enzyme in the intercellular spaces near the synapses. Acetylcholine mediates both fast excitatory and slow inhibitory synaptic responses in insects via nicotinic and muscarinic M_2 receptors, respectively[46], and activation of these different

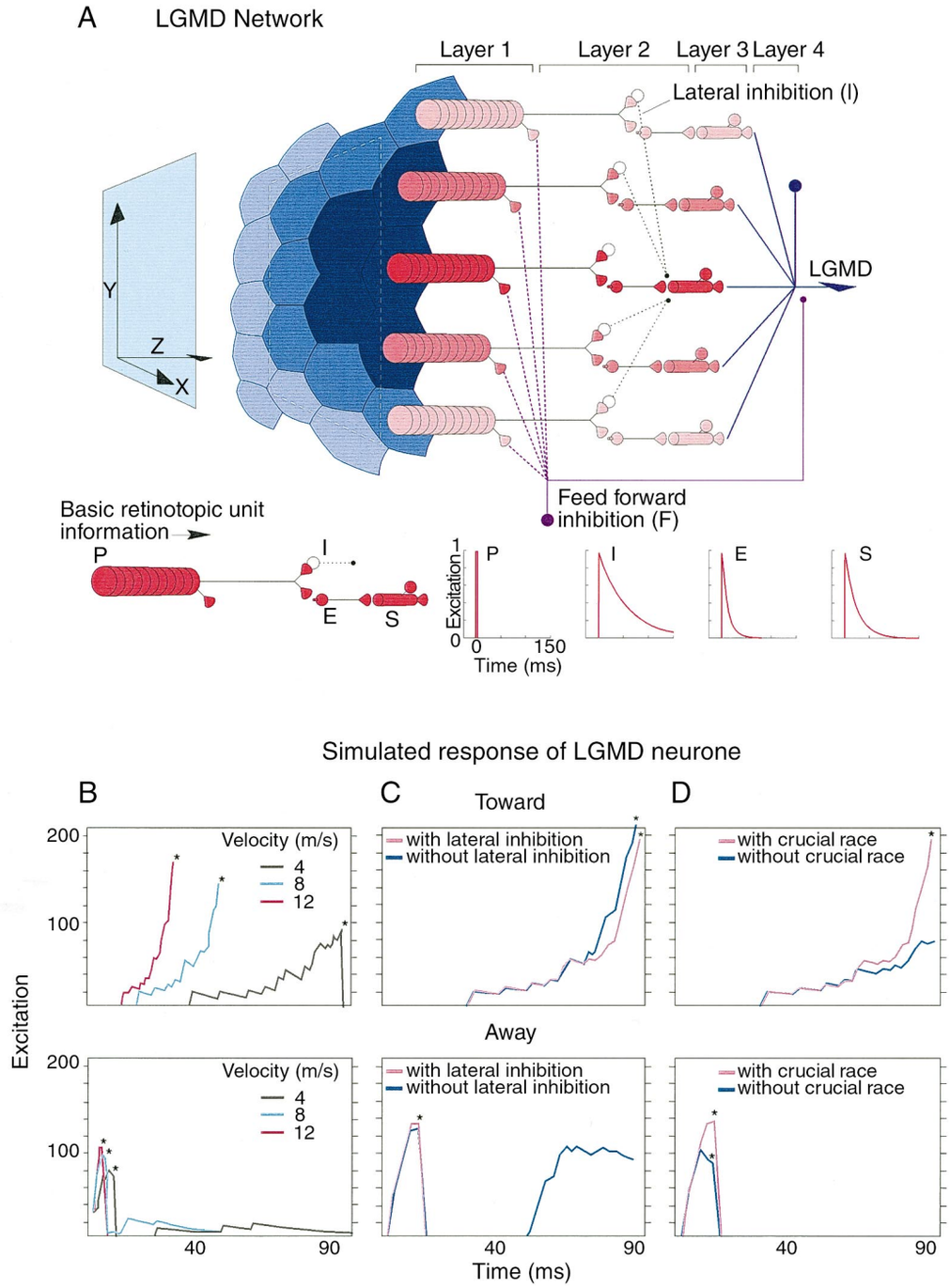

Fig. 4. ***A neural network that responds like the lobula giant-movement detector (LGMD) and reveals the importance of lateral inhibition to the response of the neurone.*** **(A)** *Schematic representation of the neural network LGMD. The inputs to the network were a series of computer-generated images of a moving object. The input organization of the basic retinotopic unit of the network is shown in red and labelled. The outputs of 250 of these units were summed by the LGMD unit (blue). In layer 1, images were mapped onto the photoreceptors, each of which viewed a narrow region of space, separated from that of its neighbours by 3.3°. Each photoreceptor (P unit, layer 1) in the model responded with a brief (1 ms) excitation to a change in level of illumination (graph P). In layer 2, this excitation was passed to three units: E, I and F. When excited, E passed excitation to a layer 3, S unit in the same retinotopic position. After a delay of 2 ms, I passed inhibition laterally to the six nearest S units, and then after a 4 ms delay, to the 12 next nearest layer 3, S units. F fed inhibition forward and by-passed layer 3. F was only active when a large number of photoreceptors were activated in a short time and had a delay of 4.5 ms in the simulations shown here. The E and I inputs were summed linearly by each S unit in layer 3 until a threshold level of excitation was reached and a spike was produced. A refractory period followed such activation, during which the neurone could not be activated, and excitation decayed exponentially (graph S). Layer 4 of the model consisted of a single LGMD unit that summed excitation from all active S units and inhibition from the F unit. In each layer proximity to the central retinotopic unit is indicated by the shade of red (dark red is the nearest). The time course of activation of each different unit is shown at the figure bottom. Abbreviations: E, excitatory unit (layer 2); F, feed-forward inhibitory unit; I, laterally projecting, inhibitory unit (layer 2); LGMD, final output unit (layer 4); P, photoreceptive unit (layer 1); S, excitatory summing unit (layer 3).* **(B)** *The response of the LGMD in layer 4 of the network to object approach on a collision trajectory versus object recession along the same path. The object was a 75 mm sided square that moved at constant velocity from 500–100 mm distance from the eye. Activity was plotted at 1 ms intervals throughout each simulation. Asterisks mark the arrival of feed-forward inhibition from the F unit (purple) onto the model LGMD.* **(C)** *Effects of changing the network parameters on the response of the LGMD to approaching and receding objects. Eliminating lateral inhibition decreases directional selectivity. The response to objects that move towards the eye is increased but there is also a strong delayed response to objects that move away from the eye.* **(D)** *Effects of changing the network parameters on the response of the LGMD to approaching and receding objects. When the critical race between excitation and lateral inhibition is eliminated (lateral inhibition is not delayed relative to the excitation passing down the network) the response no longer follows object approach.* Redrawn, with permission, from Ref. 43.

synapses could have a role in the shaping responses of the LGMD to moving stimuli.

Concluding remarks

When an image expands symmetrically over the retina, this is a cue indicating that an object is approaching the animal on a collision course. A number of neurones have been found that are excited by this type of stimulus. Owing to the higher spatial resolution of vertebrate eyes compared with those of invertebrates, the time to contact can be calculated while the object is still some distance away and evasive manoeuvres can be initiated at an appropriate time. Collision detecting neurones in the pigeon brain switch on ~1 s before the time of contact, when the subtense of the image at the eye can be as small as 3–5° and long before the locust LGMD fires strongly. The LGMD, by contrast, responds when collision is only 200–400 ms away. The one LGMD neurone present on each side of the locust is uniquely identifiable and its input organization has been investigated and modelled. It is fed by an extremely compact neuronal micro-circuit, which is tightly tuned to objects that are approaching on a collision course. In the locust optic

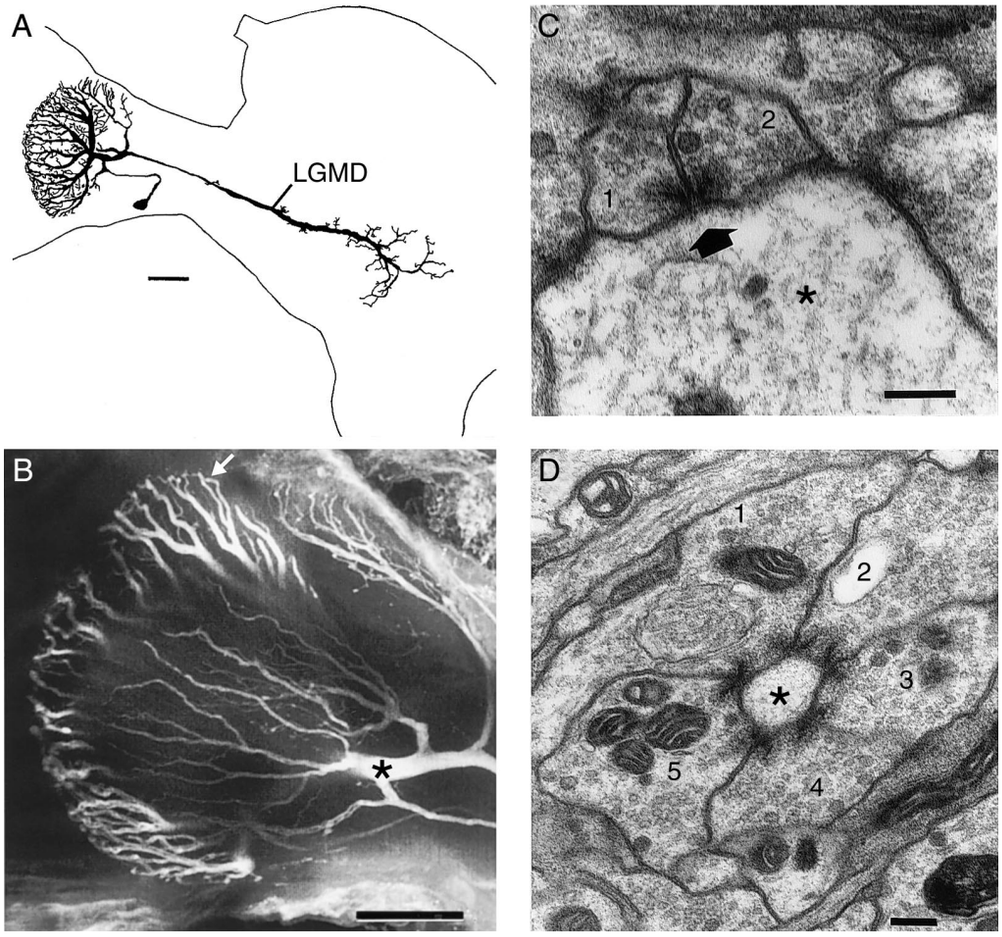

Fig 5. ***Morphology of the lobula giant-movement detector (LGMD) and its input organization.*** **(A)** *The LGMD has been stained with hexaminecobaltic chloride then viewed dorsally. The main dendritic branches of the LGMD occur in the lobula area of the optic lobe and an axon projects into the protocerebral area of the brain where it synapses with the descending contralateral-movement detector*[26,44]*. The cell body of the neurone lies in the stalk of the optic lobe.* **(B)** *The same neurone was injected with neurobiotin according to the method of Mesce* et al.[45] *then viewed dorsally using a confocal microscope. A stack of 50, 3 μm optical sections were taken through the dendrites of the LGMD in the lobula, the first 20 were then removed to reveal the underlying dendrites, which are thought to be the site of the inhibitory input onto the neurone. The base of the LGMD dendritic fan is indicated by an asterisk. An arrow indicates the area shown in* (C). **(C)** *Electron micrograph showing the paired arrangement of afferent inputs onto the LGMD dendritic fan (asterisk) in the distal lobula. Each afferent process synapses with its neighbour and the LGMD. An arrow indicates the paired presynaptic densities.* **(D)** *A small LGMD profile (asterisk) is surrounded by, and postsynaptic to, five afferent processes (numbered). Scale bars, 100 μm in* (A) *and* (B)*, and 200 nm in* (C) *and* (D). (C) and (D) reproduced, with permission, from Ref. 38.

lobe the LGMD is probably only three or four synapses distant from the photoreceptors and its postsynaptic target, the DCMD, contacts some motoneurones directly. The circuitry in this pathway is compact. The operating principles these studies have revealed could provide the inspiration for manufactured collision sensors able to respond quickly to fast-approaching objects, and the details of the neuronal circuitry could be translated into neuromorphic[47] designs for the collision-sensing vision chips of the future.

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