

COMMENTARY

The role of behavioural ecology in the design
of bio-inspired technology

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Many of today's most challenging information processing tasks can be performed using technology inspired by the highly evolved nervous systems of animals, and some of the most successful bio-inspired systems mimic the relatively simple sensory circuits of invertebrates such as insects (reviewed by Franceschini et al. 1992; Franceschini 2004; Rind 2005; Srinivasan 2006). The development of these artificial bio-inspired technologies is often tackled by interdisciplinary teams of neurobiologists, computer scientists, engineers and physicists who attempt to copy the information processing capabilities of the insect's nervous system. However, we argue that behavioural ecologists have an equally important role to play in these teams and can contribute greatly to the development of bio-inspired technologies.

Insect neural networks can sometimes provide a simple and eloquent way of processing information that has had millions of years of development through evolution (Rind et al. 2003). However, evolution develops information processing systems that can exploit particular features of the environment occupied by the insect. We argue that whereas much research is directed towards the admirable goal of understanding and copying the neural networks seen in nature, insufficient effort is dedicated to understanding differences between the behavioural ecology of the real animal and that required of the artificial agent (e.g. the robot) under development.

A well-studied example of an insect visual neuron that has also been modelled and implemented in artificial agents within novel environments is the lobula giant movement detector (LGMD) neuron of locusts (e.g.

Simmons & Rind 1992; Rind & Simmons 1999; Blanchard et al. 2000). Electrophysiological studies of the locust LGMD initially showed that it responded to small objects moving anywhere within its visual field, and so it was originally classified as a 'jittery movement detector' (reviewed by Rowell 1971; Pinter 1977). Later, it was discovered that the LGMD responded best to looming objects (Schlotterer 1977; Rind & Simmons 1992) approaching on a direct collision course with the locust (Wheatstone 1852). The characteristic response of the locust LGMD to a small looming stimulus is a train of spikes that increases in frequency as the object gets closer (Rind & Simmons 1992; Hatsopoulos et al. 1995). This spike rate broadly relates to the increasing rate at which the approaching object expands over the eye, although the relationship is not a simple linear one. Details of the input afferents to the LGMD and the connections between them have also been discovered (Rind & Simmons 1998; Rind & Leitinger 2000; Gabbiani et al. 2005; Krapp & Gabbiani 2005; Peron et al. 2007) and, as a result, it has been possible to produce biologically plausible computer models and silicon implementations of the neuron and its input circuitry (Rind & Bramwell 1996; Indiveri 1998). Much research has been conducted on the ability of the LGMD to detect imminent collisions, and models of it have been used successfully to detect imminent collisions encountered by robots (e.g. Blanchard et al. 2000). More recently, an LGMD model has been used to detect imminent collisions between pedestrians and cars from real video footage of road scenes and from interfacing the model with driving-based video games (Cuadri et al. 2005; Stafford & Rind 2005; Yue et al. 2006).

Although information processing systems such as the LGMD model are inspired by flying insects, there are few flying robotic systems (but see Srinivasan et al. 2004; Floreano et al. 2005; Franceschini et al. 2007 for examples) and the existing systems differ considerably from flying insects, particularly in manoeuvrability (although increasingly 'insect-like' robots are being developed; e.g.

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Michelson 2002). Most systems used to test simulations of insect neurons are wheeled robots, which have fewer degrees of freedom of movement than a flying insect. This means that the relationship between the information processing by the real or artificial neural network and the behaviour that it triggers in the insect or artificial agent (e.g. a robot) differs considerably. In addition, the sensory environment, part of the 'ecological niche' in which the insect lives, may be very different from that in which the artificial agent is required to function. Since insect vision has evolved to closely match the ecological niche occupied by the animal (O'Carroll et al. 1996), insect-inspired neurons might not be able to perform tasks successfully if placed into artificial agents in novel, inappropriate environments.

Here we review work on adapting the information processing capabilities of the LGMD to work in an artificial agent in a novel environment. We then consider the successes and failures of the LGMD model implemented as an automotive collision sensor. We discuss why we need to consider not only the information processing of the neuron but also the behaviour and ecology of the real locust, the physical limitations of the artificial agent and the environmental information that it must process to create successful bio-inspired solutions.

The LGMD Model

The LGMD model used in this study is the same as that used in Yue et al. (2006). It is described fully in the online [Supplementary Material](#) and is based on previous models by Rind & Bramwell (1996) and Blanchard et al. (2000). Briefly, it consists of a two-dimensional array of photoreceptor units (P units), each of which takes their input from a given pixel of a video running at 25 frames per second. The output of each of the P units is the change in luminance in successive frames over the part of the

array occupied by the P unit. This output is passed to a lateral inhibition unit (LI unit) and an excitatory summing unit (S unit) (Fig. 1). At the LI units, interactions with retinotopically neighbouring units occur; these interactions result in a blurred and expanded image of the one detected at the P units, which, in a somewhat teleological sense, can be thought of as 'predicting' the next output of the P units. The output of the LI units is delayed slightly and subtracted from the current output of the P units at the S units. Effectively, the remaining excitation in the S units is minimal under most conditions, since the 'predictive' response of the LI units matches the new excitation from the P units (Yue et al. 2006; Stafford et al. 2007). Input representing imminent collision (and certain other visual scenes; see below) is not correctly 'predicted' by the LI units and so excitation results. The excitation in the S units is summed onto the LGMD and, if a given threshold is exceeded for more than a given number of time steps, a collision alert is produced.

The output of both the real and the modelled neuron can be suppressed by a second form of inhibition called feed-forward inhibition (Palka 1967). The feed-forward pathway is thought to be triggered by large and rapid changes in the visual field, such as the onset of whole-field motion, and produces large inhibitory postsynaptic potentials in the LGMD (Rowell et al. 1977; Rind 1996; Santer et al. 2004). Other potential explanations of the functional role of feed-forward inhibition are discussed below in the context of the behavioural ecology of locusts and artificial agents.

Adapting the LGMD to Detect Collision within an Automotive Environment

In a recent study, our LGMD model was challenged with a range of automotive scenes including car crashes and

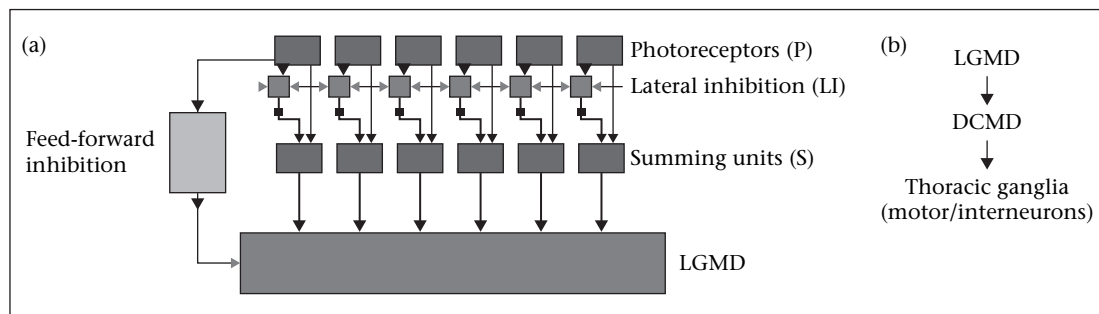


Figure 1. Generalized scheme of connectivity in the locust and model LGMDs. (a) The model LGMD mimics processing in the locust's optic lobes, presynaptic to its LGMD. In the model LGMD, each of the P, LI and S layers, although shown in the figure as only a single row of cells, is a two-dimensional array of 150 cells by 100 cells. The first layer (the P cell layer) receives input from a 150×100 pixel greyscale video image at each time step or video frame (25 s^{-1}). The value of each pixel (0–255 ranging from black to white) is mapped onto the corresponding photoreceptor unit (P layer). The output of the photoreceptors is the change in value of the pixel between successive time steps or frames. This output is passed to the retinotopic excitatory S layer and the inhibitory LI layer. The inhibition in the LI layer spreads between neighbouring LI units to spatially blur the change in image passed out of the photoreceptor units. The inhibition is delayed by one time step (0.04 s) and subtracted from the excitation, at the S units. Resultant excitation is passed to the LGMD, and collision alerts are generated if the excitation exceeds a given threshold for a given time. A feed-forward inhibition loop inhibits the LGMD after a short delay (one to five time steps, 0.04–0.20 s; values optimized by the genetic algorithm) if a given threshold value was reached by summing the outputs of all cells in the P layer. (b) In the locust, the LGMD synapses with the DCMD neuron in the brain, and spikes are reliably passed from LGMD to DCMD on a 1:1 basis. The DCMD descends to the thoracic ganglia where it synapses with motor- and interneurons that control wing and leg muscles. LGMD/DCMD activity triggers evasive gliding behaviour via these connections.

noncollision scenes (Yue et al. 2006). The functional parameters of the model were identified and parameters (or synaptic weights) were optimized to the novel automotive environment using a genetic algorithm.

The LGMD model performed well in discriminating between the imminent collisions and the vast majority of noncollision scenes in its novel automotive environment (Yue et al. 2006). However, there was one area where false collision alerts were consistently made: this was in response to translating cars moving across the LGMD model's field of view. This sequence consistently triggered a false collision alert in the modelled neuron. This is counter to work on the real locust LGMD neuron, which shows very different responses to translating and colliding stimuli (Rind & Simmons 1992; Simmons & Rind 1992). As discussed below, the reasons for the different responses of the neuron and its modelled counterpart can be explained by a consideration of behavioural ecology.

During optimization of the LGMD network to the automotive environment, no functional role for the feed-forward inhibitory pathway was found. Optimized parameters were output by the genetic algorithm which meant that the amount of excitation required to trigger a response by this feed-forward inhibition pathway was far in excess of anything that ever occurred during the processing of the automotive images (Yue et al. 2006).

Locust Behaviour and the LGMD

To understand the failings of the LGMD model in the automotive environment, we decided to reconsider the behavioural ecology of real locusts. The locust's LGMD has long been known to respond with high-frequency spikes to looming objects, and much work has focused on the possibility that it might mediate the avoidance of potentially colliding objects or swarm mates during flight (e.g. Robertson & Reye 1992; Robertson & Johnson 1993; Gray et al. 2001). Recent work also suggests that the LGMD responds with maximum spike frequencies to small, fast-moving objects, which represent the specialist avian predators that capture flying locusts (Rind & Santer 2004), and that the neuron's maximum sensitivity is in its caudal field of view (Krapp & Gabbiani 2005), suiting it to the detection of pursuing predators. Furthermore, the high-frequency spikes that occur in the LGMD and postsynaptic descending contralateral movement detector (DCMD) neurons close to the time of collision have been proposed to underlie the performance of a stereotyped gliding behaviour during flight. This gliding behaviour is interpreted as a last minute attempt to dive and escape capture by a bird predator, should steering movements fail as an evasive response (Santer et al. 2005, 2006).

It is clear that a 'predator avoidance' neuron is beneficial to the locust since capture by a predator nearly always results in death for the prey. However, a thorough understanding of the behavioural ecology of insects indicates that a collision avoidance system may be less crucial to the locust. Although collisions are often fatal to larger animals such as birds (Veltri & Klem 2005), the light weight of insects makes them incredibly robust to collisions; adult

cicadas, for example, regularly collide while flying (Hoover 2003) and flies can often be seen to fly directly into windows at high speeds and yet appear to suffer little, if any, effect from the collision. Although locusts swarm in massive numbers, it may be that they use self-organizing rules, similar to flocks of birds or shoals of fish, when swarming (Camazine et al. 2001). Using evasive glides to avoid collisions with other locusts in a swarm may be ineffective because it could result in further collisions with other individuals flying beneath them. For this reason, it may be more appropriate to think of the LGMD as predominantly a 'predator' rather than a 'collision' detector (Gray et al. 2001; Santer et al. 2005), although to do this we must step away from an explanation of neuronal function based on human intuition and look towards the one suggested by animal behaviour.

Considering the real LGMD a predator avoidance neuron that triggers a behaviour (a gliding dive) a split second before collision rather than a general collision detection neuron is important in addressing the failures of the modelled neuron in its automotive environment for two reasons. First, the biomechanics and aerodynamics of the flying locust mean that a gliding dive milliseconds before collision may allow it to lose sufficient height to evade a swooping bird's beak, if not collision with the bird's body (which may be of little consequence from the point of view of evading predation); the median time at which the gliding dive posture is fully adopted is 15 ms before collision (Santer et al. 2005). Such rapid manoeuvrability is not commonly possessed by artificial agents such as robots and is certainly not possessed by cars, which also have to evade an entire looming target to prevent collision and not just a small area of it equivalent to a bird's gaping beak to escape predation. Second, the change in angle subtended on the locust's eye by an approaching predator (or predator-sized object), which is the main cause of excitation to the LGMD, is greatest just before the point of collision. LGMD spikes at this time (between 25 and 15 ms before collision) have been shown to be crucial to glide triggering (Santer et al. 2006), meaning that the extremely rapid expansion of the predator on the locust's retina can be a cue for the triggering of avoidance behaviour. By comparison, a typical robot or automotive collision scene causes a more gradual increase in angular subtense. As a result, potential excitation of the LGMD is much higher during predator attacks than during automotive collisions (Fig. 2). This makes predator attacks much easier to detect based on the LGMD (or LGMD model) response. This higher relative level of LGMD excitation also means that predator approaches are more easily distinguished from the background excitation caused by other types of motion in the environment than automotive collisions would be.

Challenging the LGMD model of Yue et al. (2006) with stimuli previously used in experiments with the locust LGMD reveals that both can distinguish between the translating and the looming movements of a small, predator-sized object (Fig. 3; see also real results in Simmons & Rind 1992). However, the LGMD model failed at exactly this task in automotive scenes, even though the translations falsely identified as collisions occurred at velocities

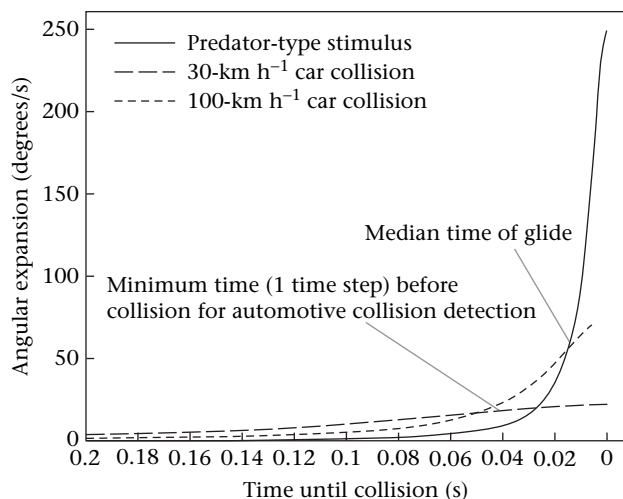


Figure 2. The mathematically derived angular expansion of a looming stimulus over the eye of a locust (or the camera acting as input to the LGMD model) as a measure of excitation entering the information processing network. Details are given for a predator-type stimulus 80 mm in diameter approaching at 5 m s^{-1} and for a car-equivalent stimulus 1.5 m in diameter moving at either 30 or 100 km h^{-1} . The excitation at the median time at which a locust performs an evasive glide is greater than the last possible situation (one frame before collision) that the LGMD model can be used for collision mitigation responses in cars.

of $30\text{--}50^\circ \text{ s}^{-1}$ (from stimuli used in Yue et al. 2006 and Stafford et al. 2007), comparable to the translating motion stimuli successfully distinguished from looming stimuli in Fig. 3. In all cases, translating movements excite the LGMD (whether the locust's or a model of it), but this is not the real issue underlying the LGMD model's inability to distinguish translations from looms in an automotive environment; this is a result of the looms themselves. Predator-like looms strongly excite the LGMD and this excitation can be distinguished easily from the weaker excitation caused by a translation; car-like looms induce less

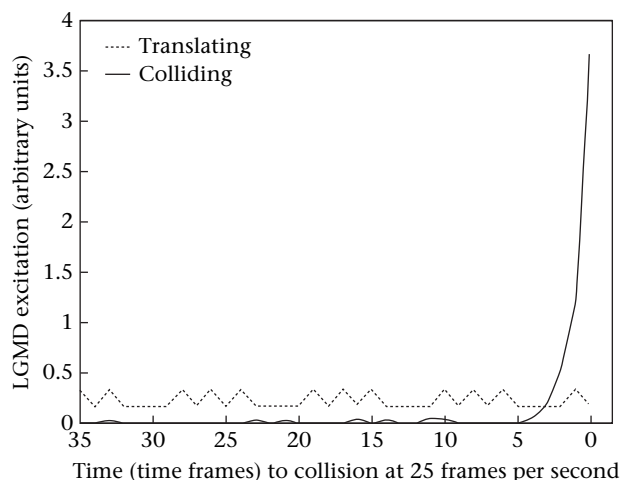


Figure 3. The excitation present in an LGMD model presented with a colliding or translating object of diameter 80 mm. The object is either approaching at 5 m s^{-1} on a direct collision course or translating at 40° s^{-1} as in a representative stimulus from an electrophysiological study of the locust LGMD (Simmons & Rind 1992).

excitation in the LGMD simply because of their differing expansion profiles (Fig. 2), meaning that there is less difference between it and that caused by translation, and these two stimuli are not easily distinguished (Yue et al. 2006; Stafford et al. 2007).

Compromises and Solutions to Match the Agent to the Environment

In the previous section, we showed that an LGMD model rigidly based on the real locust LGMD is not well suited to the detection of automotive collisions, but this does not mean that such applications of bio-inspired technology are doomed to failure. These bio-inspired solutions can be extremely effective if we take the time to understand differences between the behavioural ecologies of insect and agent and adapt the bio-inspired network to take account of these differences.

The LGMD model is under development as an automotive collision detector and, crucially, it did not fail to detect collisions in its new automotive environment; it did this very successfully (Yue et al. 2006). It was possible to increase the time before collision when an alert was given. The modelled system was capable of detecting collisions $>0.25 \text{ s}$ before impact and $>0.5 \text{ s}$ before impact in some cases. This time compares to a median time of the gliding posture being fully adopted 15 ms before impact in the locust (Santer et al. 2005; see above).

This earlier detection time was possible because the automotive collision detector did not need to have the near- 180° field of view of that the locust LGMD needs to monitor predators; this was reduced to $\sim 45^\circ$, allowing the point of focus of the video camera to effectively be well in front of the car, thus detecting expanding objects earlier. Detection times were also increased because the initial expansion of larger objects, such as cars, occurs earlier than smaller objects, such as bird predators (Fig. 2), although the maximum rate of expansion is far lower. Modifying the LGMD model so that it could exploit the benefits of the artificial agent's field of view and the mathematics of the visual scenes in the automotive environment made it a more effective method of processing images for its intended task of detecting imminent collisions with objects such as cars as early as possible to allow for maximum collision mitigation responses.

However, we also need to be aware of the potential problems caused by the physical limitations of the agent and its new environment. As we describe above, the biggest problem faced is that, in the new environment, it is harder to distinguish dangerous colliding objects from objects with translating motion. This is due to the differences in the rates of expansion of colliding objects in the two environments and to the short time period required to trigger sufficient behavioural changes in the locust compared to the less-maneuvrable car. We tackled this by integrating the LGMD model with a series of model insect-inspired directionally selective movement detectors. These model cells specifically detected translating motion and suppressed the model LGMD response (Stafford et al. 2007; see also Harrison 2005 for further

work on collision detection using insect-inspired directionally selective neurons). There is no need for this kind of additional processing in the locust's environment, but in an automotive environment it successfully tackled shortcomings in the model's response resulting from differing image geometry.

So far we have considered only placing the information processing capabilities of the LGMD model into a novel environment where the ability to select collision stimuli over noncollision stimuli is more difficult than in its natural environment. Often, this is not the case. Many artificial agents are robots or computer-based agents operating in a simplified laboratory or simplified real-world environment (e.g. Franceschini et al. 1992; Blanchard et al. 2000; Webb 2002; Santer et al. 2004; Floreano et al. 2005). It may be that the requirements of the artificial environment are less demanding than those of their natural environment. Nevertheless, it is worth considering differences between the animals' and the agents' behaviour and environment because this may limit the need for complexity and massive processing power in the information processing system or there may be differences between the environments or agents, such as the speed of movement of the real and artificial agents, which need accounting for.

What Does the Study of Artificial Agents Tell Us About Real Behavioural Ecology?

For the teams currently developing bio-inspired technology, the exchange of information is reciprocal: engineers take inspiration from biology and in return add to the understanding of exactly how the biological circuits work

by building them. So, might there also be a reciprocal exchange of ideas with the field of behavioural ecology?

First, the fit of the LGMD model to experimental results in real locusts and the underperformance of the unmodified LGMD model in the automotive environment are useful confirmation that the LGMD model really does process visual images in the same way as the locust LGMD, rather than simply performing a generic collision detection algorithm. Thus, it appears that the real LGMD neuron has evolved to specifically detect specialized avian predators of locusts, and the effectiveness of the modelled LGMD is diminished when removed from this niche; this insight may be important in understanding locust behaviour.

A second example of what we can learn from this study is provided by the locust LGMD neuron's feed-forward inhibition pathway. From studies using relatively small looming stimuli, some authors have proposed that this pathway cuts off an LGMD's response after a loom has finished or prevents it responding to some nonlooming types of motion (Rind & Simmons 1992; Simmons & Rind 1992; Rind 1996). However, support for these functions of feed-forward inhibition was not found when optimizing the model of the LGMD to automotive scenes (Yue et al. 2006). From studies using a range of larger looming stimuli, other authors found that feed-forward inhibition was active much earlier in a loom, causing the spike frequency of the LGMD to peak and begin declining before the point of collision (Hatsopoulos et al. 1995; Gabbiani et al. 1999, 2002, 2005; see example in Fig. 4). These authors propose that this occurs as a result of a multiplicative interaction between the feed-forward inhibitory pathway and the input to the main dendritic fan of the LGMD. Furthermore, they suggest that this peak in the responses of the

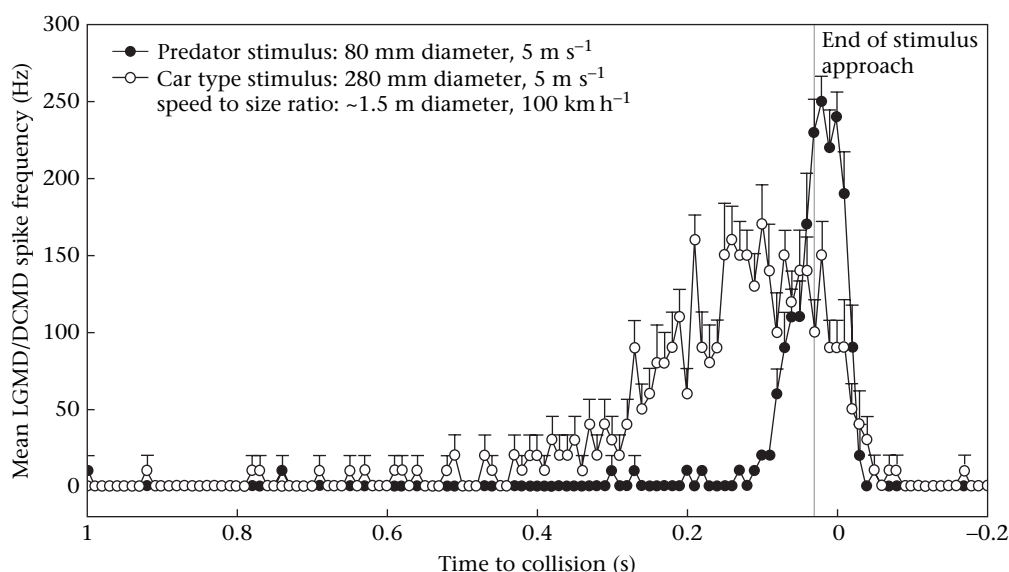


Figure 4. The mean \pm SE spike frequency of the DCMD of a locust (*Locusta migratoria* L.) presented with 10 approaches of a predator-like stimulus and 10 approaches of a stimulus with approximately the same size to speed ratio as a car colliding at 100 km h⁻¹. Data are in 10-ms bins. Predator-type stimulus was a dark circle of diameter 80 mm with simulated approach speed of 5 m s⁻¹ stopping 150 mm from the locust's eye, subtending a final angle of 29.9°. Car-type object was a dark circle of diameter 280 mm with simulated approach speed of 5 m s⁻¹ stopping 150 mm from the locust's eye, subtending a final angle of 86.1°. This gives approximately the same size to speed ratio as a theoretically circular object of car size (diameter 1.5 m) travelling at 100 km h⁻¹ (diameter to speed ratio of (1) car = 54 ms; large object = 56 ms; (2) small object/predator = 16 ms). Further experimental details are given in electronic [Supplementary Material](#).

LGMD and DCMD (the point where the spike frequency begins to decrease), rather than a prolonged burst of high-frequency spikes, is used to trigger collision avoidance behaviours in the locust, although this is currently disputed (Hatsopoulos et al. 1995; Matheson et al. 2004; Rind & Santer 2004; Santer et al. 2006).

Considering the LGMD as a specialized predator detector may help in reconciling these results. For small or fast-moving objects with small diameter to speed ratios (≤ 16 ms; e.g. a 80-mm circle looming at 5 m s^{-1}), equivalent to small, fast-moving locust predator-type stimuli, the maximum DCMD response occurs at or after the point of collision, with prolonged high spike rates suitable for triggering evasive glides occurring just before collision (Fig. 4; see also Figure 3 in Gabbiani et al. 1999). Thus, the peak (the point at which the spike frequency begins to decrease) is unsuitable as a trigger for the gliding behaviour or other responses to small, fast, predator-like stimuli (see also Rind & Simmons 1992; Money et al. 2005; Santer et al. 2005 for DCMD responses to small objects that do not show peaks before collision). Responses where LGMD activity peaks 100–200 ms before collision and then begins to decline (an order of magnitude earlier than when the gliding behaviour occurs) occur for much larger or slower-moving objects with the same approximate size: speed ratios as those of the car collisions considered in this paper (Fig. 4; see also Figure 3 in Gabbiani et al. 1999). Since predators of locusts appear as small, fast-moving visual stimuli (Rind & Santer 2004) and we consider the LGMD a predator rather than a collision detector, an alternative explanation for the maximum spike frequency occurring 100–200 ms before collision may be more appropriate. We suggest that, in response to large or slow objects, suppression of the LGMD and DCMD responses (and thus suppression of evasive glides) occurs through feed-forward inhibition as a response to a nonpredator-like stimulus. In effect this would prevent emergency predator avoidance behaviour in an inappropriate behavioural context. This would also explain why no role for feed-forward inhibition could be found when optimizing the LGMD model to a novel environment; this is simply because these larger, slower approaches were precisely those that it had to detect. Again, these insights are gained by studying the behavioural ecology of the animal rather than just focusing on the neural processing of visual information.

Conclusions

This paper has examined the integration of the environment, the physical capabilities and behaviour of an agent and the information processing ability of that agent for both a real life agent (a locust) and an artificial agent (a car). Its prime objective was to show that, in nature, an organism must integrate all of these processes to successfully exploit its ecological niche (see also O'Carroll et al. 1996). In the transition from natural to artificial systems it is important to consider not only the information processing capabilities of the biological system that one wishes to exploit but also whether these information processing capabilities are capable of serving a useful role given the mechanical and environmental constraints of the new artificial agent.

Often these insights can be gained by a thorough understanding of the behavioural ecology of the organism.

For models of the locust LGMD neuron to process collision information in artificial agents such as cars, we need to recognize two constraints: first, that the car's manoeuvrability is significantly lower than that of the locust and it needs to move further to successfully evade collision and, second, that the environment that the artificial agent occupies is different from that of the real insect. Detecting collisions by analysing object expansion is much harder in the car's environment because of the lower expansion rate of the car compared to that of a bird predator. This makes selectivity for colliding over non-colliding stimuli much harder in artificial than in real environments and makes the model LGMD more prone to incorrectly detect collisions where there are none. By studying the behavioural ecology of the real animal, the constraints and environment of the artificial agent and the neural networks used to process the information, better and more useful bio-inspired artificial agents can be produced. For this reason, the field of behavioural ecology has important contributions to make to the development of bio-inspired technologies.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2007.07.015.

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