# What Computer Vision Can Learn from Insect Vision

Luat T. Vuong, Doekele G. Stavenga and Geoffrey L. Barrows

The superb vision of insects biospeculatively combining optical preprocessing and small brains offers an intriguing example for the development of lightweight visual systems for unmanned aircraft systems and other applications.





#### Insect eyes showing multiscale, meso-ordered optics

Left: A green long-legged fly (top) and its characteristic facet pattern with alternating rows of corneal interference reflectors (bottom). Center: The Mourning Cloak, a diurnal butterfly (top) and the polycrystalline domains of corneal nanostructures on one of its facet lenses (bottom). Right: A *Hemianax papuensis* dragonfly (top) with fractal nanostructures (bottom) on its wings. D.G. Stavenga et al. J. Comp. Physiol. A **203**, 23 (2017) / K. Lee et al. Sci. Rep. **6**, 28342 (2016) / E.P. Ivanova et al. PLOS One **8**, e67893 (2013); CC-BY 4.0

here is an increasing demand for robust, rapid-response computer vision systems. But perceptions of the natural world can be overwhelming in their complexity. Given that the computational costs of machine learning grow faster than the size of computed data, how can we scale machine learning for large volumes of data—including patterned or delayed information embedded as "noise"?

Clearly, as human beings, evolution has provided us with the ability to efficiently navigate an ever-changing world, interpret our experience and make decisions—an astonishing capability, given the immense volumes of data that we process, its moderate likelihood of being distorted, its fickle temporal availability and its variable information content. Flies and other insects, facing their own version of this problem, have evolved optical and neural mechanisms that rapidly and efficiently filter visual information to find what is important amid variable environmental conditions. In thinking about the data-processing demands of machine vision, we can probably learn a lot from insects.

In this feature article, we look at some of the ways insect visual systems have solved the information problem—and how those solutions could inform computer vision architectures. After summarizing some essential aspects of insect vision and their intricate optical and neural components, we propose an insect-inspired design framework that involves optical encoding, sparse sampling with spatial compression, and shallow hardware postprocessing. Such a framework, we believe, can produce machine vision systems that can reliably extract higher-level signals in the face of noise—and can do so with lower computational costs than systems based on deep learning.

#### From bio-inspiration to "biospeculation"

Fast-flying insects such as flies offer a particularly illuminating place to start. As anyone who has attempted to swat one can attest, flies have record-speed reflexes, as measured by their light-startle response. They physically react to a flash within milliseconds, faster than a typical camera frame rate. A speedy fly can travel about 10 m/s, covering a thousand times its body length in only a second—the equivalent of Superman flying at 10 times the speed of sound. The fly manages a range of impressive, high-speed maneuvers in response to visual stimuli—and the mechanisms it has evolved for doing so may well offer a key for robust high-speed analyses in optical image processing and future camera designs.

Moths offer another inspiring case. These insects can fly and find their way in cluttered environments at extremely low light levels and see with sensitive color vision. Their special eye structures and visual capacities may well provide an example for low-light camera systems.

# Flies and other insects have evolved optical and neural mechanisms that rapidly and efficiently filter visual information to find what is important amid variable environmental conditions.

These insect examples for imaging technology, however, raise other questions. How can computer vision systems actually achieve the robust, high-speed signal processing of flying insects? How do insects find each other in noisy environments? How do they efficiently sample data with so few receptors and quickly process the information with their small brains?

Extensive studies on insects' visual sense suggest many things that would be desirable to reverse-engineer. Today's high-field-of-view optics are often heavy or bulky; lidar scanning systems have a limited angular acuity; computer vision approaches can be complex and energy intensive. Most unmanned aircraft systems (UAS) currently offload computing to ground-based computers or use GPS or other networked, distributed data for navigation. The fly's obstacle-avoidance and landing abilities would be useful in UAS technology. Insects' capacity to locate each other—again, despite having few sensors—could inspire the development of tranceivers for free-space communication systems. Arthropod-inspired designs have already been successfully applied in wide-field-of-view and 3D cameras.

We should be cautious about interpreting too much function from form. Nature does not globally optimize, but rather evolves based on adjacent possible steps. Though we might associate form and function, insect morphology may not always produce the specific functions we impute to it. Current UAS integrated vision sensor technologies do not mimic biological systems directly, but instead advance through improvements based on subtle understanding of insects' systems.

Research in this domain thus involves considerable "biospeculation," through which one can move beyond bio-inspiration to inverse-engineer and assert the possible functionality apparently possessed by insects. Biospeculation deals with functions that, while they may exist, would be hard to validate—yet, nonetheless, they serve the conceptual development of technological applications.

#### Insect eyes, insect brains

Extensive studies on arthropod eyes, especially in recent decades, have yielded detailed insight into their inner workings. Insects have compound eyes composed of numerous anatomically identical building blocks, the ommatidia, each one capped by a facet lens. This structure allows an easy estimation of the number of "pixels" of an insect eye. In the tiny fruit fly *Drosophila*, about 800 ommatidia make up an eye; in the larger dragonflies, this number can go up to 20,000. In a 2009 review of the fruit fly's imaging system, the neurobiologist Alexander Borst asked rhetorically: "Who would buy a digital camera with a fisheye lens and a 0.7 kilopixel chip, representing a whole hemisphere by a mere 26×26 pixels?" Flies quite sensibly do.

Fly eyes have eight photoreceptors per ommatidium, but in most other insects, such as bees, butterflies and dragonflies, an ommatidium contains nine photoreceptor cells, each with a characteristic spectral and polarization sensitivity. Together, each of these pixels captures information from a limited angular space, generally on the order of one degree half-width.

The facet lenses focus incident light onto the photoreceptors, where it is absorbed by their visual pigment molecules, the rhodopsins. These molecules trigger a molecular phototransduction chain, which depolarizes the photoreceptor's membrane potential. This is then fed forward to the higher neuronal ganglia, which together form the visual brain.

Vision is central to a fly's life; approximately 70% of its brain is dedicated to processing incoming visual data. Generally, flying insects have brains with 100,000 to 500,000 neurons and a mass of less than 1 mg (estimated from a volume of 0.08 mm<sup>3</sup>, assuming a dry weight of 0.25 mg). With an estimated 50-mW power demand, the brain consumes 10% of the animal's total metabolic power. With that basic equipment, insects achieve image-processing speeds as high as 200 fps—about an order of magnitude faster than humans' response to visual stimuli.

#### Clustered sensors and typologies

The construction of the eyes, the polarization and spectral properties of the photoreceptors, and the organization of neuronal processing strongly correlate with an organism's lifestyle and habitat. In the apposition eyes of diurnal insects, like bees, the photoreceptors in an ommatidium strictly receive light only via their overlying facet



Left: In apposition eyes, ommatidia are optically isolated. The rhabdomeres—visual pigment-containing organelles of the photo-receptor cells—together form a fused rhabdom (red), which receives light through a single facet lens. Right: In superposition eyes, several lenses focus light onto a rhabdom across the clear zone (CZ).



The eye of the aquatic insect *Notonecta glauca* includes zones of preferential polarization absorption, dictated by variations in microvilli orientations of adjacent R7 and R8 polarization-sensitive photoreceptors across different zones in the compound eye.

E.J. Warrant, Phil. Trans. R. Soc. B **372**, 20160063 (2016) / Adapted from T. Heinloth et al. Front. Cell. Neurosci. **12**, 50 (2017), CC-BY 4.0



shallow protrusions with spectral gratings. Right: Hovering butterflies and moths have ordered, raised corneal nanostructures.



Some butterfly and moth compound eyes have lenses coated with additional raised nanostructures. Those of the Mourning Cloak butterfly (shown here) are polycrystalline with random rotational order, and defects between crystals at grain boundaries.

W.C. Smith and J.F. Butler, J. Insect Physiol. **37**, 287 (1991) / D.G. Stavenga et al. Proc. R. Soc. B **273**, 661 (2005) / K. Lee et al. Sci. Rep. **6**, 28342 (2016), CC-BY 4.0

lens. By contrast, in the optical-superposition eyes of nocturnal insects, like moths, a photoreceptor gathers light from up to hundreds of facets.

Furthermore, in many cases, eyes are regionalized. Male fly eyes have a specific area, the "love spot," dedicated to detecting potential mates. Honeybee drones have specialized the main dorsal part of their eyes for spotting a honeybee queen as a contrasting dot in the sky. Ant and cricket eyes have a dorsal rim, dedicated to analyzing the polarization pattern of sky light. But the common backswimmer, *Notonecta glauca*, has ventral eye parts endowed with polarization vision.

The facet lenses of insect eyes are often covered with intricate nanostructures that vary from earwigs to bees to butterflies and moths. These nanostructures may offer antireflective and glare-reducing surfaces or provide anti-wetting hydrophobic surfaces to keep lenses clean.

Transmission electron microscopy identifies distinct optical patterns in the facet lenses of daytime predatorial insects and hovering insects. These are mostly random, flat patterns, but the facet lenses of horseflies and deer flies, scorpionflies, dragonflies, and long-legged flies carry 1D interferometric Fabry-Pérot spectral filters. Meanwhile, in moths and butterflies, polycrystalline lattices made up of corneal nanonipples exhibit more periodic patterns. Preliminary phylogenetic analyses and optical modeling of these structures suggest that daytime and nighttime insect structures differ in their optical function. Patterns on the insect eyes can exhibit multiple scales of order and photonic-crystal-like arrays.

Moving from lens to brain, several broad neural-circuit models of insect perception involving optical flow or polarization detection have been advanced. Reichardt detectors are neural-circuit models that rest on identifying motion. These include a low-signal-to-noise adaptation that provides an event signature—that is, a nonzero signal when an object passes with a time delay across adjacent inputs—and a high-signal-to-noise adaptation, providing more complex, differential-movement information. Higher-level memory, cognition, decision-making and sensorimotor responses build on these outputs in more complex neural systems that include circular networks.

Another broad neural-circuit model, studied in the horsefly *Tabanus bromius*, rests on combined polarization, spectral and intensity information. Specifically, the difference signals between orthogonally oriented microvilli are mixed with the difference between signal intensities from nonpolarized receptors. This mixture provides spatially encoded polarization information in a single output signal. The construction of the eyes, polarization and spectral properties of the photoreceptors, and organization of neuronal processing strongly correlate with an organism's lifestyle and habitat.

#### From fly vision to UAS vision

It's interesting to note that, while there's been substantial progress in implementing computer vision on small UAS for autonomous navigation and obstacle negotiation, the results of the algorithm-centered pipelines of UAS vision systems remain generally inferior to the evolved abilities of flying insects.

Conventional UAS pipelines process images from one or more cameras, and often the video data are composed of high-pixel-count, low-frame-rate image sequences. Subsequent frame-by-frame image processing predicts 3D movement in the environment by detecting and tracking features. Such a framework generally demands additional filtering to remove outliers and generate reliable 3D models. These real-time calculations—requiring throughputs of trillions of operations per second (TeraOPS)—are viable only with GPUs or specialized hardware designed for parallelized calculations.

In addition, such feature-detection algorithms often miss small, few-pixel-wide or pixel-sized objects, complicating aerial negotiation around cables, bare tree branches and netting. In photon-starved environments, a typical camera's setting is limited to either a short integration time, resulting in noisy pixels, or a long integration time, resulting in motion blur—both of which adversely affect the performance of feature-detection algorithms. Dirt or condensation on camera lenses result in image degradation from blur or scattering that further compromises algorithm performance. And when a feature-detection algorithm fails for these or other reasons, the entire computer vision pipeline fails, rendering the UAS unsafe to operate.

We have wondered if some key components of the fly's snapshot reflexes might lie not only in its neural processing but also in its optics—and how those components might be applied to UAS vision systems that can operate with low size, weight and power (SWaP). In advanced integrated vision sensors, modules leverage optics that pair with vision chips and tailored processing units. The processor can be programmed with firmware to operate and acquire visual information in tightly integrated devices that are optimized for high performance and small size. In such a framework, optics can encode information in such a way as to flatten the computational needs associated with image processing. The general scheme involves optical preprocessing, sparse sampling and high-speed, shallow optimization, mimicking the neural-circuit models of insect vision in quick, feed-forward calculations.

#### The virtues of "small brains"

Rather than use high-resolution images and multiple layers (with relatively long optimization times), as in conventional UAS vision pipelines, integrated vision sensors modeled on insect vision, enabled by optical preprocessing, can focus on low-pixel-density images,

#### Small-brain feed-forward neural circuits

Data flow from inputs at the top to correlation at the bottom, where inputs are signals from different photoreceptors.



Proposed Reichardt detectors, hypothetical neural circuits postulated for insect brain motion tracking. It is thought that processing switches from (left) event signals to (right) motion signals with an increasing signal-to-noise ratio.



Neural circuits associated with *Tabanus bromius* horseflies mix polarization and intensity signals, processing input from paired polarization-sensitive detectors (R7 and R8) in orthogonal horizontal and vertical microvilli, coupled with unpolarized signals from other photoreceptors (R1 to R6).

T. Haslwanter, Wikimedia Commons, CC-BY-SA 3.0 / A. Meglič et al. Proc. Natl. Acad. Sci USA **116**, 21843 (2019), CC-BY-NC-ND 4.0

Integrated vision sensors modeled on insect vision, enabled by optical preprocessing, can focus on low-pixel-density images, coarse image reconstruction and quick, back-end calculations.

# The power of optical preprocessinginputs<br/> $x_i^{(0)}$ weights $w_{ij}^{(n)}$ score: $a_i^{(n)} = \sum_j w_{ij}^{(n-1)} x_i^{(n-1)}$ outputs<br/> $y_i$ activation function: $x_i^{(n)} = f(a_i^{(n)})$ loss or cost function: $C(y_i, g(x_i^{(0)}))$ composite response: $g(x_i^{(0)}) =$ $f^{(n)}(W^{(n)}(f^{(n-1)}(W^{(n-1)}...f^{(0)}(W^{(0)}(x_0)))))$ Schematic view of a dense, fully connected multilayer neural<br/>network used for image processing in which inputs are trans-<br/>formed to outputs via a learned model.



Preprocessing with optical encoders can provide spatial signal compression to minimize the model size, either for detecting features, for example for image classification (center), or for filtering noise, for example for image reconstruction (bottom). In both cases, the optical preprocessing results in a smaller model with reduced computational load.

coarse image reconstruction and quick, back-end calculations. This kind of system can be described as one having optically encoded signals that are decoded by a "small brain." With machine-learned neural-network (NN) models, small brains (whether they are initialized as small or become small via brain pruning) can have faster inference speeds after training, lower storage requirements, minimized in-memory computations and reduced data-processing power costs. The disadvantage is that the small-brain NN system's learned functions are highly dependent on training, meaning the outcomes are data- and task-driven (and thus generally less adaptable to truly novel situations).

Such an approach has already been demonstrated using the simplest of all optical encoders—pinhole optical encoders. These diffractive encoders, which achieve a field of view of almost 180 degrees, offer high signal compression and coarse image reconstruction—potentially significant advantages for applications that prioritize high-speed reconstruction and lightweight hardware. Although the level of image coarseness from pinhole encoders prevents them from picking out details, they are capable of registering small obstacles in real time in a way that onboard high-definition cameras cannot.

In future integrated vision sensors, preprocessing from corneal nanostructures may serve in ways that go beyond antiglare optical functions—a design approach that is commonly ignored by researchers implementing insect-vision-inspired UAS. A pipeline involving corneal nanostructures would be in the spirit of lensless diffusers and other encoded computational-imaging approaches employed in computer vision today (see "Losing the Lens," OPN, July/August 2021). In the specific pipelines that involve sparse sampling and shallow, feed-forward processing, an insect-inspired model could offload significant computation costs to parallel optical preprocessing by corneal encoders.

In sum, the advantages of small-brain electronic decoding are speed and robustness—and, in a NN framework, lower training-data requirements. For certain technologies such as UAS, speed and robustness may be prioritized over high-resolution image reconstruction. Certainly, the fly's evolutionary commitment to this approach has been successful.

# Modes of optical preprocessing

Insect eyes and insect brains may use a variety of optical-preprocessing schemes to support visual systems of unparalleled efficiency. Here are some examples.

#### Colorimetric encoding and filtering

Colorimetric encoding could enable filtering of noise, isolation of object spectral signatures or interpretation of 3D structure



for a white object. For instance, the long-legged Condylestylus fly, a daytime predator, is far from stealthy; its entire body, including eyes and wings, is shiny and iridescent, making it easy to spot. The fly's compound eyes comprise alternating redand green-reflecting rows. Like dark-field condensers, the ommatidia of these flies accept filtered conical spatial modes. In a similar

spirit, the rainbow dispersion from thin films has been leveraged in 3D computational-imaging systems.

Insects commonly have a visual range extending into the UV and less into the red wavelength range. One explanation is that IR information is noisy due to thermal blackbody radiation, particularly for nighttime photon-starved vision. As a 2021 review by C.J. van der Kooi and colleagues pointed out, "the solar half of the sky contains more long-wavelength light, but the antisolar half contains more UV radiation." From an information-theoretic standpoint, the cues from UV signatures are more reliable, more robust and less noisy, providing higher-contrast imaging for some insects.

#### Compressed sensing

Compressed sensing refers to the ability to achieve a higher resolution compared with the conventional Nyquist sampling measures, through sparse signals and signal mixing.



Sparse photoreceptor arrays in Drosophila

When signals are spatially mixed, multiple dimensions of information-shape, color and polarization, for example -may be captured in fewer measurements.

It has been proposed that micro-saccadic eye and body movements improve visual acuity and spatial resolution. Disorder in optical encoders may provide a similar function in engineered systems (and in insect eyes): disordered materials provide signal mixing, which offers the sensing of more information with fewer measurements.

#### Polarization encoding and filtering

The natural environment is full of polarized information, from light reflected off of surfaces to light scattered from the sky. Polarimetric sensing could ease object surface detection and texture identification, enabling rapid feature extraction and navigation. Insects rely on their sense of polarization; semi-aquatic insects, for instance, can be fooled into laying their eggs on



synthetic reflective surfaces, such as cars, glass and polished stones, and in "polarization light traps" rather than water. Other insects rely on the celestial polarimetric signatures from the sky for navigation, an ability that can be severely limited by night-glow or light pollution from urban areas.

Polarization information also can enhance the signal or image in turbid media, enable seeing of otherwise

length of sunlight can be as long as

tens of microns-still large relative

coherent optical image processing

would appear to be more prominent

with nocturnal insects. With night-

time insects, visual data are spatially

pooled in superposition eyes, and the

partial coherence of light for visual

signal processing in such eyes plays

While moonlight appears less

spatially coherent than light from the

sun, the coherence length of starlight

is expected to be higher than that of

to nanometer length scales. Even so,

Scarab beetle polarization

invisible objects and be used to interpret the shape and refractive index of objects, among other things. Polarimetric encoding via simple pixel sensors thus opens possibilities for inferring higher-dimensional information in the environment.

#### Coherent optical preprocessing

Analog optical signal processing generally requires coherent light. Sunlight, while generally thought of as spatially incoherent, is coherent over small distances. The spatial coherence



M. stellatarum superposition compound eye

back-end decoders.

sunlight, since the angle subtended on the Earth from stars is smaller. Starlight's coherence length thus is potentially on the order of kilometers. There are numerous examples of coherent and analog image processing in optics, some of which may be decoded with simple electronic

an important role.

Beetle and photoreceptor images published with permission of Springer Nature. Complete image credits are available online at **optica-opn.org/link/1123-insect-vision**.



Simple optical preprocessing with pinhole diffraction provides a 180-degree field of view. The printed pinhole (shown between forceps) is mounted on a Centeye 125-mg TinyTam 16×16 sensor. A US penny is provided for scale. Courtesy of Centeye

In work over the past several years, we have attempted to quantify some of those benefits. In our experiments, vortex encoders were used in front of a lens, and linear intensity pixels were captured in the Fourier plane, which spatially compresses the intensity pattern. This pattern was then fed to a shallow single- and dual-layer NN—composed of linear and nonlinear activation functions—which was found to stably achieve image contrast.

We found that in our small-brain setup, when noise was added in the image and in the optically encoded sensor plane measurements, the image contrast remained, although parts of images disappeared. On the other hand, using a more complex, deep-learning convolutional NN under similar noise conditions, the reconstructed images became almost unrecognizable.



A single-layer neural network (SNN) with additional optical preprocessing (in the form of a vortex lens encoder) enabled the robust classification of MNIST handwritten digits. At low noise levels (high SNR), classification accuracies are comparable to deep-learning convolutional neural networks (CNNs). At high noise levels (low SNR), the SNN with vortex encoders significantly outperforms the CNNs. Insets show noisy images without encoding.

B. Muminov and L.T. Vuong, Proc. SPIE 11388 (2020), doi: 10.1117/12.2558983

In other words, the tradeoff of having a model that produces lower-fidelity images in the absence of noise is robustness and reliable performance in the presence of noise.

Meanwhile, nonlinearities in the form of logarithmic responses can give a sensor the ability to operate over a wide dynamic range of lighting conditions. An insect flying through a forest in daylight may simultaneously observe a bright sunlit patch of ground and a nearby deep-shadowed area with a radiance three orders of magnitude lower. The logarithmic response at a front-end sensor means it can easily capture pixels embodying environmental information at a range of ambient light levels.

# Toward insect-vision-inspired flight control

How far can we take the insect vision model? Whether low-resolution vision systems can be used to guide a flying machine has been studied extensively. Early experiments, published in 2000, used a single, downward-aimed optical flow sensor to provide a fixed-wing aircraft with autonomous altitude hold while flying forward. The biologically inspired optical flow algorithm relied on input from 18 rectangular logarithmic-response pixels and analog image-processing circuitry, with processing performed with an 8-bit microcontroller running at about 1.5 million operations per second (MOPS)-and acquired imagery at a 1.4-kHz frame rate. Later implementations, involving an 88-pixel analog neuromorphic-vision sensor chip operated by a 10-MOPS microcontroller, achieved a high degree of reliability, including holding altitude over snow on a cloudy day.

Like a compound eye, sensor arrays may support obstacle avoidance using optical flow algorithms based on fruit flies. In experiments reported in 2002, three

### The psychologist William James wrote that "the art of being wise is the art of knowing what to overlook." Insect vision embodies this philosophy.

88-pixel optical flow sensors aimed in the forward-left, forward and forward-right directions were able to trigger sharp execution of fixed-sized turns based on the difference in optical flow between the sensors. In 2012, vision-based hover-in-place via omnidirectional optical flow sensors was demonstrated with an 18-cm-wide coaxial helicopter. In 2010, a ring of eight vision chips acquiring a total of 512 rectangular pixels (half horizontal and half vertical) grabbed eight optical flow measurements around the yaw-plane that were used to estimate position based on a model of global optical flow processing neurons found in the blowfly. A few years later, a 250-pixel setup enabled similar behavior-in an implementation weighing only 3 grams that included the eight vision chips, optics, interconnects and an 8-bit microcontroller running at 60 MOPS.

As these examples demonstrate, useful vision-based flight control can be performed with integrated visual circuits involving sensors with hundreds or thousands instead of millions of pixels—and at data throughputs many orders of magnitude smaller than the TeraOPS levels of conventional UAS vision systems that require sophisticated GPUs. In the work we briefly surveyed above, no GPS, motion capture, external computation or position systems were used. We speculate that with the added front-end processing provided by optical encoders—again, biospeculative optical preprocessing achieved by insect eyes—more advanced behaviors may be supported by these low-SWaP systems.

#### When less is more

The psychologist William James wrote that "the art of being wise is the art of knowing what to overlook." Insect vision embodies this philosophy. To close this article, we offer some examples of what the fly has "learned to overlook"—with lessons for those designing machine vision systems:

**Rely less on more distortable information.** Insects see in the UV, which provides greater image contrast and is less vulnerable to environmental and sensor thermal noise than the IR.

**Capture more multidimensional information with fewer pixels.** Insects sample sparsely and leverage polarization, which enables greater higher-level inferences.

**Encode sensor data to capture more information.** The seemingly random domains of corneal nanostructures could spatially disperse data and provide the capacity to collect, filter, process and map more visual data.

**Reduce computational complexity.** Insects leverage shallow computation and feed-forward algorithms to make rapid decisions.

**Do not assume more is better.** Coarse, high-frame-rate image processing offers robustness in variable natural environments. **OPN** 

Luat T. Vuong (luatv@ucr.edu) is with the University of California Riverside, Riverside, CA, USA. Doekele G. Stavenga is with the University of Groningen, Netherlands. Geoffrey L. Barrows is with Centeye in Washington, DC, USA.

#### References and Resources

- G.L. Barrows and C. Neely. "Mixed-mode VLSI optic flow sensors for in-flight control of a micro air vehicle," in *Critical Technologies for the Future of Computing*, SPIE Proc. 4109, 52 (2000).
- ► G.L. Barrows et al. "Biologically inspired visual sensing and flight control," Aeronaut. J. 107, 159 (2003).
- D.G. Stavenga et al. "Light on the moth-eye corneal nipple array of butterflies," Proc. R. Soc. B 273, 661 (2005).
- ► A. Borst. "Drosophila's View on Insect Vision," Curr. Biol. 19, R36 (2009).
- H. Haberkern and V. Jayaraman. "Studying small brains to understand the building blocks of cognition," Curr. Opin. Neurobiol. 37, 59 (2016).
- D.G. Stavenga et al. "Photoreceptor spectral tuning by colorful, multilayered facet lenses in long-legged fly eyes (Dolichopodidae)," J. Comp. Physiol. A 203, 23 (2017).
- E.J. Warrant. "The remarkable visual capacities of nocturnal insects: vision at the limits with small eyes and tiny brains," Phil. Trans. R. Soc. B 372, 20160063 (2017).
- B. Muminov and L.T. Vuong "Fourier optical preprocessing in lieu of deep learning," Optica 7, 1079 (2020).
- ► C.J. van der Kooi et al. "Evolution of insect color vision: From spectral sensitivity to visual ecology," Annu. Rev. Entomol. 66, 435 (2021).
- T. Wang et al. "Image sensing with multilayer nonlinear optical neural networks," Nat. Photonics 17, 408 (2023).

For complete references and resources, go online: **optica-opn.org/link/1123-insect-vision**.

Acknowledgments: L.T.V. acknowledges support from DARPA Young Faculty Award D19AP00036. D.G.S. acknowledges support from AFOSR/EOARD grant FA9550-19-1-7005. G.L.B. acknowledges support under NSF contract CCF-0926148 and Air Force contract FA8651-06-C-0127.

Image credits, p. 31. Clockwise from top left: T. Shahan / Getty Images; G. Horváth et al. in G. Horváth (ed.), *Polarized Light and Polarization Vision in Animal Sciences*, pp. 147–170, Springer (2014), published with permission of Springer Nature; A. Stöckl et al. Proc. R. Soc. B **289**, 20220758 (2022), CC-BY 4.0; J.P. Kumar, in A. Singh and M. Kango-Singh (eds), *Molecular Genetics of Axial Patterning, Growth and Disease in Drosophila Eye*, pp. 97–120, Springer (2020), published with permission of Springer Nature.

#### Complete References and Resources

#### Insect nanostructures

- D.G. Stavenga et al. "Photoreceptor spectral tuning by colorful, multilayered facet lenses in long-legged fly eyes (Dolichopodidae)," J. Comp. Physiol. A 203, 23 (2017).
- D.G Stavenga et al. "Light on the moth-eye corneal nipple array of butterflies," Proc. R. Soc. B 273, 661 (2005).
- E.P. Ivanova et al. "Molecular organization of the nanoscale surface structures of the dragonfly *Hemianax papuensis* wing epicuticle," PLOS ONE 8, e67893 (2013).
- K. Lee et al. "Mesostructure of ordered corneal nano-nipple arrays: The role of 5−7 coordination defects," Sci. Rep. 6, 28342 (2016). doi:10.1038/srep28342
- C. Bernhard et al. "Function of the corneal nipples in the compound eyes of insects," Acta Physiol. Scand. 58, 381 (1963).

#### Neural circuits and small brains

- ► J. Haag et al. "Fly motion vision is based on Reichardt detectors regardless of the signal-to-noise ratio," Proc. Natl. Acad. Sci. U.S.A. **101**, 16333 (2004).
- H.S. Cheong et al. "Multi-regional circuits underlying visually guided decision-making in Drosophila," Curr. Opin. Neurobiol. 65, 77 (2020).
- H. Haberkern and V. Jayaraman. "Studying small brains to understand the building blocks of cognition," Curr. Opin. Neurobiol., 37, 59 (2016).
- R. Behnia and C. Desplan. "Visual circuits in flies: Beginning to see the whole picture," Curr. Opin. Neurobiol. 34, 125 (2015).
- E.J. Warrant. "The remarkable visual capacities of nocturnal insects: Vision at the limits with small eyes and tiny brains," Philos. Trans. R. Soc. B 372, 20160063 (2017).

#### Insect polarization vision

- T. Heinloth et al. "Insect responses to linearly polarized reflections: Orphan behaviors without neural circuits," Front. Cell. Neurosci. 12, 50 (2018).
- R. Schwind. "Evidence for true polarization vision based on a two-channel analyzer system in the eye of the water bug, Notonecta glauca," J. Comp. Physiol. A, 154, 53 (1984).
- A. Meglič et al. "Horsefly object-directed polarotaxis is mediated by a stochastically distributed ommatidial subtype in the ventral retina," Proc. Natl. Acad. Sci. U.S.A. 116, 21843 (2019).
- ► G. Horváth (ed.). Polarized Light and Polarization Vision in Animal Sciences, Springer (2014).

#### Insect spectral and coherent information processing

- ► K. Hamdorf et al. "Insect visual pigment sensitive to ultraviolet light," Nature 231, 458 (1971).
- T.W. Cronin and M.J. Bok. "Photoreception and vision in the ultraviolet," J. Exp. Biol. 219, 2790 (2016).
- ► C.J. van der Kooi et al. "Evolution of insect color vision: From spectral sensitivity to visual ecology," Annu. Rev. Entomol. 66, 435 (2021).
- D.G. Stavenga. "Partial coherence and other optical delicacies of lepidopteran superposition eyes," J. Exp. Biol. 209, 1904 (2006).
- ► G.D. Bernard. "Evidence for visual function of corneal interference filters," J. Insect Physiol. 17, 2287 (1971).
- G. Belušič et al. "A cute and highly contrast-sensitive superposition eye—the diurnal owlfly *Libelloides macaronius*," J. Exp. Biol. **216**, 2081 (2013).

#### Insect polarization signal processing

- T. Heinloth et al. "Insect responses to linearly polarized reflections: Orphan behaviors without neural circuits," Front. Cell. Neurosci. 12, 50 (2018).
- G. Belušič et al. "A cute and highly contrast-sensitive superposition eye—the diurnal owlfly Libelloides macaronius," J. Exp. Biol. 216, 2081 (2013).
- N.J. Marshall et al. "Polarisation signals: A new currency for communication," J. Exp. Biol. 222, jeb134213 (2019).
- R.A.R. Childers et al. "A hypothesis for robust polarization vision: An example from the Australian imperial blue butterfly, *Jalmenus evagoras*," J. Exp. Biol. **226**, jeb244515 (2023).

#### Visual acuity in insects

- ► J. Kemppainen et al. "High-speed imaging of light-induced photoreceptor microsaccades in compound eyes," Commun. Biol., 5, 203 (2022).
- ► J. Theobald. "Insect flight: Navigating with smooth turns and quick saccades," Curr. Biol. **27**, R1125 (2017).
- M. Juusola et al. "Microsaccadic sampling of moving image information provides *Drosophila* hyperacute vision," eLife 6, e26117 (2017).

#### Engineered 3D and colorimetric imaging

- J. Chang and G. Wetzstein. "Deep optics for monocular depth estimation and 3D object detection," Proc. IEEE/CVF Intl. Conf. Comp. Vis. 2019, 10193 (2019).
- Q. Guo et al. "Compact single-shot metalens depth sensors inspired by eyes of jumping spiders," Proc. Natl. Acad. Sci. U.S.A. 116, 22959 (2019).
- N. Antipa et al. "DiffuserCam: Lensless single-exposure 3D imaging," Optica 5, 1 (2017).
- V. Boominathan et al. "Recent advances in lensless imaging," Optica 9, 1 (2022).

#### Polarimetric imaging

- E. Arbabi et al. "Full-Stokes imaging polarimetry using dielectric metasurfaces," ACS Photonics 5, 3132 (2018).
- N.A. Rubin et al. "Matrix Fourier optics enables a compact ► full-Stokes polarization camera," Science **365**, eaax1839 (2019).
- J. Feng et al. "Insect-inspired nanofibrous polyaniline multiscale films for hybrid polarimetric imaging with scattered light," Nanoscale Horiz. **7**, 319 (2022).
- X. Weng et al. "Non-line-of-sight full-Stokes polarimetric imaging with solution-processed metagratings and shallow neural networks," ACS Photonics 10, 2570 (2023).
- Y.Y. Schechner and N. Karpel. "Recovery of underwater visibility and structure by polarization analysis," IEEE J. Ocean. Eng. 30, 570 (2005).

#### Encoded coherent signal processing

- J.W. Goodman. Introduction to Fourier Optics, McGraw-Hill Physical and Quantum Electronics Series, W.H. Freeman (2005).
- ► S. Divitt and L. Novotny. "Spatial coherence of sunlight and its implications for light management in photovoltaics," Optica 2, 95 (2015).
- ► G.S. Agarwal et al. "Coherence properties of sunlight," Opt. Lett. **29**, 459 (2004).
- ▶ Y. Zhou et al. "Flat optics for image differentiation," Nat. Photonics 14, 316 (2020).
- H. Mashaal et al. "First direct measurement of the spatial coherence of sunlight," Opt. Lett. 37, 3516 (2012).
- ► G. Wetzstein et al., "Inference in artificial intelligence with deep optics and photonics," Nature **588**, 39 (2020).
- B. Muminov and L.T. Vuong. "Fourier optical preprocessing in lieu of deep learning," Optica 7 1079 (2020).

#### Compressive sensing

- E.J. Candes and M.B. Wakin. "An introduction to compressive sampling," IEEE Signal Process. Mag. 25(2), 21 (Mar. 2008).
- ► J. Feng et al. "Polarimetric compressed sensing from insect-inspired meso-ordered encoders," submitted.
- A. Liutkus et al. "Imaging with nature: Compressive imaging using a multiply scattering medium," Sci. Rep. 4, 5552 (2014).
- T. Wang et al. "Image sensing with multilayer nonlinear optical neural networks," Nat. Photonics 17, 408 (2023).
- ▶ B. Muminov and L.T. Vuong. "Vortex Fourier encoding for small-brain classification of MNIST digits with no hidden layers," *in* Proc. SPIE Vol. 11388, Image Sensing Technologies: Materials, Devices, Systems, and Applications VII, 113880T, pp. 79-84 (2020).

#### Toward real-time applications for UAS

- ▶ G.L. Barrows et al. "Biologically inspired visual sensing and flight control," Aeronaut. J. **107**, 159 (2003).
- G.L. Barrows and C. Neely. "Mixed-mode VLSI optic flow sensors for in-flight control of a micro air vehicle," *in* Proc. SPIE Vol. 4109, Critical Technologies for the Future of Computing, pp. 52–63 (2000).
- L.F. Tammero and M.H. Dickinson. "The influence of visual landscape on the free flight behavior of the fruit fly Drosophila melanogaster," J. Exp. Biol. 205, 327 (2002).
- A.M. Hyslop and J.S. Humbert. "Autonomous navigation in three-dimensional urban environments using wide-field integration of optic flow," J. Guid. Control Dyn. **33**, 147 (2010).
- F. Rodriguez et al. "Sequentially trained, shallow neural networks for real-time 3D odometry," in Artificial Intelligence for Security and Defence Applications VII, SPIE, September 2023.
- ► H.G. Krapp et al. "Dendritic structure and receptive-field organization of optic flow processing interneurons in the fly," J. Neurophysiol. **79**, 1902 (1998).
- ► G.L. Barrows et al. "Vision based hover in place," US Patent 20120197461A1, Aug. 02, 2012.