

# Collision Detection as a Model for Sensory-Motor Integration

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Annu. Rev. Neurosci. 2011. 34:1–19

First published online as a Review in Advance on March 10, 2011

The *Annual Review of Neuroscience* is online at [neuro.annualreviews.org](http://neuro.annualreviews.org)

This article's doi: 10.1146/annurev-neuro-061010-113632

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0147-006X/11/0721-0001\$20.00

## Keywords

single neuron computation, looming, neuroethology, escape behavior, LGMD, DCMD

## Abstract

Visually guided collision avoidance is critical for the survival of many animals. The execution of successful collision-avoidance behaviors requires accurate processing of approaching threats by the visual system and signaling of threat characteristics to motor circuits to execute appropriate motor programs in a timely manner. Consequently, visually guided collision avoidance offers an excellent model with which to study the neural mechanisms of sensory-motor integration in the context of a natural behavior. Neurons that selectively respond to approaching threats and brain areas processing them have been characterized across many species. In locusts in particular, the underlying sensory and motor processes have been analyzed in great detail: These animals possess an identified neuron, called the LGMD, that responds selectively to approaching threats and conveys that information through a second identified neuron, the DCMD, to motor centers, generating escape jumps. A combination of behavioral and *in vivo* electrophysiological experiments has unraveled many of the cellular and network mechanisms underlying this behavior.

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## INTRODUCTION

How does an animal brain use the sensory information it acquires from the outside world to generate appropriate motor actions? When multiple behavioral choices are available, which neural mechanisms underlie making a particular decision? These questions have been the subject of intense research for decades. For the most part, sensory and motor physiology have been studied separately to characterize the input and output stages of the nervous system. However, owing to the inherent variability in both sensory and motor responses, their relation and the neural transformations that occur between them cannot be fully appreciated unless they are studied simultaneously.

Behaviors that are critical for survival provide a favorable model for sensory-motor integration because many animals have evolved specialized neural circuitry to execute them. Studying their underlying neural mechanisms provides an opportunity to understand basic principles of sensory-motor integration, which may generalize to other behaviors as well. In this review, we focus on visually evoked collision-avoidance and escape behaviors. Their investigation is particularly feasible in the laboratory because approaching objects can be effectively simulated using two-dimensional

projections on a computer screen, called looming stimuli.

In the following sections, we first discuss what is known about the psychophysics of collision-avoidance behaviors across different animal species, from humans to insects. Next, we present a comparative overview of the structure and function of specialized looming-sensitive neurons and their hypothesized role in generating escape responses. Finally, we focus on the locust, the model system in which the neural mechanisms underlying visually evoked escape behaviors are best understood. Despite the relatively small size of their brains, these animals are champions in executing such behaviors. At the sensory-motor interface, they possess identified neurons that detect looming stimuli and are part of a compact neural network that transforms sensory signals to the motor commands required for collision avoidance. Thus, in the locust, investigators can undertake detailed studies of the neural processing that occurs between the sight of a threat and the execution of an escape behavior.

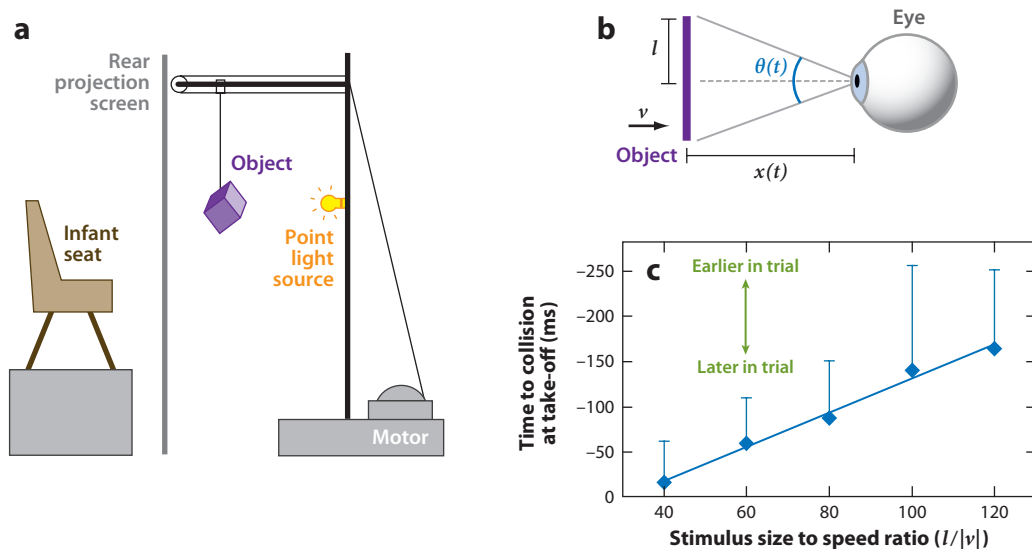
## VISUALLY EVOKED COLLISION-AVOIDANCE BEHAVIORS

Virtually all animals endowed with spatial vision exhibit an avoidance response to objects approaching on a collision course. To be effective, such responses should be executed in a timely manner and only if the approaching object might be a real threat. Thus the properties of the approaching object must be monitored in real time for the animal to decide whether, at which moment, and in which direction, to generate an escape response.

The psychophysics of visually evoked collision-avoidance behaviors has been studied for many decades, across different animal species (e.g., humans: Ball & Tronick 1971, King et al. 1992; monkeys: Schiff et al. 1962; pigeons: Wang & Frost 1992; turtles: Hayes & Saiff 1967; frogs: Ingle & Hoff 1990, King & Comer 1996, King et al. 1999, Yamamoto et al. 2003; goldfish: Preuss et al. 2006; crabs:

### Looming stimulus:

the two-dimensional expanding shadow associated with an approaching object by central projection on a screen



**Figure 1**

Looming stimuli and evoked behavior. (a) Schematics of the experiments of Ball & Tronick (1971). The subject is seated in a chair and views either a real approaching object (without projection screen) or the object's expanding shadow projected on the screen (looming stimulus). Reactions to the two types of stimuli are indistinguishable. (b) Kinematic variables characterizing a looming stimulus viewed monocularly. A solid disc is characterized by its half-size,  $l$ , and its constant approach speed,  $v$ . The distance to the eye is  $x(t)$  and the subtended angle,  $\theta(t)$ . The time course of  $\theta$  is fully determined by the size-to-speed ratio,  $l/|v|$  (see sidebar, Approach Kinematics and Angular Threshold). (c) In locusts, the time of jump relative to collision as a function of the looming stimulus size-to-speed ratio is well fitted by a line [ $\rho = 0.6$ , data points are mean and standard deviation pooled over 13 animals; adapted from Fotowat & Gabbiani (2007)].

Hemmi 2005, Oliva et al. 2007, Sztarker & Tomsic 2008; crayfish: Wine & Krasne 1972, Glantz 1974; flies: Holmqvist & Srinivasan 1991, Tammero & Dickinson 2002, Hammond & O'Shea 2007, Card & Dickinson 2008, Fotowat et al. 2009; locusts: Robertson & Johnson 1993, Santer et al. 2005a,b, Fotowat & Gabbiani 2007). In response to impending collision, most animals generate a motor response that moves them away from the threat, covers the most vulnerable parts of their body, or generates a fast, unpredictable movement trajectory. For example, Ball & Tronick (1971) reported that human infants, 2–11 weeks old, presented with approaching objects, moved their head back and away from the object and brought their arms to their face. They found that such collision-avoidance behaviors were extremely robust and invariant with age, suggesting that they either are innate or require minimal learning. Additionally, the authors found that the two-dimensional shadow of an

approaching object was equally effective in generating avoidance responses (Figure 1a), and they concluded that either human infants are not capable of extracting depth information or such information is not necessary for generating the avoidance response. Similarly, both infant and adult rhesus monkeys show a “persistent fear response” to the symmetrically expanding shadows of physically approaching objects (Schiff et al. 1962). Thus, the symmetrical two-dimensional expansion of a silhouette is sufficient to simulate the approach of an object on a collision course and to generate avoidance responses. For such two-dimensional stimuli, referred to as looming stimuli, the “time of collision” is defined as the moment when the angular size subtended by the silhouette on the retina reaches  $180^\circ$  (Gibson 1958). In the particular case of monocular stimulation, the temporal dynamics of the retinal image of an object with half size  $l$ , approaching on a collision course with a constant approach speed,  $v$ ,

## APPROACH KINEMATICS AND ANGULAR THRESHOLD

In reference to **Figure 1b**, let  $x > 0$  be the object's position with respect to the subject's eye; i.e.,  $x = 0$  at collision. Define  $t = 0$  as the time of expected collision and  $t < 0$  before collision. Consequently, the object's speed,  $v$ , is  $< 0$  when the object is approaching and  $-v = |v|$ , the absolute value of  $v$ . The object's position is given by  $x(t) = vt$  and by trigonometry,

$$\tan \theta(t)/2 = l/(vt) \quad \text{or} \quad \theta(t) = 2 \tan^{-1}[l/(vt)]. \quad 1.$$

Assume that the time of an event relative to collision depends linearly on  $l/|v|$ , as is the case for jump time in **Figure 1c**. Then

$$-t_{event} = \alpha l/|v| - \delta \quad (> 0 \text{ before collision}), \quad 2.$$

where  $\alpha$  is the slope of this linear relation (dimensionless) and  $\delta$  the intercept with the ordinate axis (in units of ms). Equivalently, the angle,  $\theta_{thres}$ , subtended by the looming stimulus  $\delta$  ms before the event (i.e., at time  $t_{event} - \delta$ ) is independent of the stimulus size-to-speed ratio,  $l/|v|$ . To see this, use successively Equations 1 and 2,

$$\tan \theta_{thres}/2 = l/[v(t_{event} - \delta)] = l/[-v\alpha l/|v|] = \alpha^{-1}$$

which is indeed independent of  $l/|v|$ . Furthermore, the threshold half-angle's tangent,  $\tan \theta_{thres}/2$ , is the inverse of the slope,  $\alpha$ .

can be fully characterized by its size-to-speed ratio,  $l/|v|$  (**Figure 1b**) (Gabbiani et al. 1999). Therefore, for a given object size, a faster approach speed implies a faster expansion rate and a smaller  $l/|v|$  ratio. Varying the  $l/|v|$  ratio thus allows investigators to manipulate the temporal dynamics of the looming stimulus to study which of its various aspects are used by the animal to guide its behavior.

For example, in response to looming stimuli, locusts jump and fly away, and the time of take-off relative to collision varies linearly with  $l/|v|$  (**Figure 1c**). This linear relationship shows that the jump does not occur at a fixed time before collision, but implies rather that it occurs at a fixed delay after the stimulus reaches a threshold angular size on the retina (see sidebar, Approach Kinematics and Angular Threshold). Retinal image size has also been reported to be a critical stimulus parameter for

triggering visually evoked escape responses in several other species (frogs: Ingle & Hoff 1990, Yamamoto et al. 2003; goldfish: Preuss et al. 2006; fruit fly: Fotowat et al. 2009). An estimate of time to collision, on the other hand, may be relatively easily extracted from looming stimuli (Lee 1976) and, a priori, seems better suited than retinal image size for triggering collision-avoidance behaviors because it is not confounded by object size. There is, however, little evidence implicating time to collision in responses to approaching objects. Time to collision, however, has been linked to other types of avoidance behaviors, e.g., the triggering of wing folding in diving gannets (Lee & Reddish 1981), landing in the house fly (Wagner 1982), and various interception tasks in humans (Tresilian 1999). In the case of landing, other visual variables may also be used (Borst & Bahde 1988, Srinivasan et al. 2000), and it is likely that separate neural pathways drive collision-avoidance and landing behaviors (Tammero & Dickinson 2002).

Another interesting aspect of visually guided escape responses is their preparatory phase. For example, locusts (Santer et al. 2005b) and fruit flies (Card & Dickinson 2008) use their middle legs to displace their center of mass laterally and thus tilt the direction of their jump away from the approaching object. Additionally, fruit flies raise their wings prior to take-off (Hammond & O'Shea 2007, Fotowat et al. 2009), and locusts prepare for take-off by storing the required energy in the elastic elements of their hind legs (Heitler 1974). Whether the same neural pathways control collision-avoidance preparation and its final execution remains unknown.

In many animals, looming-evoked escape responses are probabilistic and habituate over repeated stimulus presentations (Hayes & Saiff 1967, Holmqvist & Srinivasan 1991, Yamamoto et al. 2003, Fotowat & Gabbiani 2007, Hammond & O'Shea 2007, Oliva et al. 2007, Fotowat et al. 2009). Interestingly, in locusts, the dynamics of habituation have been linked to the social lifestyle of the animals (solitary or swarming; Matheson et al. 2004).

Because visually evoked escape responses are natural, robust, probabilistic, and often multi-staged, planned behaviors, they provide an excellent context for studying the neural mechanisms of sensory-motor integration. Efficient detection of approaching threats is the critical first step for generating an escape response; hence many animal species possess neurons specialized in this task. In the next section, we discuss the properties of such looming-sensitive neurons and the different ways by which they could convey information about approaching objects to downstream motor centers.

## LOOMING-SENSITIVE NEURONS

Electrophysiological recordings, electrical and pharmacological stimulation, and lesion studies have been carried out in many different animal species, revealing classes of neurons and neuronal pathways preferentially activated by objects approaching on a collision course in the context of visually guided collision-avoidance or escape behaviors. These neurons and pathways are commonly located in regions of the brain thought to be involved in sensory-motor integration, such as the superior colliculus and some of its target nuclei (monkeys: King & Cowey 1992; rats: Sahibzada et al. 1986, Mitchell et al. 1988a,b, Redgrave et al. 1988, Dean et al. 1989, Westby et al. 1990; hamsters: Northmore et al. 1988). In nonmammalian vertebrates, the optic tectum is homologous to the superior colliculus, and looming-sensitive neurons are found in midbrain nuclei along the tectofugal pathway in pigeons (Wang & Frost 1992, Wu et al. 2005), the optic tectum of frogs (King et al. 1999, Nakagawa & Hongjian 2010), and the nucleus isthmi in fish (Gallagher & Northmore 2006). The nucleus isthmi in birds may also be implicated in detecting looming stimuli in the context of spatial visual attention (Asadollahi et al. 2010). In mice, looming-sensitive neurons have been reported as early as in the retina (Münch et al. 2009). In the frog retina, synchronized activity of dimming-detectors plays an important role in generating looming-evoked escape behaviors (Lettvin

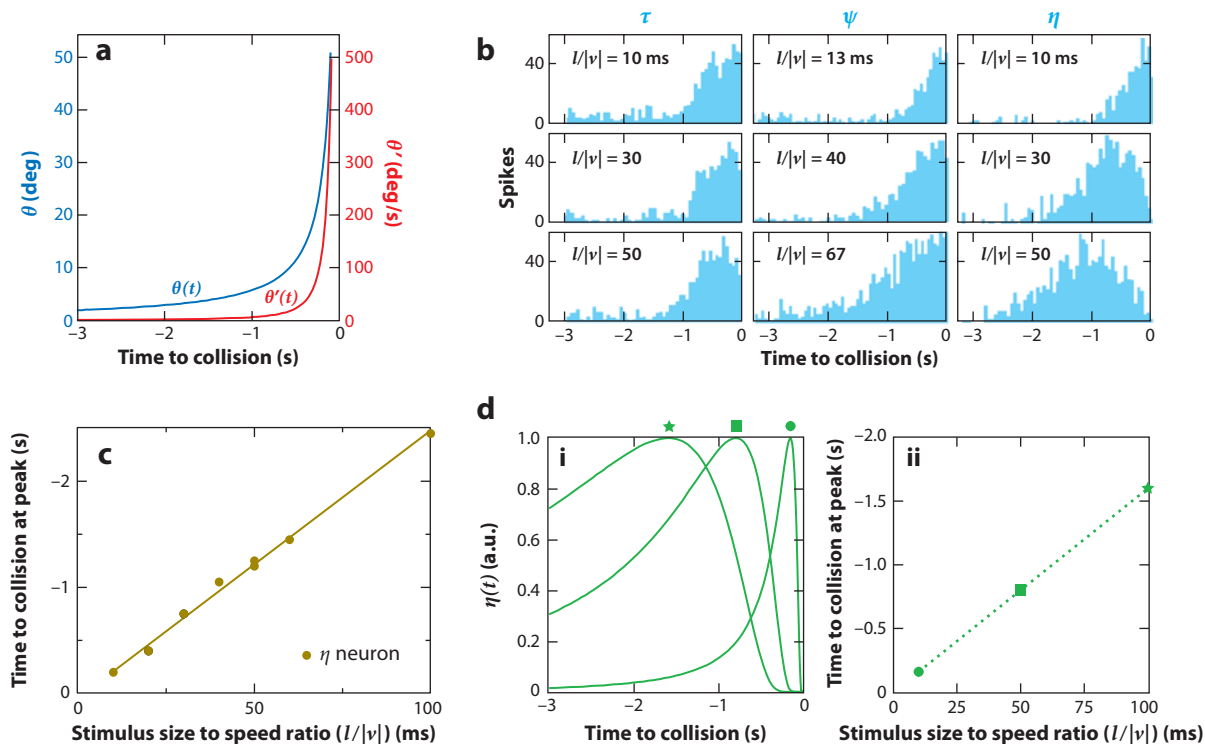
et al. 1968, Ishikane et al. 2005). Investigators have also identified looming-sensitive neurons in the brains of crustaceans, teleost fish, and insects [lobula giant neurons of crabs: Medan et al. 2007, Oliva et al. 2007, Sztarker & Tomsic 2008; medial giant neurons of crayfish: Wine & Krasne 1972; Mauthner cell of goldfish: Preuss et al. 2006; lobula giant movement detector (LGMD) of locusts: Schlotterer 1977, Rind & Simmons 1992, Hatsopoulos et al. 1995; neurons in the moth optic lobe: Wicklein & Strausfeld 2000).

Despite many differences in brain structure and behavioral repertoire, these neurons and pathways seem to share some common features. For example, many looming-sensitive neurons possess large dendritic fields, consistent with wide-field integration of sensory inputs (O'Shea & Williams 1974, Wicklein & Strausfeld 2000, Medan et al. 2007). They are sensitive to collision-bound trajectories across a substantial fraction of the visual field (Wang & Frost 1992, Gabbiani et al. 2001, Medan et al. 2007, Rogers et al. 2010) and respond very weakly, if at all, to optic flow stimuli, such as those generated by self-motion (O'Shea & Rowell 1975a, Wang & Frost 1992, Gabbiani et al. 2002, Medan et al. 2007). Additionally, these neurons are often multimodal. For example, looming-sensitive neurons in goldfish and locusts also respond to auditory stimuli (Zottoli 1977, O'Shea 1975, Zottoli & Faber 2000), and three of the four identified classes of looming-sensitive neurons in crabs respond to mechanical stimuli (Medan et al. 2007). In rats, the neural projection from the superior colliculus to the cuneiform area, which is implicated in generating collision avoidance to looming stimuli, is multimodal as well (Westby et al. 1990). Electrical and pharmacological stimulation of those neuronal populations leads to changes in respiration and heart rate, as well as blood pressure (Keay et al. 1988, 1990). Similarly, Wang & Frost (1992) reported that increases in heart rate correlate with increases in the activity of looming-sensitive neurons in pigeons. Thus, looming-sensitive neurons are likely to provide input to the autonomic nervous system in

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**LGMD:** lobula giant movement detector

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**Figure 2**

Kinematics of looming stimuli and associated neural responses. (a) During looming, both stimulus angular size,  $\theta(t)$  (blue curve), and speed,  $\theta'(t)$  (red curve), grow nonlinearly with time. (b) Responses of neurons in the nucleus rotundus of pigeons to looming stimuli (sum of 5 trials; 50 ms bins). A representative of the first class ( $\tau$ , left) starts firing at a fixed time to collision, independent of  $I/|v|$ . Neurons of the  $\psi$  class (middle) start to fire when the stimulus angular speed exceeds a threshold and neurons of the  $\eta$  class (right) exhibit a peak that shifts relative to collision time with  $I/|v|$ . (c) The time of peak firing rate of  $\eta$  neurons is linearly related to  $I/|v|$ . (d) Their firing rate time course is well described by the  $\eta$  function described in the text, (i), whose peak time varies linearly with  $I/|v|$  as well, (ii). Symbols mark the correspondence to different  $I/|v|$  values. Panels a and d adapted from Laurent and Gabbiani (1998); panels b and c adapted from Sun & Frost (1998).

vertebrates, in addition to their involvement in motor aspects of collision-avoidance behaviors.

Which kinematic variables of an approaching object are extracted by looming-sensitive neurons in different animal species, and what are the similarities and differences in the computations they perform? Using the time course of retinal image expansion, these neurons could, in theory, compute several time-varying quantities associated with an approaching object, e.g., angular size and speed, time remaining to collision, or various combinations thereof. A defining characteristic of looming stimuli is that, as collision becomes imminent, both the angular size,  $\theta(t)$ , and speed,  $\theta'(t)$ , grow nonlinearly

(Figure 2a), whereas time remaining to collision,  $\tau$ , decreases linearly.

Among all vertebrate species, looming-sensitive neurons have been best characterized in the pigeon, where three distinct classes of neurons sensitive to distinct kinematic variables have been reported in the midbrain nucleus rotundus (Sun & Frost 1998). Neurons of the first class always initiate their response at the same time remaining to collision, i.e., after  $\tau$  reaches a threshold. Thus, their response onset time relative to collision does not vary with the stimulus size or speed (Figure 2b,  $\tau$ ). The time course of the firing rate of neurons in the second class differs because it starts earlier

relative to collision for larger or slower objects (**Figure 2b**,  $\psi$ ), and its onset is well described by a threshold in the angular speed of the stimulus. After response onset, the temporal slope of the firing rate is not different for stimuli with different size-to-speed ratios, suggesting that these neurons do not track the stimulus angular speed per se, but rather begin responding after it reaches a threshold. The response profile of the third class of neurons is similar to the second one in that it initiates earlier for larger or slower objects, but it is different in that it decreases when the stimulus reaches large angular sizes showing a distinct peak, which also occurs earlier for larger or slower objects (**Figure 2b**,  $\eta$ ). Furthermore, the timing of the peak varies linearly with the stimulus size-to-speed ratio (**Figure 2c**). Just as in the case of locust jump escape behaviors, this linear relationship indicates that the peak occurs a fixed delay after the stimulus reaches a threshold angular size on the retina (Gabbiani et al. 1999). Such a pattern of neural activity could be achieved if the neurons in this class were following a nonlinear function of the stimulus angular size,  $\theta(t)$ , and speed,  $\theta'(t)$ , which first increases and then decreases toward the end of the approach. A simple multiplication of angular speed with a negative exponential of angular size fulfills this requirement:  $\eta(t) = C\theta'(t - \delta)\exp(-\alpha\theta(t - \delta))$  (**Figure 2d**). Here, the constant,  $C$  (converting angular velocity to firing rate), as well as  $\alpha$  (related to the threshold angular size), and  $\delta$  (implementing neural delays), can be fitted to experimental data. This function initially increases in parallel with angular speed, but eventually decreases as the negative exponential of size overwhelms it. Thus,  $\eta(t)$  exhibits a peak that occurs earlier relative to collision for larger or slower objects and varies linearly with the object's size-to-speed ratio,  $l/|v|$ . In fact, this function had first been proposed to fit the time course of activity of an identified, looming-sensitive neuron in the locust, the LGMD (Hatsopoulos et al. 1995). This multiplicative combination of angular speed and a negative exponential of size is essentially unique in being able to reproduce

the characteristic linear relation between peak firing rate and  $l/|v|$  (appendix 3 of Gabbiani et al. 1999) and was later found to fit the time course of looming-evoked excitatory postsynaptic potentials in the Mauthner cell of goldfish, as well (Preuss et al. 2006).

The locust LGMD is perhaps the most extensively studied looming-sensitive neuron (O'Shea & Rowell 1976, Rowell et al. 1977, Schlotterer 1977, Rind & Simmons 1992, Hatsopoulos et al. 1995, Judge & Rind 1997, Gabbiani et al. 1999, Gabbiani et al. 2002, Matheson et al. 2004, Krapp & Gabbiani 2005, Guest & Gray 2006, Peron et al. 2009, Peron & Gabbiani 2009). It makes a strong synapse with the descending contralateral movement detector (DCMD) (O'Shea & Williams 1974, Rind 1984, Killmann & Schürmann 1985), whose large axon travels down the animal's contralateral nerve cord and contacts motor and interneurons involved in generating jumps and flight steering (Burrows & Rowell 1973, O'Shea et al. 1974, Simmons 1980). Therefore, the LGMD-DCMD system provides an excellent framework for studying the sensory-motor transformations that occur during looming-evoked collision-avoidance behaviors. In the following sections, we first review the known anatomical and physiological properties of the LGMD neuron and next describe the role of the LGMD-DCMD system in the sensory-motor integration mechanisms that underlie visually evoked collision-avoidance behaviors.

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**DCMD:** descending contralateral movement detector

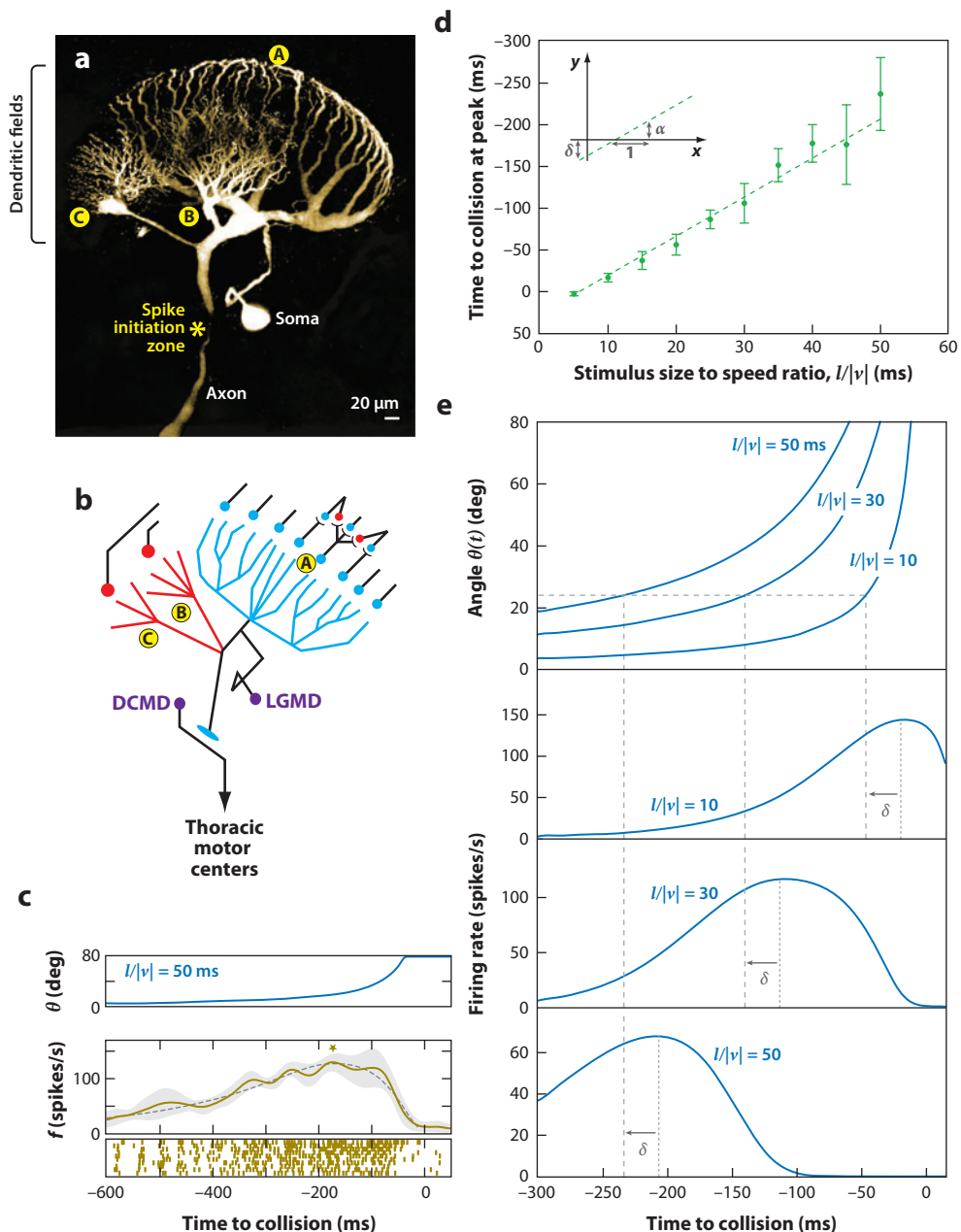
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## THE LOBULA GIANT MOVEMENT DETECTOR NEURON OF LOCUSTS

The LGMD of locusts is an identified neuron located in the lobula neuropil of each of their optic lobes. As in other insects, the two bilaterally symmetric optic lobes consist of a photoreceptor layer, the retina, and three hierarchically organized neuropils, the lamina, medulla, and lobula, connected by two optic chiasmata. Thus, the lobula is three synapses away from the photoreceptors. Each LGMD neuron receives visual input through three distinct

dendritic fields (**Figure 3a**). The largest one, field A, is ellipsoidal in shape, just like the eye, and receives  $\sim 15,000$  excitatory retinotopic inputs from the entire visual hemifield (O'Shea & Williams 1974, Strausfeld & Nüssel 1981, Krapp & Gabbiani 2005, Peron et al. 2007). The retinotopic organization of this projection

is remarkably precise and preserved down to the level of single ommatidia or facets (Peron et al. 2009). In contrast, the LGMD's other two smaller dendritic fields, B and C, each receive  $\sim 500$  nonretinotopic, feedforward inhibitory inputs, which are best activated by large, transient changes in luminance (Palka 1967,





Rowell et al. 1977, Hatsopoulos et al. 1995, Gabbiani et al. 2005). In addition, the excitatory pathway is endowed with a lateral inhibitory network activated by wide-field motion that protects the LGMD's responses from habituation (**Figure 3b**) (O'Shea & Rowell 1975a).

The LGMD neuron responds to small stimuli translating in its visual receptive field but is maximally activated by objects approaching on a collision course with the animal or by looming stimuli (Rowell et al. 1977, Schlotterer 1977, Rind & Simmons 1992, Hatsopoulos et al. 1995). The selectivity of the LGMD for looming versus translating stimuli is due in part to spike frequency adaptation mediated by SK-like (small  $K^+$  conductance) potassium channels located immediately adjacent to the LGMD's spike initiation zone (Gabbiani & Krapp 2006, Peron & Gabbiani 2009). This conductance acts as a veto mechanism, effectively shutting off synaptic excitation when it is not maximally activated. In response to looming stimuli, the firing rate of the neuron increases as the stimulus angular size increases but then declines as it exceeds a threshold (**Figure 3c**). This decline is caused by the feed-forward inhibitory inputs onto dendritic fields B and C. Feedforward excitation and inhibition are activated concurrently during a looming stimulus, with excitation slightly leading inhibition. As a result, the firing rate peak occurs well before excitation or inhibition has ceased (Gabbiani et al. 2002, 2005). The peak time of LGMD activity

is linearly related to  $l/|v|$ , occurring earlier relative to collision for larger size-to-speed ratios (**Figure 3d**) (Gabbiani et al. 1999). Again, this finding indicates that the peak occurs a fixed delay after the stimulus reaches a threshold angular size on the retina (**Figure 3e**), where the delay and threshold angular size can be simply calculated from the slope and intercept of the linear fit (see sidebar, Approach Kinematics and Angular Threshold). This angular size threshold is invariant to changes in the shape, texture, and direction of the approaching object (Gabbiani et al. 2001, Rogers et al. 2010), presumably enabling the locust to respond similarly to the wide range of predators it experiences in the wild (Kuitert & Connin 1952, Preston-Mafham 1990).

In response to looming stimuli, the time course of the LGMD firing rate can be described as a function of the angular speed of stimulus expansion multiplied by a negative exponential of its angular size (Hatsopoulos et al. 1995, Gabbiani et al. 2002), similar to the  $\eta$  function used to fit the response of looming-sensitive neurons in pigeons. Experimental evidence suggests that this multiplicative operation is carried out within the LGMD itself rather than presynaptically (Gabbiani et al. 2002). How could the LGMD biophysically compute the  $\eta$  function using the visual inputs it receives? Information about the angular speed of the stimulus is conveyed by the excitatory input to the LGMD (from

### Figure 3

Anatomy, circuit properties, and responses of the LGMD to looming stimuli. (a) Stain of the LGMD neuron illustrating its dendritic fields A, B, and C, and the location of the spike initiation zone (\*). (b) Schematics of the input-output circuitry of the LGMD. Field A receives retinotopic, feedforward excitatory synaptic input from the entire visual hemifield (light blue). A lateral inhibitory network (red dots) between adjacent excitatory inputs to field A lies presynaptic to the LGMD (purple dot). Fields B and C receive nonretinotopic feedforward inhibition (red). The LGMD makes a synaptic contact with the DCMD neuron (purple dot) in the protocerebrum, which in turn sends its axon toward thoracic motor centers. (c) Response to a looming stimulus ( $l/|v| = 30$  ms). The angular size subtended by the stimulus at the retina is illustrated on top (dark blue curve). The firing rate is illustrated in the middle panel (dark yellow line and gray fill, indicating standard deviation), as well as the multiplicative model discussed in the text (dashed gray line). Ten spike rasters representing ten different trials are illustrated at the bottom. Time of peak is indicated by a star. (d) Plot of peak time as a function of the size-to-speed ratio of the looming stimulus. The relation is close to linear and has an intercept  $\delta$  with the y-axis and a slope  $\alpha$  (top left inset). Data in panels c and d are from different animals. (e) Diagram illustrating the significance of the parameters  $\alpha$  and  $\delta$  derived from the linear fit in panel d. The time course of the angle  $\theta(t)$  is depicted on top for three  $l/|v|$  values. The bottom three panels illustrate the mean firing rate of the LGMD in response to these three looming stimuli. Note that in each case, the angular size of the object is equal to  $24^\circ$  at a delay  $\delta = 27$  ms before the peak DCMD activity (horizontal and vertical dashed lines). Adapted from Gabbiani et al. (1999, 2002).

dendritic subfield A; Krapp & Gabbiani 2005), whereas feedforward inhibition conveys information about stimulus size (from subfields B or C; Gabbiani et al. 2005). Thus, if the excitatory input were proportional to the logarithm of angular speed,  $\log \theta'$ , and the inhibitory input to angular size,  $-\alpha\theta$ , these two signals could be added and exponentiated within the LGMD to yield the desired  $\eta$  function. A complete verification of this hypothesis requires a quantitative description of the time course of excitation and inhibition along the feedforward pathways leading to the LGMD and their interaction within its dendritic tree. In support of this hypothesis, the transformation between membrane potential and firing rate at the spike initiation zone of the LGMD is well approximated by a third-order power law, close to the exponentiation postulated above (Gabbiani et al. 2002). Thus, the locust LGMD is an example of a single neuron within a compact nervous system able to carry out a complex nonlinear computation within its dendritic tree. Mammalian neurons are endowed with many types of active dendritic conductances (Johnston & Narayanan 2008) potentially allowing them to carry out complex, nonlinear computations (Polsky et al. 2004), although their relation to sensory and motor processing remains less well understood.

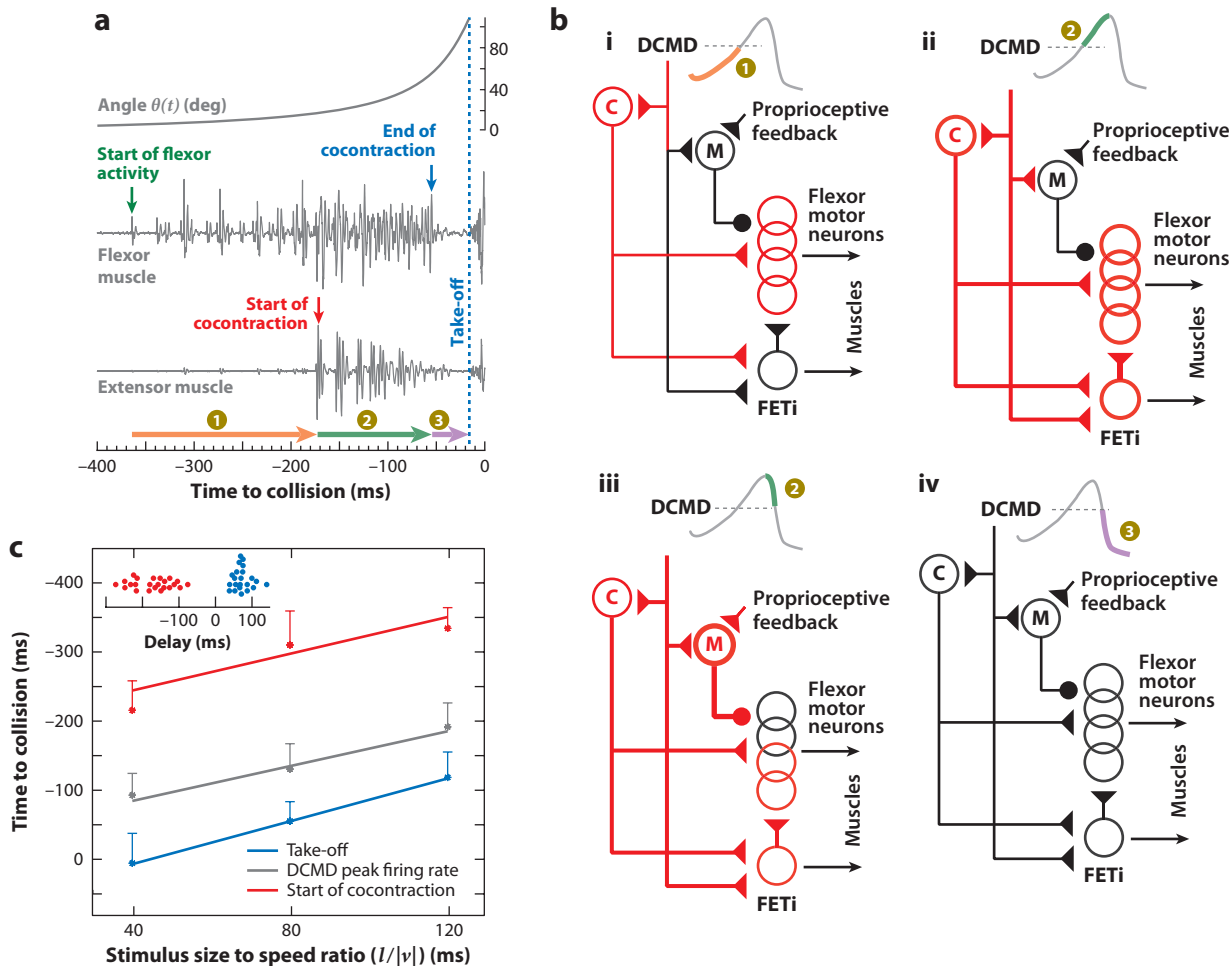
In the brain, each LGMD neuron makes a mixed chemical and electrical synapse (Killmann & Schürmann 1985) with the DCMD neuron (O'Shea et al. 1974). The LGMD-DCMD synapse is so strong that every LGMD spike generates a spike in the DCMD (O'Shea & Rowell 1975b, Rind 1984). The DCMD axon crosses the midline in the brain, enters the contralateral nerve cord, and eventually reaches downstream motor ganglia in the thorax. Because the LGMD-DCMD spikes are 1:1, the DCMD acts as a faithful relay of the LGMD activity to motor centers. The DCMD axon is located peripherally in the dorso-medial segment of the nerve cord and has one of the largest diameters (15–17  $\mu\text{m}$ ; O'Shea et al. 1974), making it amenable to high signal-to-noise ratio extracellular recordings.

In the thorax, the DCMD axon forms a single branch within the first or prothoracic ganglion and three branches in the second (meso-) and third (meta-) thoracic ganglia, where it makes synapses with identified motor and interneurons implicated in the generation of jump and flight (Burrows & Rowell 1973, O'Shea et al. 1974, O'Shea & Williams 1974, Pearson et al. 1980, Simmons 1980, Pearson & Robertson 1981). Because of its selectivity to approaching objects and its postsynaptic targets, the DCMD neuron has long been thought to play an important role in triggering visually evoked escape behaviors. In the next section, we describe recent findings on the role played by the DCMD in triggering escape jumping.

## ROLE OF THE DCMD IN LOOMING-EVOKED ESCAPE BEHAVIORS

The DCMD neuron is thought to be involved in generating escape jumps in response to looming stimuli (Fotowat & Gabbiani 2007, Santer et al. 2008), as well as in-flight collision-avoidance behaviors (Santer et al. 2006). Here, we focus on looming-evoked jump escape behaviors for which electrophysiological data are available in freely behaving animals (Fotowat et al. 2011).

The locust jump is a ballistic movement, requiring about ten times more power than what can be provided by the extensor muscles of the hind legs (Bennet-Clark 1975). Locusts, therefore, prepare to jump by storing mechanical energy in the elastic elements of their hind legs. The jump motor program consists of three phases (**Figure 4a**) (Godden 1975, Heitler & Burrows 1977, Burrows 1995, Burrows & Morris 2001). First, the flexor tibiae motor neurons become active. After its full flexion, the tibia becomes locked into the femur through an engaging lump near the joint. Next, the extensor motor neurons become active as well, resulting in the isometric cocontraction of flexors and extensors and the distortion of spring-like elastic elements of the joints, which act as energy storage devices (Burrows & Morris 2001).



**Figure 4**

DCMD's involvement in the motor sequence leading to a jump. (a) In response to a looming stimulus (top,  $l/|v| = 40$  ms), flexor motor neurons start to fire (green arrow), causing the tibia to flex and align itself with the femur. Next, the fast extensor motor neuron starts to fire, initiating the cocontraction phase (red arrow). Finally, the flexors become inhibited, signaling the end of the cocontraction phase (blue arrow). This leads shortly thereafter to take-off (dashed blue vertical line). The corresponding three jump phases are indicated by three colored arrows at bottom and three dark yellow circled numerals. (b) (i–iv) Simplified diagram of the circuitry involved in jump escape behaviors in response to looming stimuli and the postulated relation between DCMD firing phases, the activation of the circuit generating the jump, and motor phases of the behavior. Triangles and the circle indicate excitatory and inhibitory synapses, respectively. See text for details. Thick and thin red lines indicate strong and weakly activated pathways, respectively, at a time point within the given time interval (dark yellow circled numeral). Colors on schematized DCMD firing rate profile correspond with arrows indicating motor phases in panel a. (i) The rising phase of the DCMD activity coincides with the initial flexor activity until the DCMD firing rate crosses a threshold (dashed horizontal line), after which the cocontraction starts. (ii) Following this threshold, the DCMD maximally excites the fast extensor tibiae (FETi) motor neuron during the cocontraction phase. (iii) Around the DCMD peak activity, contingent upon the presence of sufficient proprioceptive feedback input, the M interneuron becomes activated, contributing to the inhibition of flexor motor neurons. (iv) The decline in the DCMD firing rate contributes further to the silencing of flexors as well as the FETi motor neuron, resulting in the end of cocontraction and take-off. (c) Time of start of cocontraction (red), DCMD peak firing rate (gray) and take-off (blue) as a function of stimulus size to speed ratio (mean and standard deviation across multiple trials and animals). The inset illustrates representative delays between DCMD peak and cocontraction onset (red) and between peak and take-off (blue) in single trials. Positive delays correspond to events after the peak. Thus the time of peak firing always follows cocontraction onset and precedes take-off. Modified and adapted from Fotowat & Gabbiani (2007) and Fotowat et al. (2011).

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**FETi:** fast extensor tibiae (muscle and corresponding motor neuron)

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Finally, once the required level of energy storage is achieved, the flexor tibiae motor neurons become inhibited, the lock gets released, and the tibia extends, leading to take-off.

Many of the identified motor neurons and interneurons that contribute to the generation of this motor pattern receive excitatory input from the DCMD (**Figure 4b**) (Burrows 1996). Each DCMD makes an excitatory connection with the C (Cocking) interneurons, a bilaterally symmetric pair located in the second (meso-) thoracic ganglion (Pearson & Robertson 1981). The C interneurons in turn make excitatory connections with both the fast extensor of the tibia (FETi) and flexor motor neurons. They can evoke spikes in both, provided that the tibia is in a fully flexed position, and therefore contribute to the cocontraction phase of the jump. Each DCMD also directly excites the FETi motor neuron of both hind legs, which in turn makes excitatory connections with flexor motor neurons. This highly unusual connection between antagonistic motor neurons, found only at the level of the hind legs, is most likely active during cocontraction as well (Hoyle & Burrows 1973, Burrows et al. 1989). In the third thoracic ganglion, each DCMD innervates a pair of interneurons called M (Multimodal). These interneurons, which also receive proprioceptive feedback from the hind legs and make inhibitory connections with the flexor motor neurons, are thought to contribute to the release of cocontraction, allowing take-off (Pearson et al. 1980; Steeves & Pearson 1982; Gynther & Pearson 1986, 1989). Therefore, on the basis of these anatomical connections, the DCMD neuron could contribute to both triggering and release of cocontraction.

Tethered locusts respond to looming stimuli by flexing their hind legs, and this behavior was shown to coincide with the time when the DCMD firing activity is largest [ $>150$  spikes (spk)/s, Santer et al. 2008]. However, simultaneous recordings obtained from the DCMD and the FETi motor neuron in fixed locusts have shown that spiking in the DCMD is typically insufficient to activate the FETi (Burrows & Rowell 1973, Rogers et al. 2007), leaving

unsolved the role of the DCMD in triggering the cocontraction and take-off (Burrows 1996).

In freely behaving locusts, however, the firing rate of the DCMD neuron can reach much higher values ( $>250$  spk/s), and the cocontraction is triggered after the DCMD firing rate exceeds a threshold [**Figure 4b(ii)**] (Fotowat et al. 2011). The timing of such a threshold also varies linearly with  $1/|v|$  (Gabbiani et al. 2002), thus the cocontraction phase is triggered after the approaching object reaches a threshold angular size. It is important to note, however, that although a DCMD threshold firing rate appears necessary for triggering cocontraction, it is not sufficient (Fotowat et al. 2011). For example, cocontraction cannot start before the hind leg is fully flexed (Burrows & Pflüger 1988). After the onset of cocontraction, the FETi motor neuron spikes closely follow those of the DCMD (Fotowat et al. 2011) and thus the onset of cocontraction appears to act as a switch that promotes the DCMD input to a major source of excitation for this neuron.

The DCMD's characteristic peak in firing rate occurs after the onset of cocontraction and well before take-off (**Figure 4c**), rendering the DCMD maximally active during cocontraction. Furthermore, the timing of take-off can be predicted with high accuracy from the timing of the DCMD peak firing rate, suggesting that the postsynaptic targets of the DCMD control the time of take-off on the basis of the time of DCMD peak activity, most likely through at least two parallel pathways. First, the postsynaptic M interneuron, which has a high firing threshold (Pearson et al. 1980), is likely to be maximally excitable around the DCMD peak firing time. Thus, given concurrent proprioceptive feedback excitation that signals the level of stored energy, the M interneuron could eventually shut off the flexor motor neurons [**Figure 4b(iii)**] (Pearson et al. 1980, Gynther & Pearson 1989). Second, the end time of cocontraction will be influenced by the DCMD peak time through the subsequent reduction in DCMD activity, resulting in decreased excitation to the flexors and extensors [**Figure 4b(iv)**]. This complex sequence of

events illustrates how the elements of a local neuronal network may use different aspects of a sensory neuron's activity to generate various components of a motor behavior.

Because looming-evoked escapes in freely behaving locusts are probabilistic, they provide the opportunity to study the contribution of sensory and motor neuron activity to the final decision to escape. Recordings in freely behaving locusts have revealed that in trials where locusts do not jump, the cocontraction is still triggered, though significantly later. Additionally, in those trials, the number of DCMD spikes fired after cocontraction onset is significantly lower, whereas the timing of the DCMD peak firing rate remains unchanged. A corollary of these observations is that the occurrence of a jump can be predicted on a trial-by-trial basis from both sensory and motor aspects of the discharge patterns evoked by looming stimuli (Fotowat et al. 2011). It would be useful to identify the sources of sensory response variability that ultimately influence the behavioral outcome. One possible source of such variability is the modulation of the DCMD activity by identified octopaminergic neurons in the medulla, whose axons arborize in the optic lobe and respond to stimuli that increase locust arousal (Rowell 1971b, Bacon et al. 1995, Rind et al. 2008). Therefore, in an aroused locust, increased levels of octopamine could increase the excitability of the DCMD and, consequently, the excitatory drive to the downstream motor circuits.

Is the DCMD the sole source of looming information to the jump motor circuitry, or are there other parallel visual pathways that could generate escapes, as reported in other species (zebrafish: Liu & Fetcho 1999; fruit fly: Fotowat et al. 2009)? In fact, each locust nerve cord contains the axon of a neuron that carries to motor centers a nearly identical copy of the information provided by the DCMD. This neuron is called the descending ipsilateral movement detector (DIMD), and its axon runs in the nerve cord ipsilateral to the eye from which it receives input, i.e., opposite to that of the DCMD (Rowell 1971a, Burrows &

Rowell 1973). This redundancy allows a locust with one ablated nerve cord to still react and jump in response to stimuli presented to either eye (Santer et al. 2008, Fotowat et al. 2011). The DIMD has yet to be identified anatomically but is thought to have a large axon like the DCMD. Furthermore, its spikes are thought to summate with those of the DCMD at the level of the FETi neuron (Rowell 1971a, Burrows & Rowell 1973). The looming-evoked responses in the DCMD and DIMD are very similar, with indistinguishable peak time and amplitude (Fotowat et al. 2011). In addition to the DIMD, laser ablation of the DCMD has revealed other contralateral descending neurons that respond to looming; however, their peak activity occurs much later than that of the DCMD or DIMD. In the absence of these two neurons, locusts still flex their hind legs in preparation for cocontraction; however, they rarely take off, and when they do, it is after projected collision (Fotowat et al. 2011). These results suggest that the activity of the DCMD or DIMD is likely not necessary for the initial flexion stage [Figure 4*b(i)*] but plays a critical role in generating correctly timed jump take-offs.

In summary, studies in freely escaping locusts illustrate how different aspects of the activity of single sensory neurons, e.g., firing rate threshold, spike count, peak firing rate, or decreases in firing rate following a peak, could be used in parallel by downstream neural networks to trigger distinct stages of complex behaviors. Moreover, sensory response variability itself can contain ample information about the variability in behavior, as well as its final outcome, i.e., to jump or not.

## DISCUSSION AND FUTURE DIRECTIONS

Recent evidence increasingly indicates that sensory neurons tuned to looming stimuli share many physiological features across widely different animal species, including fruit flies, fish, frogs, locusts, and pigeons. These features include (*a*) specific tuning for approaching, as opposed to, e.g., translating, object motion;

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**DIMD:** descending ipsilateral movement detector

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(*b*) encoding of an angular threshold size in their peak firing rate; (*c*) the ability to segment effectively an approaching object from whole field optic flow, caused, e.g., by ego-motion; and (*d*) invariant responses to many aspects of looming stimuli, such as texture, shape, contrast, or approach angle. Elucidation of the underlying algorithms and of the biophysical implementation that gives rise to these features will bring us closer to understanding how collision-avoidance behaviors are generated and, more generally, will shed light on how the brain processes sensory information in a natural context, at the levels of both single neurons and neural circuits. This program is being pursued in the locust visual system by taking advantage of its identified neurons, the relatively compact neural circuitry involved, and the ability to carry out many types of electrophysiological experiments *in vivo*. Other species will undoubtedly offer complementary advantages to progress toward the same goal, for example, the use of genetic techniques in fruit flies or zebrafish (Pfeiffer et al. 2008, Scott 2009).

In locusts, the emerging picture suggests that distinct aspects of a single neuron's time-varying activity could be used by different elements of downstream networks during motor planning and execution. Moreover, proprioceptive feedback plays a role in shaping sensory-motor integration and the final behavioral outcome. Simultaneous monitoring of sensory input and proprioceptive feedback will thus be important in unraveling details about the process of sensory-motor integration.

On the basis of studies in fixed animals, the DCMD had long been thought incapable of driving visually evoked escape behaviors. Yet, in

freely behaving animals, the DCMD firing rate reaches significantly higher levels and can drive spiking in motor neurons such as the FETi. These results call for the study of sensory-motor integration in freely behaving animals (Fotowat et al. 2011, Maimon et al. 2010).

Finally, the role of neuromodulators in shaping the outcome of collision-avoidance behaviors remains largely open to investigation. Looming-sensitive neurons often show pronounced habituation, or fluctuations in overall responsiveness, usually attributed to neuromodulation. The fact that trial-by-trial variations in LGMD-DCMD activity are related to the final outcome of collision-avoidance behaviors indicates that neuromodulators are an integral part of the sensory-motor circuitry that mediates them. Mapping out the associated neural components and characterizing their impact would thus constitute an important step in understanding how sensory-motor integration contributes to decision making in the context of collision-avoidance behaviors.

Although there are striking similarities regarding the sensory processing of looming stimuli between animals such as locusts, fish, and pigeons, they possess quite distinct motor networks and muscular machinery for generating escape behaviors. Relatively little is known about how different motor networks use sensory activity for generating complex behaviors and whether common sensory-motor transformation rules are exploited in different species that possess similar sensory processing stages. Comparative studies are thus necessary to draw general conclusions about the biophysical implementations of these neural computations.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We gratefully acknowledge support for our work over the years from the AFRL, HSFP, NIMH, NSF, as well as the Sloan and Gillson Longenbaugh Foundations. We thank Mr. P.W. Jones, as well as Drs. N. Chen, N.J. Cowan, R.B. Dewell and R. Krahe for comments.

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## Errata

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