

# Studying sensorimotor integration in insects

Stephen J Huston and Vivek Jayaraman

Sensorimotor integration is a field rich in theory backed by a large body of psychophysical evidence. Relating the underlying neural circuitry to these theories has, however, been more challenging. With a wide array of complex behaviors coordinated by their small brains, insects provide powerful model systems to study key features of sensorimotor integration at a mechanistic level. Insect neural circuits perform both hard-wired and learned sensorimotor transformations. They modulate their neural processing based on both internal variables, such as the animal's behavioral state, and external ones, such as the time of day. Here we present some studies using insect model systems that have produced insights, at the level of individual neurons, about sensorimotor integration and the various ways in which it can be modified by context.

## Address

19700 Helix Drive, Janelia Farm Research Campus, Howard Hughes Medical Institute, Ashburn, VA 20147, United States

Corresponding author: Jayaraman, Vivek ([vivek@janelia.hhmi.org](mailto:vivek@janelia.hhmi.org))

Current Opinion in Neurobiology 2011, 21:527–534

This review comes from a themed issue on  
Sensory and Motor Systems  
Edited by Sascha du Lac and Rachel Wilson

Available online 24th June 2011

0959-4388/\$ – see front matter

© 2011 Elsevier Ltd. All rights reserved.

DOI 10.1016/j.conb.2011.05.030

## Introduction

Going by numbers, insects are the most successful metazoans on the planet [1]. A large part of their success is derived from their ability to perform sophisticated sensorimotor tasks despite their comparatively limited neural hardware. For example, specialized sensorimotor processing allows dragonflies to hunt prey in visually cluttered landscapes [2], and ants to mount foraging expeditions and return to their nests in barren deserts [3]. Importantly for experimenters, these robust and complex behaviors are enabled by comparatively tractable neural circuits with individually identifiable and, often, physiologically accessible neurons. Such features make insects attractive model systems for studying the neural basis of sensorimotor integration.

To produce sensory-guided behavior the nervous system must extract behaviorally relevant features of the input, then transform and integrate this information to generate a

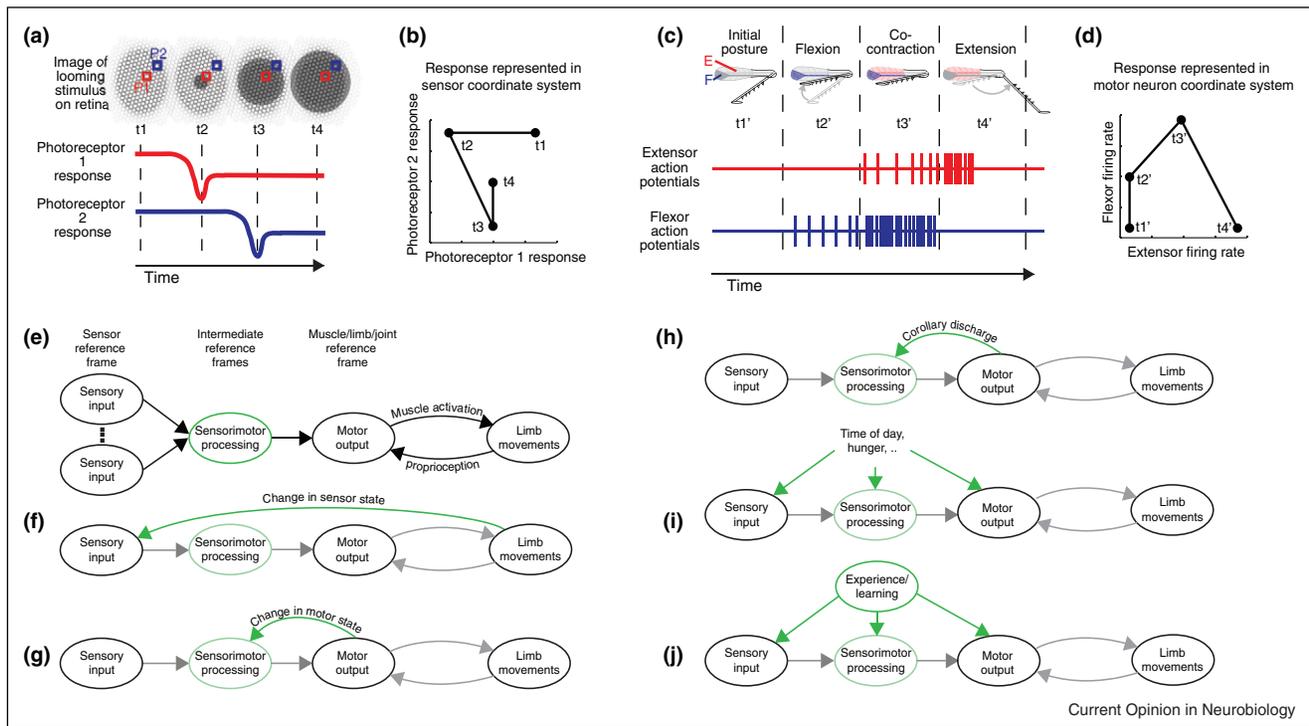
behaviorally useful output. Such sensorimotor integration occurs, for example, when a looming visual stimulus triggers a locust to jump. The locust's brain must detect the visual expansion that occurs in coordinates of the photoreceptor array, then transform this information into an appropriate motor output that is generated in the coordinates of the leg musculature (Figure 1a–d) [4].

Sensorimotor integration is computationally challenging because the transformations involved need to be flexible. The same sensory input may be converted into different patterns of muscle output depending on contextual factors, prominent examples of which are:

- Posture (Figure 1e). For example, a grooming locust will target its leg to the site of tactile stimulation on its wing using different limb trajectories depending on proprioceptive information about the leg's initial position [5]. In addition, the relative positions of the sensory and motor reference frames can change. For example, when making visually targeted leg movements locusts must transform information between their eyes and leg muscles even though the two are constantly moving relative to each other [6].
- Timing. Active sampling strategies such as locust peering (reviewed in Ref. [7]) often require sensory inputs to be processed differently depending on the motor context or timing (Figure 1f).
- Behavioral state (Figure 1g; later section). For example, whether the animal is standing still or engaged in active locomotion.
- Self-generated versus external sensory stimuli. Whether the sensory input arises from an external source or the insect's own actions (Figure 1h; later section).
- Internal state. For example, hunger and external variables such as the time of day (Figure 1i; later section).
- Experience. For example, whether a particular odor triggers a proboscis extension motor sequence in a honeybee can depend on the odor's prior association with a sucrose reward [8] (Figure 1j).

To understand the neural representations, transformations, and circuit dynamics underlying such sensorimotor phenomena requires, in our opinion, a physiological strategy motivated by behavior. In such an approach, the circuit involved is assumed to extract features relevant to the behavior, and this guides the choice of stimuli used to probe the system. Here we highlight some examples of insect neural circuits that implement the different features of sensorimotor processing discussed above, with a focus on computations of behavioral relevance (see Table 1 for examples of insect behaviors

Figure 1



Overview of sensorimotor processing. Example sensorimotor behavior: locust escape response. **(a)** As the image of a looming stimulus expands across a locust's retina, it sequentially modulates the activity of each photoreceptor (two schematized examples shown). **(b)** The resulting pattern of photoreceptor activity over time (t1–t4) can be projected into a multidimensional coordinate system, with each axis representing the activity of a single photoreceptor (only two axes shown for clarity). **(c)** In response to the looming stimulus, the locust initiates the jump motor pattern: an initial flexion of the tibiae, followed by co-contraction of both flexor and extensor muscles, followed by a rapid extension of its legs [54]. The schematized activity of flexor and extensor motor neurons is shown. **(d)** This motor output can be represented in a motor coordinate system where the position along each axis is determined by the activity of a different motor neuron or muscle (only two motor neurons shown for clarity). The corresponding change in motor neuron action potential rates over time (t1'–t4') results in a particular trajectory through the motor coordinate system (only two axes shown for clarity). To correctly generate the escape jump in response to a looming stimulus, the locust's nervous system must correctly transform the incoming visual inputs from a trajectory in sensory coordinates to the correct trajectory in the motor coordinate system [4\*]. **(e)–(j)** Some recognizable motifs in sensorimotor integration (see text for instantiations in insects). **(e)** A simple sensorimotor transformation can be represented as being primarily feedforward, taking inputs from multiple sensory organs and converting them into a posture-dependent motor output. However, a more accurate model of the process would contain multiple feedback loops and modulation at every stage. Prominent examples of this are shown in the following panels. **(f)** During active sensation the animal probes the environment by either emitting a signal that can be detected by its own sensors, or by moving the sensor in a search pattern. **(g)** The properties of the sensory system are often modulated according to the current motor state to fine-tune them to the current behavioral requirements. **(h)** If the animal's motor output has predictable sensory consequences, the nervous system may use a corollary discharge to subtract the predictable components from the incoming sensory stream. **(i)** The nervous system must implement flexible sensorimotor transformations to take account of contextual variables such as time of day or hunger. **(j)** The mapping from sensory input to motor output may display experience-dependent plasticity.

suitable for functional investigations of sensorimotor integration).

### Neural basis of a direct visual-motor transformation: fly gaze stabilization

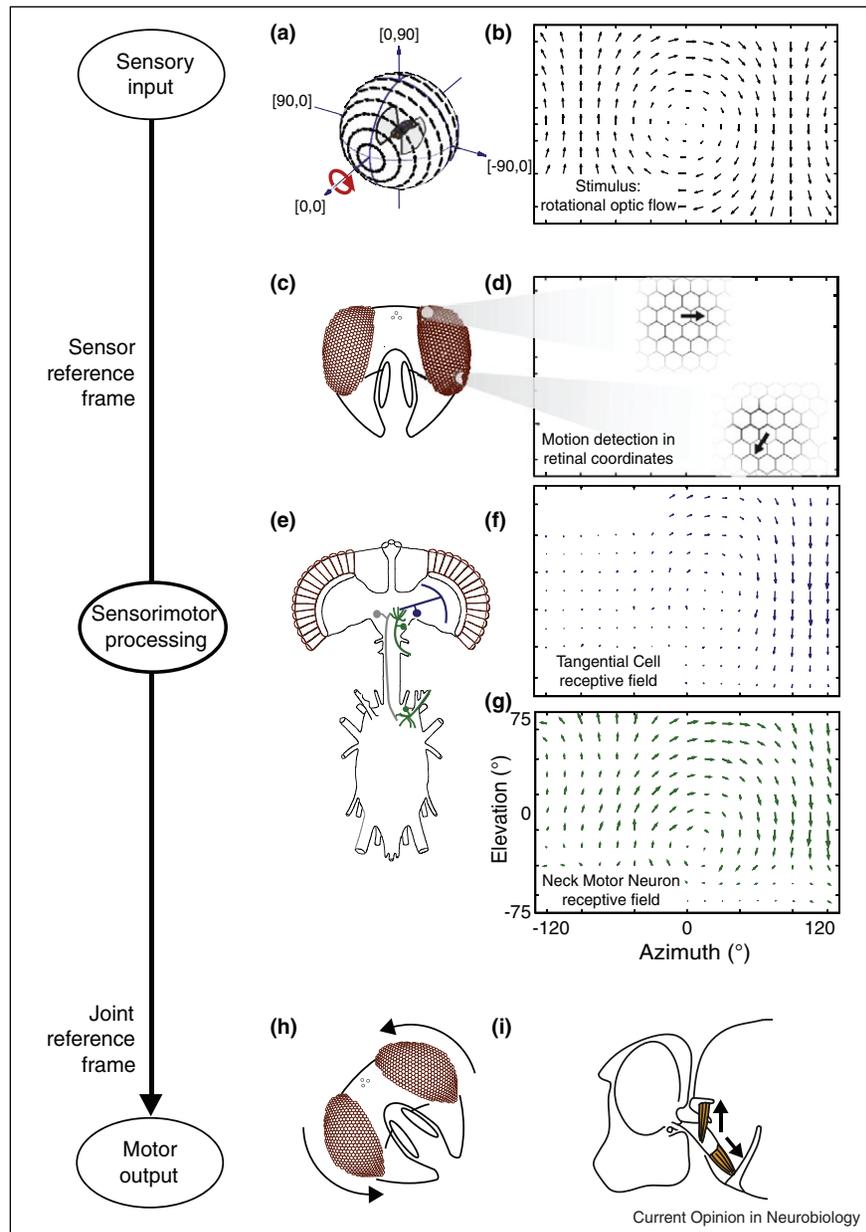
During flight, a fly's gaze-stabilization system visually detects self-rotations and generates compensatory head movements to maintain a level gaze [12]. As visual information passes from sensory input to motor output in this system, it is filtered at the periphery, integrated into behaviorally relevant signals, and transformed into motor coordinates. The process starts at the eye, where visual motion information is detected locally in coordinates of the hexagonal eye-lattice (Figure 2c and d). At a

later level of visual processing, 'vertical system' (VS) and 'horizontal system' (HS) lobula plate tangential cells (LPTCs) (Figure 2e) integrate these local inputs across their wide dendrites, with each cell's dendrites combining inputs from across a different strip of visual space. LPTC axons then connect laterally with each other via gap junctions. Both electrophysiology [27] and imaging [28\*] studies have shown that these lateral connections serve to widen each cell's receptive field making the LPTC responses, and those of downstream neurons [29], less susceptible to local contrast fluctuations and more representative of the global visual motion pattern. Detailed measurements of the resulting receptive fields show that, across one visual hemisphere, they are

**Table 1****Examples of insect sensorimotor integration.**

Behavioral goal	Sensory input	Motor output	Modulation and plasticity	Example model systems
Grooming	Mechanosensory, for example, tactile stimulation of wing. Chemosensory, for example, localized noxious stimulus.	Targeted leg scratching movements.	Leg trajectory compensates for leg initial position [5]. Leg movements adapt to changes in proprioceptive feedback [9].	Locust [5].
Gap crossing/ Obstacle avoidance	Visual, for example, terrestrial edges. Mechanosensory, for example, antennal contact.	Reaching leg movements. Changes in step size and posture.		Locust [6], fly and cockroach [10,11].
Course and gaze stabilization	Visual: optic flow.	Change in direction of locomotion and gaze.	Behavioral gain depends on state: flight, walking or standing [12].	Fly, bee, snout beetle
Feeding	Gustatory, for example, sugar water. Olfactory, for example, food odor.	Extension of proboscis.	Modulated by: Hunger state. Olfactory conditioning [8].	Bee [8], fly [13].
Sound localization	Auditory, for example, species specific song.	Change in direction of locomotion.		Parasitoid fly ( <i>Ormia</i> ) [14], cricket [15].
Chasing	Visual: small objects, for example, prey or conspecifics.	Change in direction of locomotion.		Housefly, hoverfly [16], dragonfly [2].
Object fixation/ discrimination	Visual patterns.	Change in direction of locomotion.	Behavioral choices modulated by prior experience [17-19].	Bee [17], fly [18,19].
Olfactory localization/ Discrimination	Olfactory, for example, attractive odor.	Change in direction of locomotion.	Modulated by visual surround [20]. Can be modified by prior experience [21].	Moth, fly [22].
Escape	Visual: looming. Mechanosensory: wind cues.	Jump, flight initiation or avoidance maneuvers.	Preparatory leg movements for escape jump depends on initial posture [23]. Behavior can habituate.	Locust [4*], fly, cockroach, cricket.
Navigation	Skylight; polarization pattern.	Change in direction of locomotion.		Cricket, locust [24*], butterfly [25], honeybee [26].

Figure 2



How visual information is sequentially transformed as it passes through the fly gaze-stabilization pathway. **(a)** Flies rotate during flight, resulting in the image of the world counter-rotating across the retina. **(b)** The resulting panoramic pattern of visual motion is termed 'rotational optic flow'. The optic flow resulting from a roll rotation is shown in (b) in a cylindrical projection where  $[0, 0]$  [azimuth, elevation] is directly in front of the fly. The direction and magnitude of local image velocity is represented by the direction and magnitude of the arrows. **(c)** and **(d)** Visual motion is initially detected in the local coordinates of the fly's hexagonal eye-lattice. **(e)** Simplified diagram of the neurons involved in the gaze-stabilization pathway. The tangential cells (blue) integrate inputs from the early visual system (eye shown in dark red) and synapse both directly and, via descending neurons (gray), indirectly onto neck motor neurons [green, 55]. Neck motor neurons control the fly's head movements. **(f)** The receptive field of one tangential cell (VS7). The direction and length of the arrows indicate the cell's preferred motion direction and sensitivity at different points within visual space (axes are the same as for b). Tangential cells integrate local motion cues from across an entire eye, resulting in a receptive field that is similar to one half of the optic flow stimulus (compare to right hand side of b). **(g)** The receptive field of a neck motor neuron. Neck motor neurons appear to integrate tangential cell inputs from both sides of the brain to generate binocular receptive fields matched to the entire optic flow stimulus generated by a particular rotation of the fly (compare to b). **(h)** and **(i)** The final motor output is generated in coordinates defined by the pulling planes of the muscles. Neck motor neurons drive neck muscles (**(i)** side-view of part of the fly neck musculature) that generate head movements to compensate for the initial imposed rotation and keep the fly's gaze level despite the body rotating (**(h)**). Panels b, d, f and g are plotted in the same axes. Figure adapted with permission from [12,31\*,55,56].

matched to the complex pattern of optic flow that occurs during particular rotations of the fly ([30], compare right hand side of Figure 2f to b). LPTCs, however, still respond to both rotation and translation of the fly, whereas the gaze-stabilization system is primarily tuned for rotations [12]. This ambiguity is partially resolved by neck motor neurons (NMNs) [31<sup>•</sup>] and some descending neurons (DNs) [32] which integrate LPTC inputs from both sides of the brain, resulting in binocular receptive fields (Figure 2g) that are more specifically tuned to rotations than translations ([31<sup>•</sup>], compare Figure 2g to b). The NMNs then drive the neck muscles responsible for head movements. Thus, the system takes inputs in retinal coordinates and, through successive layers of neural integration, produces an appropriate motor output in the coordinates of the motor system.

### Sensorimotor integration as a dynamic, actively modulated, adaptive process

The above example describes visual-to-motor integration as a largely feed-forward process, with sensory inputs being transformed by successive banks of spatial and temporal filters. There are, in reality, few static filter banks in the nervous system: neural responses at almost every stage of a sensorimotor pathway are modified at short and long timescales by biophysical and synaptic processes, recurrent and feedback connections, and learning, as well as many other internal and external variables. In the sections to follow, we briefly review a sampling of physiological investigations into these different aspects of sensorimotor integration.

#### Behavioral state-dependence of visual-motor transformation in flies

The motion vision circuitry described above is important for course stabilization during locomotion. However it is energetically expensive to maintain a circuit in a state of high gain all the time [33]. Accordingly, LPTC [34,35<sup>•</sup>,36<sup>•</sup>] (Figure 3a) and NMN [37] responses are amplified when flies walk or fly, but not when they stand still. In addition, HS LPTCs change their tuning depending on locomotor state, increasing their response gain to higher image speeds during walking [36<sup>•</sup>] (Figure 3b), a possible mechanism to process these faster speeds only when they are behaviorally relevant. Octopamine, a neuromodulator released during flight, has been shown to modulate photoreceptors and LPTCs [38], suggesting a potential mechanism for the observed phenomenon.

It should be noted that both the LPTCs and DNns respond to noncompound eye inputs as well [39–41]. The NMNs receive massive multisensory convergence [42] including antennal [37] and haltere inputs that gate and temporally structure the visual responses [43]. Thus, some part of the behavior-dependent gain increases observed in LPTCs and NMNs could also arise from other sensory inputs to the motion-vision pathway.

#### Corollary discharge in the cricket auditory system

The brain must distinguish sensory input that is generated externally from that generated by the insect's own actions [44]. For example, crickets sing to ward off rivals and attract mates, and, in turn, respond to the singing of conspecifics. However, it would not be advantageous for a cricket to respond to its own song and potentially desensitize its auditory neurons [45]. Its nervous system avoids this by using a corollary discharge that selectively suppresses sensory responses during its own chirping (Figure 3c–e) [46]. The thoracic central pattern generator that drives motor activity underlying wing movement and song production sends a copy of the motor commands to a corollary discharge interneuron (CDI). The CDI then inhibits the interneurons that receive auditory input, thereby reducing the sensory system's response to the cricket's own song. This strategy may be similar to that of forward models used in control theory, in which a future state is predicted from the integration of the current state and an external control signal [47]. How prevalent such a strategy is in the insect brain remains to be seen.

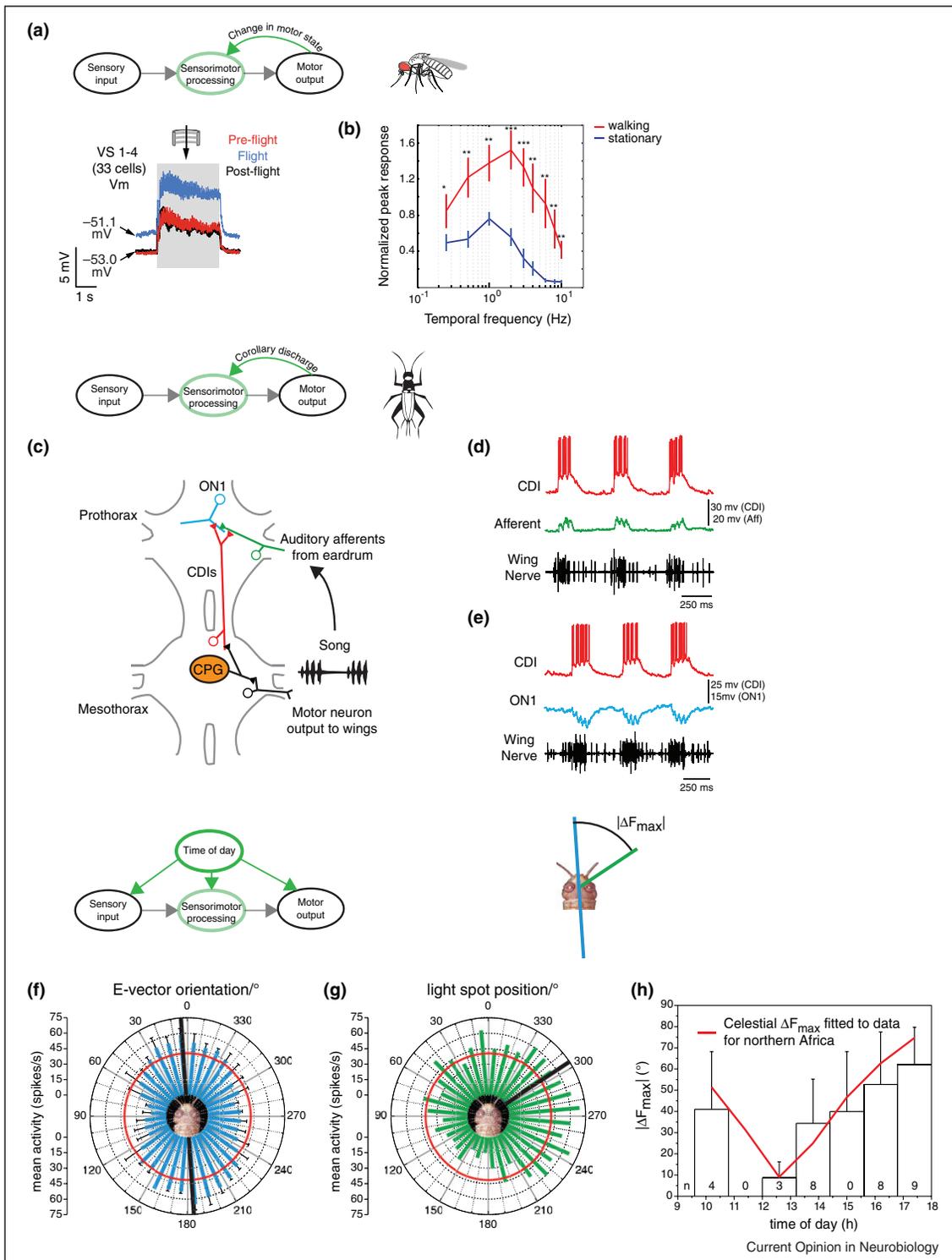
#### Circadian modulation of sensorimotor maps

Several insects, such as locusts and monarch butterflies, use skylight cues to maintain a fixed heading during long migratory flights. The two main cues, sun position and sky polarization pattern, are represented in well-organized maps in higher brain areas, such as the central complex [24<sup>•</sup>], suggesting their role in heading maintenance. However, both cues change over the course of a day, limiting the value of a static neural map to maintain heading. The brain appears to employ an elegant solution to this problem, using circadian information from its clock centers to adjust the tuning of the relevant input neurons, thereby shifting the map to compensate for the changing position of the sun in the sky during the day [48,49<sup>•</sup>] (Figure 3f–h).

#### Opportunities in insect sensorimotor integration

Insects provide a diverse repertoire of innate and learned behaviors that can be used to study sensorimotor processing, from the multisensory integration required in fly courtship [50] to the plasticity required in honeybee associative learning [8]. What makes working with insects particularly advantageous is that these behaviors are accomplished with a compact nervous system, whose neurons can be uniquely identified and examined across individuals. These features make it possible to explore circuit mechanisms that produce interesting sensorimotor phenomena. In the specific case of *Drosophila melanogaster*, an additional advantage for experimenters is the array of genetic tools available to label, target, and manipulate specific subsets of its neurons [51]. Such tools are making it increasingly tractable to identify and track information flow across a sensorimotor pathway [52<sup>•</sup>]. The use of RNAi [53] and viral approaches may make such strategies feasible in other insects as well, further boosting the

Figure 3



Behavioral relevance of feedback in sensorimotor integration. **(a)** Whole-cell patch clamp recording of a vertical system (VS) neuron in the *Drosophila* optic lobe shows that membrane potential and response to motion in the preferred direction are increased when the insect is flying. (a) Adapted with permission from [35\*]. **(b)** Temporal frequency (motion speed) tuning curves under different behavioral conditions derived using two-photon GCaMP3.0 calcium imaging of horizontal system (HS) LPTC dendrites. Tuning curve shifts toward faster speeds during walking, a behavioral regime when processing such speeds might be more relevant for the fly. (b) Adapted from [36\*]. **(c)** Paired intracellular recordings from one of the bilaterally paired corollary discharge interneurons (CDIs) and an auditory afferent **(d)** or an auditory interneuron ON1 **(e)** from the thoracic ganglia of cricket *Gryllus bimaculatus* during fictive singing. Central pattern generators (CPGs) that drive wing song motor activity also drive CDIs that inhibit the cricket auditory

potential of using insect systems to understand the many facets of sensorimotor integration.

## Acknowledgments

The authors would like to thank Gwyneth Card for useful discussions and comments on the manuscript, and Michael Reiser, John Tuthill and Eugenia Chiappe for their useful feedback on the manuscript. We also thank Stijn Cassenaer for discussions on the use of viral approaches in insects.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
  - of outstanding interest
1. May RM: **How many species are there on earth.** *Science* 1988, **241**:1441-1449.
  2. Olberg RM, Seaman RC, Coats MI, Henry AF: **Eye movements and target fixation during dragonfly prey-interception flights.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2007, **193**:685-693.
  3. Wehner R: **Desert ant navigation: how miniature brains solve complex tasks.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2003, **189**:579-588.
  4. Fotowat H, Harrison RR, Gabbiani F: **Multiplexing of motor information in the discharge of a collision detecting neuron during escape behaviors.** *Neuron* 2011, **69**:147-158.  
A novel telemetry system permits recordings from a collision detecting neuron in freely moving locusts, revealing components of the neural response that predict parameters of the jumping escape behavior.
  5. Durr V, Matheson T: **Graded limb targeting in an insect is caused by the shift of a single movement pattern.** *J Neurophysiol* 2003, **90**:1754-1765.
  6. Niven JE, Buckingham CJ, Lumley S, Cuttle MF, Laughlin SB: **Visual targeting of forelimbs in ladder-walking locusts.** *Curr Biol* 2010, **20**:86-91.
  7. Srinivasan MV, Poteser M, Kral K: **Motion detection in insect orientation and navigation.** *Vision Res* 1999, **39**:2749-2766.
  8. Giurfa M: **Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2007, **193**:801-824.
  9. Page KL, Matheson T: **Functional recovery of aimed scratching movements after a graded proprioceptive manipulation.** *J Neurosci Off J Soc Neurosci* 2009, **29**:3897-3907.
  10. Triphan T, Poeck B, Neuser K, Strauss R: **Visual targeting of motor actions in climbing *Drosophila*.** *Curr Biol* 2010, **20**:663-668.
  11. Harley CM, English BA, Ritzmann RE: **Characterization of obstacle negotiation behaviors in the cockroach, *Blaberus discoidalis*.** *J Exp Biol* 2009, **212**:1463-1476.
  12. Hengstenberg B: **Gaze control in the blowfly *Calliphora*: a multisensory, two-stage integration process.** *Semin Neurosci* 1991, **3**:19-29.
  13. Chabaud MA, Devaud JM, Pham-Delegue MH, Preat T, Kaiser L: **Olfactory conditioning of proboscis activity in *Drosophila melanogaster*.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2006, **192**:1335-1348.
  14. Mason AC, Oshinsky ML, Hoy RR: **Hyperacute directional hearing in a microscale auditory system.** *Nature* 2001, **410**:686-690.
  15. Hedwig B, Poulet JF: **Complex auditory behaviour emerges from simple reactive steering.** *Nature* 2004, **430**:781-785.
  16. Nordstrom K, O'Carroll DC: **Feature detection and the hypercomplex property in insects.** *Trends Neurosci* 2009, **32**:383-391.
  17. Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV: **The concepts of 'sameness' and 'difference' in an insect.** *Nature* 2001, **410**:930-933.
  18. Liu G, Seiler H, Wen A, Zars T, Ito K, Wolf R, Heisenberg M, Liu L: **Distinct memory traces for two visual features in the *Drosophila* brain.** *Nature* 2006, **439**:551-556.
  19. Neuser K, Triphan T, Mronz M, Poeck B, Strauss R: **Analysis of a spatial orientation memory in *Drosophila*.** *Nature* 2008, **453**:1244-1247.
  20. Frye MA, Tarsitano M, Dickinson MH: **Odor localization requires visual feedback during free flight in *Drosophila melanogaster*.** *J Exp Biol* 2003, **206**:843-855.
  21. Claridge-Chang A, Roorda RD, Vrontou E, Sjulson L, Li H, Hirsh J, Miesenböck G: **Writing memories with light-addressable reinforcement circuitry.** *Cell* 2009, **139**:405-415.
  22. Carde RT, Willis MA: **Navigational strategies used by insects to find distant, wind-borne sources of odor.** *J Chem Ecol* 2008, **34**:854-866.
  23. Card G, Dickinson MH: **Visually mediated motor planning in the escape response of *Drosophila*.** *Curr Biol: CB* 2008, **18**:1300-1307.
  24. Homberg U, Heinze S, Pfeiffer K, Kinoshita M, el Jundi B: **Central neural coding of sky polarization in insects.** *Philos Trans R Soc Lond B Biol Sci* 2011, **366**:680-687.  
The authors review a classic series of locust papers from the Homberg lab, as well as work from other insects and labs, showing representation and transformation of polarized light e-vector information in the insect brain.
  25. Reppert SM, Gegear RJ, Merlin C: **Navigational mechanisms of migrating monarch butterflies.** *Trends Neurosci* 2010, **33**:399-406.
  26. Kraft P, Evangelista C, Dacke M, Labhart T, Srinivasan MV: **Honeybee navigation: following routes using polarized-light cues.** *Philos Trans R Soc Lond B Biol Sci* 2011, **366**:703-708.
  27. Farrow K, Borst A, Haag J: **Sharing receptive fields with your neighbors: tuning the vertical system cells to wide field motion.** *J Neurosci Off J Soc Neurosci* 2005, **25**:3985-3993.
  28. Elyada YM, Haag J, Borst A: **Different receptive fields in axons and dendrites underlie robust coding in motion-sensitive neurons.** *Nat Neurosci* 2009, **12**:327-332.  
The authors use a combination of imaging, electrophysiology, and modeling to show that gap junction coupling of neighboring lobula plate tangential cell axons smoothes fluctuating visual signals without disrupting computations occurring in their electrically compartmentalized dendrites.

**(Figure 3 Legend Continued)** system during singing. Spikes in CDIs produce primary afferent depolarizations (PADs) in auditory afferents (d), and inhibitory postsynaptic potentials (IPSPs) in ON1 (e) after a constant delay, thus preventing desensitization of the auditory pathway during the cricket's own song. Adapted with permission from [57,58]. **(f)** Spiking responses of a polarization-sensitive anterior optic tubercle neuron (TuTu1) of the North African locust brain to different orientations of polarized blue light (blue bars in **(f)**) in the zenith, and different azimuthal positions of a green light spot that mimics the sun (green bars in **(g)**). Red circle represents spontaneous activity of the neuron. Black bars represent mean tuning preference angles. The absolute angular difference between the angles ( $\Delta\phi_{\max}$ ) is plotted in **(h)**. The locust could use this information to perform compass navigation. However, the angular separation between the solar azimuth and e-vector orientation in the sky, that is, the celestial  $\Delta\phi_{\max}$ , depends on solar elevation, which changes during the day in a manner dependent on geographical coordinates. The TuTu1  $\Delta\phi_{\max}$  is, in fact, appropriately modulated, compensating for diurnal changes in the sun's elevation and sky polarization pattern (red line in **(h)** shows fit to data for coordinates of northern Africa). This can allow the locust to maintain a constant heading during long-range navigation. Adapted with permission from [24\*].

29. Wertz A, Gaub B, Plett J, Haag J, Borst A: **Robust coding of ego-motion in descending neurons of the fly.** *J Neurosci* 2009, **29**:14993-15000.
30. Krapp HG, Hengstenberg R: **Estimation of self-motion by optic flow processing in single visual interneurons.** *Nature* 1996, **384**:463-466.
31. Huston SJ, Krapp HG: **Visuomotor transformation in the fly • gaze stabilization system.** *PLoS Biol* 2008, **6**:e173.  
Electrophysiology recordings from motor neurons reveal how they combine the outputs of well-characterized visual neurons to generate a robust behavioral output.
32. Wertz A, Borst A, Haag J: **Nonlinear integration of binocular optic flow by DNOVS2, a descending neuron of the fly.** *J Neurosci* 2008, **28**:3131-3140.
33. Niven JE, Laughlin SB: **Energy limitation as a selective pressure on the evolution of sensory systems.** *J Exp Biol* 2008, **211**:1792-1804.
34. Rosner R, Egelhaaf M, Warzecha AK: **Behavioural state affects motion-sensitive neurones in the fly visual system.** *J Exp Biol* 2010, **213**:331-338.
35. Maimon G, Straw AD, Dickinson MH: **Active flight increases the gain of visual motion processing in *Drosophila*.** *Nat Neurosci* 2010, **13**:393-399.  
The authors use whole-cell patch clamp technique in tethered flying *Drosophila* to show that motion-sensitive VS neurons in the optic lobe increase their sensitivity and gain during flight.
36. Chiappe ME, Seelig JD, Reiser MB, Jayaraman V: **Walking • modulates speed sensitivity in *Drosophila* motion vision.** *Curr Biol* 2010, **20**:1470-1475.  
Two-photon calcium imaging is used in tethered *Drosophila* behaving on a ball to show that HS neurons in the early motion-vision pathway increase their sensitivity and tuning to faster image motion during walking.
37. Haag J, Wertz A, Borst A: **Central gating of fly optomotor response.** *Proc Natl Acad Sci U S A* 2010, **107**:20104-20109.
38. Longden KD, Krapp HG: **Octopaminergic modulation of temporal frequency coding in an identified optic flowprocessing interneuron.** *Front Syst Neurosci* 2010, **4**:153.
39. Parsons MM, Krapp HG, Laughlin SB: **Sensor fusion in identified visual interneurons.** *Curr Biol: CB* 2010, **20**:624-628.
40. Haag J, Wertz A, Borst A: **Integration of lobula plate output signals by DNOVS1, an identified premotor descending neuron.** *J Neurosci Off J Soc Neurosci* 2007, **27**:1992-2000.
41. Gronenberg W, Strausfeld NJ: **Descending neurons supplying the neck and flight motor of Diptera: physiological and anatomical characteristics.** *J Comp Neurol* 1990, **302**:973-991.
42. Strausfeld NJ, Seyan HS: **Convergence of visual, haltere, and prosternal inputs at neck motor neurons of *Calliphora-Erythrocephala*.** *Cell Tissue Res* 1985, **240**:601-615.
43. Huston SJ, Krapp HG: **Nonlinear integration of visual and haltere inputs in fly neck motor neurons.** *J Neurosci* 2009, **29**:13097-13105.
44. Vonholst E, Mittelstaedt H: **Das Reafferenzprinzip – (Wechselwirkungen Zwischen Zentralnervensystem Und Peripherie).** *Naturwissenschaften* 1950, **37**:464-476.
45. Poulet JF, Hedwig B: **A corollary discharge mechanism modulates central auditory processing in singing crickets.** *J Neurophysiol* 2003, **89**:1528-1540.
46. Poulet JF, Hedwig B: **The cellular basis of a corollary discharge.** *Science* 2006, **311**:518-522.
47. Webb B: **Neural mechanisms for prediction: do insects have forward models?** *Trends Neurosci* 2004, **27**:278-282.
48. Pfeiffer K, Homberg U: **Coding of azimuthal directions via time-compensated combination of celestial compass cues.** *Curr Biol* 2007, **17**:960-965.
49. Heinze S, Reppert SM: **Sun compass integration of skylight • cues in migratory monarch butterflies.** *Neuron* 2011, **69**:345-358.  
The authors find potential neural substrates for the Monarch butterfly's ability to maintain heading during long migratory flights. Paper characterizes directionally tuned, and time-of-day compensated polarized and unpolarized light responses in central complex areas of the Monarch butterfly similar to those previously reported in locust (see Homberg et al. [24]).
50. Griffith LC, Ejima A: **Multimodal sensory integration of courtship stimulating cues in *Drosophila melanogaster*.** *Ann N Y Acad Sci* 2009, **1170**:394-398.
51. Simpson JH: **Mapping and manipulating neural circuits in the fly brain.** *Adv Genet* 2009, **65**:79-143.
52. Ruta V, Datta SR, Vasconcelos ML, Freeland J, Looger LL, Axel R: **A dimorphic pheromone circuit in *Drosophila* from sensory input to descending output.** *Nature* 2010, **468**:686-690.  
Optical, electrophysiological, and genetic techniques are used to track information flow across three synapses from olfactory sensory neurons to descending neurons in a pheromone-processing pathway guiding innate sexual behavior in *Drosophila*.
53. Belles X: **Beyond *Drosophila*: RNAi in vivo and functional genomics in insects.** *Annu Rev Entomol* 2010, **55**:111-128.
54. Burrows M: *Neurobiology of an Insect Brain.* Oxford: Oxford Univ. Press; 1996.
55. Strausfeld NJ, Seyan HS, Milde JJ: **The neck motor system of the fly *Calliphora-Erythrocephala*. 1. Muscles and motor neurons.** *J Comp Physiol A Sens Neural Behav Physiol* 1987, **160**:205-224.
56. Krapp HG: **Repräsentation von Eigenbewegungen der Schmeißfliege *Calliphora erythrocephala* in VS-Neuronen des dritten visuellen Neuropils.** In *Fakultät für Biologie.* Edited by Tübingen. University of Tübingen; 1995.
57. Crapse TB, Sommer MA: **Corollary discharge across the animal kingdom.** *Nat Rev Neurosci* 2008, **9**:587-600.
58. Poulet JF, Hedwig B: **New insights into corollary discharges mediated by identified neural pathways.** *Trends Neurosci* 2007, **30**:14-21.