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Insect-Inspired Vision and Visually Guided Behavior

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Definition

Many insects are capable of remarkably fast and precise visually guided behavior. These impressive feats are achieved despite low-resolution vision and limited neural resources, constraints that have led to elegant neural and behavioral strategies which are of interest to engineers seeking to emulate insect-level performance with lightweight hardware. Insect-inspired visual systems – in which engineers incorporate design principles derived from insect behavior – have been adopted for many tasks, from the biomimetic design of visual hardware through to the development of parsimonious control algorithms for autonomous agent control.

Introduction

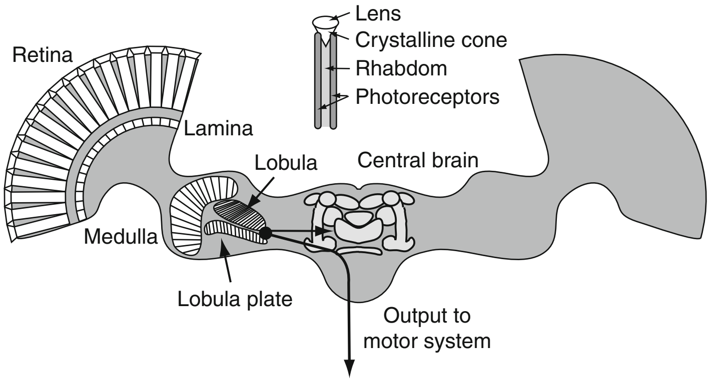
The insect world offers many examples of remarkable visually guided behavior. Two such behaviors which are no less remarkable for their familiarity are the precise, extremely fast flight control of flies and the long distance landmark navigation of bees and ants. These behaviors are all the more impressive because of the limitations that insects overcome in terms of visual resolution and available neural processing power. For the biomimetic engineer, the visual systems of insects therefore provide aspirational examples of parsimonious and economical strategies for visual tasks which can be evidently performed with minimal lightweight hardware [1].

Investigations of insect vision over many years and at various levels of study, from optical anatomy up to behavioral observation, have shown how visually guided behaviors are the product of dedicated circuits which have evolved in specific ecological niches, leading to the tight coupling of sensory apparatus, visual processing, and behavior. The basic organizational principles of insect visual systems are reviewed and, in each case, it is considered how these principles influence the design of artificial systems.

The Insect Visual Pathway

In insects, the visual pathway begins with the compound eye, which differs fundamentally from simple eyes (i.e., single lens eyes like human eyes) because there are multiple lenses with differing viewing directions but a fixed focal length (Fig. 1). There are two basic forms of compound eye [2], apposition and superposition. This Chapter focuses on the former as diurnal insects, the majority of which have apposition-type compound eyes, produce well-studied behaviors such as flight control, collision detection, and navigation that have inspired engineers.

In the apposition compound eye (Fig. 1), each lens has its own photoreceptors, and this lens-photoreceptor unit is called an ommatidium ("little eye"). Compound eyes are severely limited in terms of spatial resolution because diffraction limits the resolution possible for a given aperture size. For instance, to replicate foveal human visual acuity, which is of the order 1 min of arc, a compound eye would have to have many more lenses, and each lens would have to be much bigger, leading to a bulky sphere with a diameter of over 10 m. This limitation means that the highest visual acuity in insects is found in the large eyes of the dragonfly at about 0.5°. To mitigate this limitation, the density of ommatidia is not uniform but is adapted to environment, mode of locomotion, and behavior. Arthropods that move close to flat surfaces such as water or mud flats have greater acuity in the equatorial part of the visual field, which views the horizon where landmark information is to be found. Insects that fly in dense vegetation have a low density of ommatidia in the lateral parts of the eye to increase the detection of motion signals from objects moving from front to back across the eye's surface. Similarly, insects that need to resolve and track small targets, such as potential mates or rivals, have evolved specialized high acuity eye regions that are adapted to encoding small and often fast moving targets. Despite the limitations in acuity, compound eyes still offer advantages for insects and potentially engineers too. The hardware of the compound eye allows for a better temporal resolution (up to 300 Hz rather than 30 Hz for human vision) and, because of the convex shape of a compound eye, insects can create a very wide field of view (FOV). These properties are particularly beneficial for processing motion information (which is discussed in section Using Motion Information).



Insect-Inspired Vision and Visually Guided Behavior, Fig. 1 *Left*. The compound eyes of a Robber Fly (*Holcocephala fusca*). Photo: Magnus Manske, used with permission under a Creative Commons license. *Right*. A schematic of the major regions in a typical insect visual pathway. Redrawn after [1]. *Inset*. The major components of a single ommatidium

The parallel output from the ommatidia is processed further in the Lamina and Medulla (Fig. 1). In these structures, information remains retinotopically organized. Although the functional organization of these structures is still not fully understood, it is generally taken that information is high-pass filtered in the lamina to emphasize dynamic components of the input before subsequent extraction of local motion information in the medulla [3]. It is thought that motion information is extracted using correlational filters, where the signal from one point in space is correlated with time-delayed signals from adjacent points in space. These supposed filters are known as Elementary Motion Detectors (EMDs).

One step further along the visual pathway are the Lobula and Lobula Plate. Here there is a massive convergence of the motion-filtered signals from all parts of the visual field. These brain regions house a limited number of highly specialized neurons that are at the service of specific behaviors. For instance, single cells act as matched filters for particular patterns of optic flow generated in flight, or for the motion of small objects against patterned backgrounds. The output of these cells often passes directly to flight muscles without further processing in the central brain. This highlights the economical, specialized nature of insects' visual circuits [1, 3].

Artificial Compound Eyes

Artificial compound eyes are desirable because they promise a wide FOV without the bulk of single lens imaging systems. It is true that a large FOV can be achieved with multi-camera systems, panoramic mirrors, or even mirror and lens hybrid arrangements that are cheap and easy to use. Indeed, these kind of panoramic imaging systems are widely used tools for biologists using modeling and robotic approaches to study animal visual behavior [4]. They can also be mounted on medium to large wheeled [5] and flying [6] robots for autonomous navigation. However, future miniature platforms, such as micro unmanned aerial vehicles (MUAVs) need to minimize payload and thus require much smaller visual systems and so approaches inspired by compound eyes have been explored. Moreover, artificial compound eyes of a comparable scale to insect eyes would have many applications in space-limited situations.

There have been some successes replicating the optical arrangements of compound eyes. One approach is to use arrays of micro-lenses to project onto CCD or CMOS cameras. The basic result is a sandwich of a micro-lens array, an aperture array and a photodetector array. These flat artificial compound eyes, which can be constructed using MEMS (microelectromechanical systems) construction technology, have the advantage of being very small and thin, but do not necessarily have a large FOV. 3D microlens arrays can improve the FOV to a maximum of 180°, even when projecting onto a flat photodetector array. However, a practical issue remains with systems of this type, owing to the difficulty in aligning the different components of the system.

One of the more striking attempts to create an artificial compound eye, owing to its stunning similarity to a real insect eye, comes from Jeong and colleagues [7]. They avoid the problem of aligning the components of a visual system by creating a self-aligning system. To construct their eye, they make a mold of the outer surface of a compound eye – a hemisphere consisting of thousands of bumps in a hexagonal array. This compound eye mold is filled with an epoxy resin and, when struck by a beam of light, each bump in the epoxy structure acts as a lens and focuses light on the material below, hollowing out a narrow cavity. By this technique, waveguides (similar to the rhabdom in the insect ommatidium, Fig. 1) are constructed in perfect alignment with each lens. The end product is remarkably similar in size, shape, and optical performance to a honeybee ommatidium.

The aforementioned approaches to building artificial compound eyes mainly focused on taking advantage of the optical, size, and FOV advantages that come with this eye design. A second approach to building insect-inspired eyes comes from neuromorphic engineering where conventional optics are used in tandem with hardware (VLSI or FPGA) which mimics the early stages of visual processing, most commonly motion extraction. So-called "eyes on a chip" successfully achieve the low weight and fast parallel processing required in artificial systems [1, 8].

Using Motion Information

Fast, precise insect behaviors, such as the ability of flies to avoid being swatted, of hoverflies to accurately maintain their position, and of locusts to avoid predator attacks, come from the capability of insect brains to rapidly extract global patterns of local motion in behaviorally relevant ways. The pattern of visual motion experienced by an animal depends on three factors: egomotion, the structure of the environment, and the movement of objects in the world. This means that insects can use motion signals to extract information about their own movements as well as the structure of the environment. In this section, some basic uses of motion information are considered.

Flight Control

For flying insects, controlling flight is complicated by air currents; thus, an insect's actual movements cannot be directly inferred from its motor output. To monitor the success of an intended movement or to check for unintended displacement, insects use the pattern and amplitude of the visual motion they experience. Behavioral experiments with bees and neurophysiological experiments with flies have demonstrated the smart tricks used by insects when using visual motion cues to control flight behavior.

Mandyam Srinivasan and colleagues [6] have spent many years observing bees flying through patterned tunnels. These experiments show that bees maintain a central position in a tunnel by balancing the image motion, or optic flow, perceived by each eye. The optic flow, F, generated by a simple object at a distance d from an observer moving with an instantaneous velocity v can be calculated as:

$$F = -\omega + \frac{v}{d}\sin\theta$$

where ω is the optic flow generated by self-rotation and θ is the angle of the object relative to the direction of travel. In the absence of self-rotation (often assumed to be subtracted out through measurement by gyroscopic sensors), balancing the optic flow on each side of the bee (i.e., at $+/-\ \theta$) would mean that d would be the same on both sides (as v is constant for both eyes). Similarly, maintaining constant optic flow requires that if the tunnel narrows, the bee must lower its velocity. This means that in more cluttered environments, the bee automatically responds appropriately by slowing down. This simple and elegant solution of balancing optic flow thus results in a bee being able to chart a safe path through a cluttered environment *without* knowing its own speed or measuring the distance to nearby objects.

A similar control scheme is used by bees to control grazing landings on flat surfaces. When landing, bees control their forward flight speed using the angular velocity perceived in the lower part of their visual field. As the bee descends, the ground appears to move at a higher angular velocity. By controlling forward thrust to maintain a fixed angular velocity, the bee "automatically" slows as its altitude falls. When the bee finally touches down, its forward speed is zero, thus ensuring a smooth landing. This algorithm also allows the bee to maintain a constant angle of descent throughout the landing, and does not require explicit measurement of flight speed, flight altitude, or estimated time to contact.

Flight Control for UAVs

The fixed-point control mechanisms observed in bee flight are clearly attractive to engineers and, following Srinivasan's work, there have been multiple instantiations of corridor-centering robots. In addition, the observation that bees use this type of control to maintain a fixed height above a surface has led to the robust control of UAVs capable of "terrain following." Notice that in the above equation, if the object is directly below an insect flying parallel to the ground, the optic flow signal will be strong and the distance, d, is the height of the agent above the ground. A UAV can therefore maintain a constant height over undulating terrain by altering its forward velocity so that the optic flow measured from a downward facing camera remains constant. This type of control has been implemented on free-flying helicopters and fixed-wing aircraft [6, 9]. Crucial to the success of these systems is the reliable extraction of optic flow signals, generally achieved through the use of simple hardware elementary motion detectors (EMDs).

Going a stage further down the visual pathway and modelling the widefield integration of the cells in the Lobula Plate has led to alternative control systems for UAV implementations. As described above, these cells take input from a large number of EMDs in the medulla and electrophysiological studies indicate that they respond preferentially to particular global patterns of optic flow, such as an expanding flowfield caused by pure forward motion. Individual cells therefore act as matched filters for translation and rotation about different axes, providing signals that insects can use to monitor movement and correct for unintended displacements or rotations [10].

Engineers have used an analog of the Lobula Plate system to generate fixed-point control algorithms for both flying and wheeled robots [11]. The output of a given neuron in the Lobula Plate can be interpreted as a comparison between the current instantaneous flow field and the flow field that would be generated by the particular movement that the neuron is configured to detect. This can be modeled as an inner product between a template flow field pattern and the instantaneous flow field. With this technique it is possible to extract information such as forward and vertical velocity and pitch rate from an optic flow field. Further, spatial Fourier components of appropriate filter outputs can be fed back into the system and thus used in fixed-point control algorithms to control for UAV stabilization.

Collision Avoidance

The depth cues available to insects are an impoverished subset of those that vertebrates can use. Two main cues are available: motion parallax and looming. Insects do not use these cues to generate a universal depth map. Rather, individual cues are used in specific visual circuits to control specific behaviors. For avoiding obstacles in free flight, many insects use parallax cues and have evolved a specific movement strategy to simplify the perception of parallax information. During translatory movements, objects closer to the animal move faster across the retina, but this signal can be swamped by the rotatory flow fields (where objects at all distances move across the retina with the same speed) produced by insect rotation. Many insects therefore move in a saccadic manner where periods of straight flight are alternated with very fast turns. In addition, small head movements are used to compensate for body rotation, such that the eyes are rotating for the least amount of time. The utility of this strategy was highlighted in a seminal piece of insect vision–inspired biorobotics [12]. Franceschini and colleagues implemented an array of electronic EMDs on the perimeter of a large, wheeled robot. The EMDs were tuned to respond to the parallax generated by objects that were on a collision course with the robot. This was possible as the robot used a fixed movement direction relative to its sensors and used a saccadic movement strategy; pure translation alternated with fast pure rotation. Given these two constraints, the robot was able to move rapidly around its environment whilst avoiding obstacles.

An alternative distance cue comes from looming, also known as image expansion. The mechanisms of looming detection have been well studied in the locust collision-avoidance response which is triggered by image expansion [13]. In locusts, a specialist neuron in the Lobula, called the Lobula Giant Movement Detector (LGMD), responds to any movement within a large visual area but is most sensitive to objects directly approaching the eye. The firing rate of this neuron increases throughout an object's approach, but responses decrease if the approaching target deviates from a collision course by a small amount. The response properties of the LGMD indicate that the cell is sensitive to movement, the total length of luminance boundaries in the image, as well as the acceleration of edges. All these parameters can be derived by conflating the output of EMDs in the medulla and the LGMD neuron therefore acts as a matched filter for impending collision using only a few processing stages.

Because the LGMD is able to reliably signal impending collisions without the need to explicitly represent the target object's physical size, distance, or approach speed, it represents an interesting model for collision avoidance in artificial systems. For instance, artificial neural networks have been constructed to account for the responses of the locust LGMD neurons and detect impending collisions on wheeled robots. Essentially, the edges of an expanding object trigger feed-forward excitation, followed a short time later by laterally spreading inhibition, with both excitatory and inhibitory signals converging on the LGMD. So long as the edges continue expanding rapidly enough to "outrun" the pursuing inhibitory signals, the LGMD's response continues to grow in strength. This model has been further developed and tested for collision warning systems in automobiles [14]. However, in order to produce satisfactory performance in an automobile context, the model had to be significantly augmented. This highlights a particular problem with biomimetics. In this example, the sensory environment and behavioral niche for locusts and cars are very different. In general, it should not be assumed that bio-inspired systems will work perfectly in novel contexts.

Economical Place and Pattern Recognition

Efficient and robust navigation using visual cues is an important capability for many animals as well as autonomous robots. By using simple strategies, insects are able to demonstrate excellent navigational ability albeit with small brains and low-resolution vision. The most famous example of this is view-based homing or snapshot guidance [15] in which insects navigate back to a location by remembering a retinotopic view of the world, or snapshot, stored at the goal position. Subsequent navigation is achieved by moving so as to make the current view of the world more similar to the remembered goal view. In general, algorithmic instantiations of this process work by iteratively comparing a parameterized view of the world from the agent's current position with a similarly parameterized view stored at the goal location. Differences between the current and goal views can then be transformed into an approximate direction to the goal. For engineers, the attraction of insect style view-based homing is that these strategies can work without having to identify landmarks. That is, they work using only the appearance of the world rather than worrying about object identification [16].

One of the simplest and most elegant implementations of snapshsot homing for robotic navigation is the Average Landmark Vector (ALV) model [5]. The ALV model works by first identifying visual features from a 360° panoramic view of the environment. The view of the world from that position is then represented as the average of unit vectors pointing from the agent to each identified feature, i.e., the ALV. The algorithm works since the vector difference between the current ALV and an ALV stored at the goal position points approximately back to the goal. The idea of encoding a visual scene as the visual center-of-mass of visual features, or even the center of mass of simple pixel intensities, is surprisingly robust and is a general purpose method for retinotopic encoding of a visual scene.

While the ALV is a particularly parsimonious visual homing algorithm, at the heart of all algorithms of this type is the fact that, within a region local to the goal image, the difference between goal and other images increases smoothly with distance. The size of this region, called the catchment area of an image, is determined by the distribution of object distances. To home successfully, the agent thus needs only to calculate the local gradient of the difference between current and goal images (whether processed or unprocessed) and move in the direction which decreases this difference. While the local gradient can be calculated by sampling the world, it has been shown that the gradient can also be estimated using matched filters which approximate the effects of forward and sideways movements on the current image [17]. This is effectively the opposite of a basic optic flow calculation. This method has been shown to work robustly in natural environments and can be implemented with simple parallel processing steps and so should be amenable to hardware implementation.

Conclusion

Insects are an existence proof that low-resolution vision and a small brain are not a barrier to the production of exquisite visually guided behavior. What's more, insects provide specific design blueprints for emulating this performance in artificial systems [1]. In summary, the early stages of insect vision are massively parallel and fast, and much visual behavior is controlled by neural matched filters that integrate across many of these parallel inputs. However, a significant lesson for engineers is that insects' visual systems have been fine-tuned by evolution such that the interactions between optics, neurons, behavioral routines, and the environment are optimized for a specific ecological niche. The niche of an artificial system has to be considered when applying biomimetic design principles.

Cross-References

▶ Biomimetics
▶ Insect Flight and Micro Air Vehicles (MAVs)

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