

to several phenomena in human object recognition and scene analysis (Leow and Miikkulainen, 1994), but it is still a long way from capturing the full variety and complexity of real-world object recognition and scene analysis. Some objects have flexible or movable components that can appear in different spatial relations with each other, such as the limbs and body of a human reaching up or picking up something from the ground. For such objects, topological relationships such as "connected-to" would be more appropriate than rigid spatial relationships (Biederman, 1987). Many objects would need to be represented in 3D rather than as 2D projections, and it should be possible to recognize them from different viewpoints and also in different scales and orientations (Hummel and Biederman, 1992; Leow, 1994; Olshausen, Anderson, and Van Essen, 1993). Also, segmentation of scenes to their components and separation from the background is perhaps not possible strictly bottom-up as VISOR currently assumes, especially when the objects can be occluded. So far, it has been possible to give only partial answers to some of these questions, and others remain wide open.

Road Map: Vision

Related Reading: Routing Networks in Visual Cortex; Thalamus; Visual Scene Perception: Neurophysiology

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Visuomotor Coordination in Flies

Alexander Borst and Martin Egelhaaf

Introduction

Motion information plays a prominent role in the visual orientation of many animal species because the retinal images are continually displaced during self-motion. The resulting retinal motion patterns depend characteristically on the trajectory described by the animal as well as on the particular three-dimensional structure of the visual environment.

Consider, for instance, three common situations. (1) When an animal deviates from its course, the retinal image of the entire visual environment is coherently displaced in the opposite direction. (2) In contrast, the approach toward an obstacle leads to an expansion of the retinal image. In other words, all elements in the image move centrifugally away from the point that the animal is approaching. (3) When the animal passes a nearby object in front of a more distant background, the retinal images of the object and the background move at different velocities. This difference leads to discontinuities in the motion pattern. All of these retinal motion patterns induced by self-motion are particularly pronounced in fast-moving animals and especially in flying animals.

If evaluated appropriately, these different types of motion patterns can be used to guide visual orientation. (1) Rotatory

large-field motion may signal to the animal unintended deviations from its course; thus, a system extracting this type of motion pattern could be an integral part of an autopilot which compensates for these deviations by corrective steering maneuvers (*optomotor response*). (2) Image expansion signals that the animal approaches an obstacle; a system evaluating this type of motion pattern may initiate deceleration and control extension of the legs to avoid crash landing (*landing response*). (3) Finally, discontinuities in the retinal motion field and small-field motion indicate nearby stationary or moving objects; therefore, mechanisms sensitive to this type of motion pattern may be part of a fixation system which induces turning reactions toward objects (*object response*).

The mechanisms underlying the extraction of these retinal motion patterns and their transformation into the appropriate motor activity have been analyzed extensively in the fly. Since the fly's orientation behavior relies heavily on motion information, its visual system was found to be highly specialized with respect to motion vision. Moreover, the fly's nervous system is amenable to an analysis on the basis of nerve cells which can be identified individually in each animal. This feature is a great advantage for an analysis of biological information processing in terms of neuronal circuits.

The Visuomotor System of the Fly

The transformation of the retinal images into appropriate motor activities is the consequence of specific biophysical properties of nerve cells and their connection patterns. Figure 1 summarizes those features of the fly's nervous system which are most relevant in the current context. The retinal images are initially transformed by a sequence of successive retinotopically organized layers of columnar nerve cells. At the level of the lobula plate, large-field elements are found which integrate the output signals of columnar neurons. These large-field cells connect to other brain areas or, through descending neurons, to the motor control centers. All of these large-field cells respond selectively to motion in a particular direction and play an important role in extracting the different types of retinal motion patterns. Because of their extraordinary structural constancy and highly invariant physiological properties, they can be identified individually in each animal (Strausfeld, 1989; Hausen and Egelhaaf, 1989). The motor output consists of indirect power muscles, which keep the thorax and the wings oscillating during flight, and a system of small steering muscles, which insert on various sclerites at the wing base and influence the wing posture during up- and downstrokes. While visual afferences to the power muscles mainly affect lift and thrust reactions of the fly, visual input to the steering muscles is important for the control of different kinds of flight maneuvers, such as torque (Heide, 1983).

Studies on Visual Orientation of the Fly

Although fly visual orientation has been studied also under free-flight conditions (Wagner, 1985), free-flight behavior is often too complex for a systematic analysis. In a more reductionist approach, therefore, most behavioral experiments were done on tethered flying animals under well-defined and sufficiently simple visual stimulus conditions which made it possible

to establish stimulus-response relationships quantitatively. Visually induced turning responses were monitored by mounting the tethered flying fly to a torque meter and stimulating it with patterns of different size which could be moved with various velocities into different directions (Buchner, 1984; Heisenberg and Wolf, 1984). Essentially the same stimulus conditions were employed to investigate the visual release mechanisms of landing. In these experiments, the extension of the fly's forelegs was monitored by means of a light barrier. The leg extension is a fixed-action pattern which characterizes the initial phase of the landing response and is accompanied by deceleration of the animal (Borst, 1990).

From this sort of black box analysis, models of the underlying mechanisms could be derived. These models allowed us to design the appropriate visual stimuli for the identification of those neurons which may correspond to the different model elements (Hausen and Egelhaaf, 1989; Borst, 1990; Egelhaaf and Borst, 1993b). The outcome of this analysis is summarized below. However, it should be kept in mind that the analysis builds on knowledge of only a few dozen neurons (mainly the large ones) among the approximately 300,000 nerve cells of a fly brain. It also considers mainly those behaviors which can be observed in the laboratory during tethered flight. Thus, the scope can only be to explain the control of some behavioral components through well-defined retinal motion patterns, and not to understand the subject of fly vision and control of aerobic flight maneuvers in its entirety.

Stages of Motion Computation

The only information available to the visual system is given by the time-dependent brightness values of the retinal image as sensed by the photoreceptors. The retinal input is transformed into the corresponding behavioral output in three principal steps: (1) Motion in the different parts of the retinal image

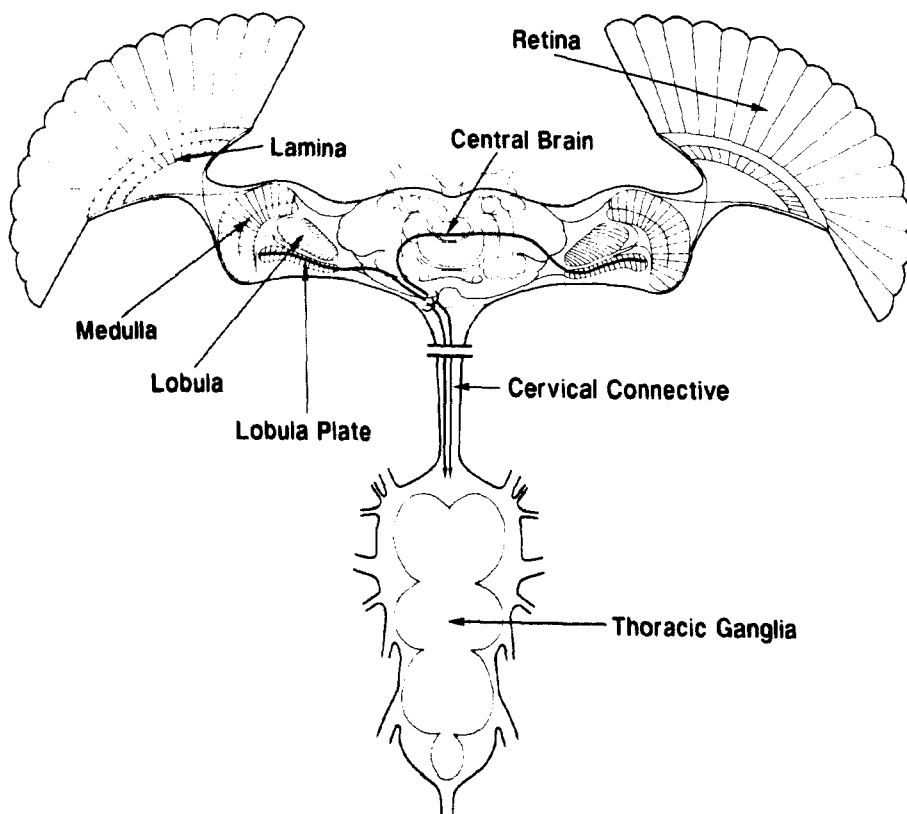


Figure 1. Schematic horizontal cross-section through the nervous system of the fly, with the retina; the three visual ganglia (lamina, medulla, and lobula complex, which is subdivided into the anterior lobula and the posterior lobula plate); the central brain; and the thoracic ganglia, with the motor control centers. (Modified from Hausen, 1984.)

is computed in parallel by two-dimensional retinotopic arrays of local movement detectors. (2) From their signals, various retinal motion patterns are extracted by spatial integration over arrays of appropriately directed local movement detectors. (3) The dynamical properties of these representations of retinal motion are tuned by temporal filtering to the needs of the fly in free flight.

Local Movement Detection

Motion in different parts of the visual field usually does not have the same direction and velocity (Figure 2, top). As a first step of motion analysis, therefore, a local representation of the different motion vectors must be computed. This process is done in parallel by local movement detectors. These are organized in two-dimensional retinotopic arrays which cover the entire visual field (Figure 2, center). On the basis of a behavioral analysis, many years ago, W. Reichardt and B. Hassen-

stein proposed a formal model of such a local movement detector, the *correlation-type movement detector* (Figure 2, bottom) (Reichardt, 1961, 1987; Buchner, 1984; Borst and Egelhaaf, 1993). It consists of two mirror-symmetrical subunits. Their output signals are subtracted from each other. Each subunit has two input channels which become multiplied after one of the signals has been delayed by some sort of temporal filtering. Interestingly, this type of motion detector does not provide an exact measurement of the local pattern velocity. Its response also depends characteristically on the structure of the stimulus pattern. As a result, the instantaneous activity profile of a two-dimensional array of correlation-type motion detectors does not encode faithfully the geometrically calculated retinal motion pattern. Thus, additional processing steps are required to gain meaningful motion information from the output of local movement detectors and, in particular, useful representations of the different retinal motion patterns.

Extraction of Different Retinal Motion Patterns

The different types of motion patterns are characterized by different directions and velocities in the different parts of the visual field. Hence, specific information about the different retinal motion patterns can be extracted by intra- and interocular spatial integration over appropriately oriented local movement detectors. In the fly, this process occurs mainly in the lobula plate (see Figure 1), where motion-sensitive neurons with large dendrites are found. All of these neurons are activated by motion in a particular direction and are inhibited by motion in the respective opposite direction (Hausen, 1984; Hausen and Egelhaaf, 1989). Two functional classes of output elements of the lobula plate are particularly important in the current context, the *horizontal cells* (HS cells) and *figure detection cells* (FD cells) (Hausen and Egelhaaf, 1989; Egelhaaf and Borst, 1993b).

There are three HS cells which cover the dorsal, medial, and ventral parts of the lobula plate (Figure 3A). They are excited by motion from the front to the back in the dorsal, medial, and ventral parts of the ipsilateral visual field, respectively. Their responses increase, although not linearly, with increasing size of the stimulus pattern (Figure 3B). As a result of synaptic input from another identified large-field element of the contralateral lobula plate, part of the HS cells also respond to motion from the back to the front in the contralateral visual field. This input organization makes the HS cells particularly sensitive to coherent rotatory large-field motion around the animal's vertical axis. In studies where the HS cells were ablated from the circuit by microsurgical, laser, or genetic techniques, the large-field optomotor response was severely impaired (Heisenberg and Wolf, 1984; Hausen and Egelhaaf, 1989). Thus, the HS cells are likely to be part of the fly's autopilot, which compensates for unintended turns of the fly from its course.

The FD cells are a group of at least four output elements of the lobula plate which are all selectively tuned to small-field motion. For example, the FD1 cell is shown in Figure 3A. Its response is greatest during stimulation with a small pattern and declines when the stimulus pattern becomes larger (see Figure 3C). In contrast to many small-field cells found in other animals which have spatially separated excitatory and inhibitory subregions of their receptive field, the FD cells are excited by a small moving object anywhere within their receptive field of the ipsilateral eye. Ablation experiments demonstrated that the small-field tuning of the FD1 cell is mediated through inhibition by a single identified neuron, the ventral centrifugal horizontal (VCH) cell: After photoinactivation of the VCH cell, the small-field tuning of the FD1 cell was selectively lost (Egelhaaf

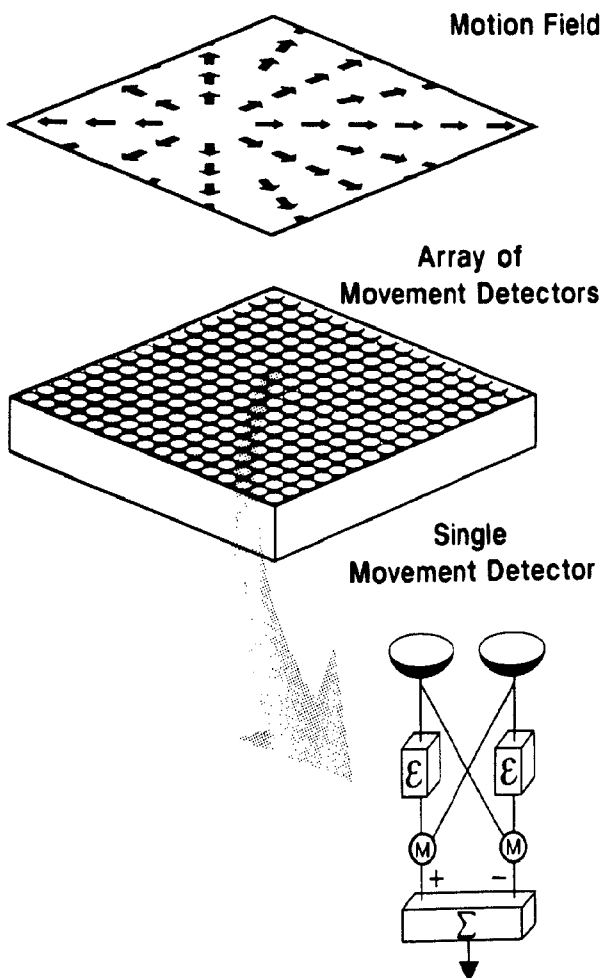


Figure 2. In the first step of motion analysis, motion in different parts of the visual field is computed in parallel by two-dimensional arrays of local movement detectors. The upper diagram shows an example of a retinal motion pattern. The middle diagram shows a two-dimensional array of movement detectors. The bottom diagram shows a correlation-type movement detector as a representative of a local motion detection mechanism. In its simplest form, its input is given by the light intensities as measured at two points in space. In each subunit, the detector input signals are multiplied (M) with each other after one of them has been delayed by some sort of temporal filter (ϵ). The outputs of both mirror-symmetrical subunits are then subtracted to give the final output signal of the detector.

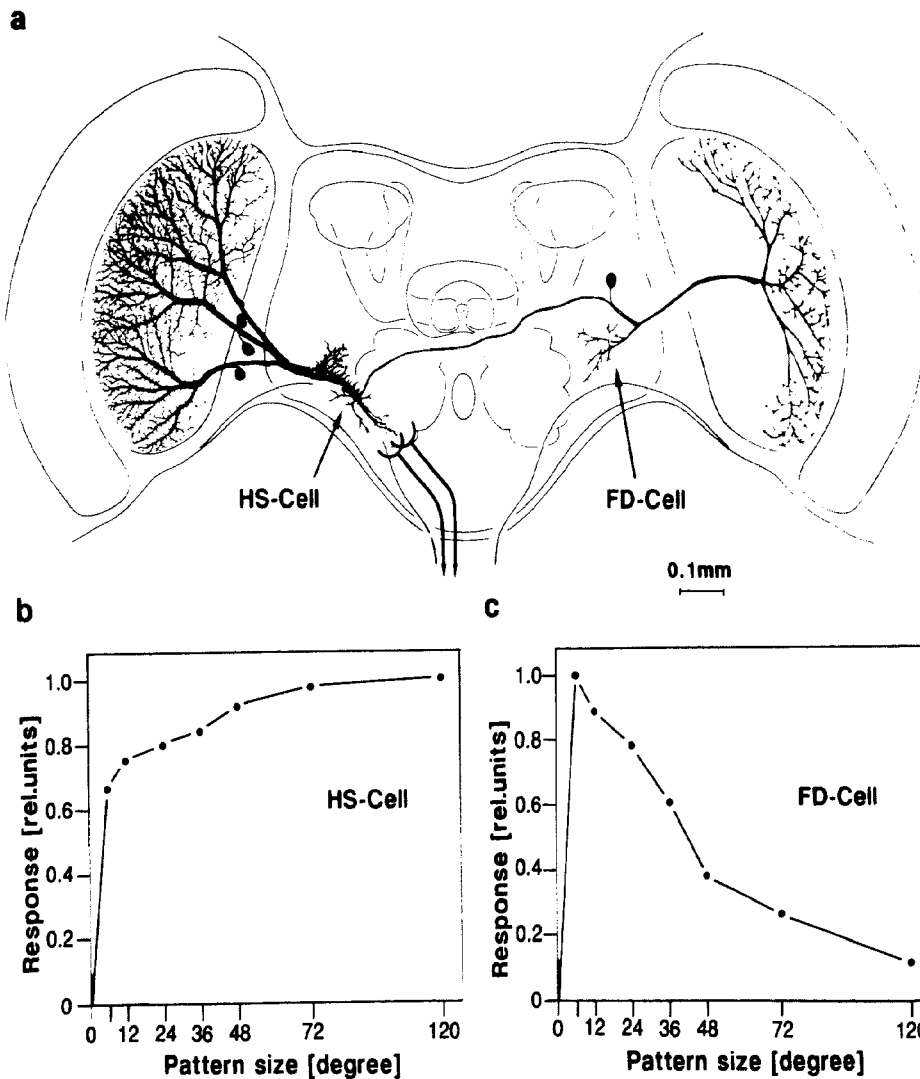


Figure 3. Spatial integration properties of neural elements in the fly's lobula plate extracting coherent rotatory large-field motion (HS cells) and small-field motion (FD cells), respectively. *A*, Frontal projection of arborizations of the three HS cells (shown in the left optic lobe) and one of the FD cells, the FD1 cell (shown in the right optic lobe). The HS cells were reconstructed from cobalt stainings (courtesy Klaus Hausen) and the FD1 cell from intracellular Lucifer yellow staining. *B* and *C*, Dependence of the mean response amplitude of an HS cell and an FD1 cell on the size of the stimulus pattern. The pattern was a random texture, the angular horizontal extent of which was varied. Whereas the response of the HS cell reaches its maximum for motion of large patterns, the response of the FD cell is strongest when a small pattern is moved in its receptive field.

and Borst, 1993b). The similarity between the functional properties of the FD cells and the dependence of visually induced turning responses on the different stimulus parameters suggests that the FD cells may control turns of the animal toward objects.

Visual interneurons extracting some representation of image expansion from the activity profiles of the retinotopic array of movement detectors have only been found in the cervical connective (see Figure 1). These cells' responses are strongest when the animal approaches an obstacle or a potential landing site. Their responses to different motion stimuli correlate well with changes in landing responses seen in behavioral experiments, suggesting that they are part of the neuronal circuit initiating landing behavior (Borst, 1990).

Temporal Tuning

The different types of motion patterns are characterized by their specific geometrical properties and also have specific dynamic features, as reflected in the temporal tuning of the respective control systems.

At the level of the lobula plate, the different motion-sensitive neurons still have similar dynamical properties (Egelhaaf and Borst, 1993a, 1993b). In the pathway tuned to coherent rotatory large-field motion, these signals become temporally low-pass filtered somewhere between the lobula plate and the steer-

ing muscles which mediate the compensatory turning responses (Egelhaaf, 1991). Since active turns of the fly in free flight are brief and rapid (Wagner, 1985), the resulting retinal large-field motion consequently is also characterized by fast changes in its direction. Because of the dynamical tuning of the fly's autopilot, these deviations from course are not well compensated for by corrective steering maneuvers. Hence, the temporal tuning might be a simple computational means to prevent the visual consequences of active turns from being compensated for by the autopilot.

Some sort of low-pass filtering is also taking place in the fly's landing system, as suggested by experiments where the latency of the leg extension which accompanies the initiation of landing was found to vary with the stimulus strength in a graded way (Borst, 1990). The low-pass filter, in combination with a threshold device, converts the stimulus strength into a wide range of response latencies. A weak stimulus, such as a slowly expanding pattern, leads only to a slow increase in the temporally integrated signal and thus to a large response latency, whereas a strong stimulus, such as a pattern expanding with a higher velocity, leads to a rapid increase in the temporally integrated signal and thus needs less time to reach threshold. This capability ensures that the fly initiates landing earlier when it approaches a potential landing site with a higher velocity than when it reaches a site with a lower velocity and, thus, leads to a safe landing.

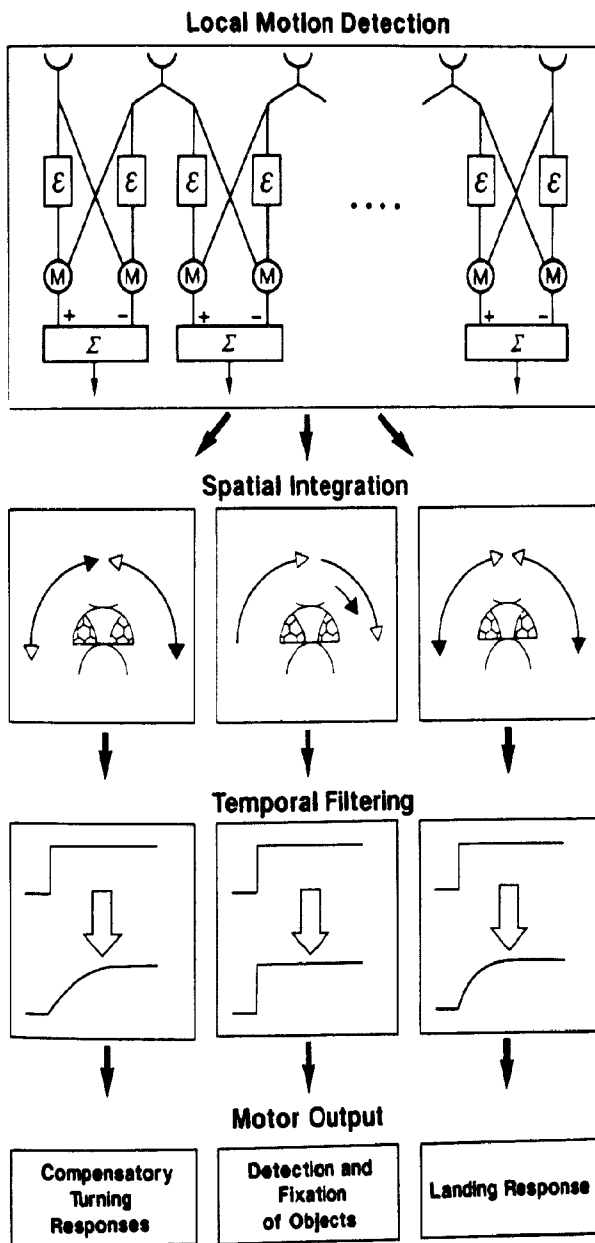


Figure 4. Summary diagram of the principal steps of motion information processing in the fly visual system. The top part illustrates detection of local motion by large retinotopic arrays of movement detectors. Only three detectors are shown (for abbreviations, see the legend of Figure 2). Next, the initial representation of local motion segregates into three pathways which extract different retinal motion patterns: rotatory large-field motion (left), relative motion of an object and its background (middle), and pattern expansion (right). The arrows indicate the direction of pattern motion; filled and open arrowheads indicate excitation and inhibition, and long and small arrows indicate large-field and small-field motion, respectively. The third part of the diagram shows temporal tuning of the representations of rotatory large-field motion and pattern expansion by some sort of low-pass filters with different time constants. The signals before and after the filters are shown in response to an onset of motion. The different pathways are involved in mediating different types of orientation behavior, as illustrated by the final part of the diagram.

Discussion

The features of the different retinal motion patterns which are important for flight control are extracted in a series of processing steps (Figure 4). (1) The initial explicit representation of motion is computed in parallel by retinotopic arrays of local motion detectors. (2) This representation is then segregated into different pathways which are selectively tuned to the different retinal motion patterns and feed different control systems of visual orientation behavior. This spatial tuning is achieved by appropriate inter- and intraocular spatial integration. (3) Before exerting their influence on the motor control centers, the signals are tuned by appropriate temporal filtering to the characteristic dynamical properties of the retinal motion fields as induced during different flight maneuvers.

Despite the relative simplicity of the computations underlying the different control systems, the problems they solve are of widespread relevance. There is good evidence from electrophysiological, behavioral, and psychophysical studies of similar mechanisms in such phylogenetically distant animals as insects and mammals, including humans (Egelhaaf and Borst, 1993a). These similarities hint at a convergent evolution and thus to some degree of optimal adaptive value of the mechanisms of motion processing exploited by biological systems. In contrast to technical systems, these mechanisms are not exact in a mathematical sense, but are fast, reliable, and robust against noisy signals. These features could make them attractive models for low-level processors in artificial seeing systems for robots (e.g., Franceschini, Pichon, and Blanes, 1992).

Road Map: Motor Pattern Generators and Neuroethology

Related Reading: Active Vision; Directional Selectivity in the Retina; Locust Flight: Components and Mechanisms in the Motor; Motion Perception; Reactive Robotic Systems

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Visuomotor Coordination in Frogs and Toads

Francisco Cervantes-Pérez

Introduction

The study of visually guided behaviors in amphibians, as in many other animals, has become significant for scientists working in a variety of fields. In neurobiology (see Llinás and Precht, 1976; Fite, 1976; Vanegas, 1984) and computational neuroscience (see articles by Arbib, Betts, Cervantes-Pérez, an der Heiden, and Lara in Ewert and Arbib, 1989), scientists are pursuing the quest for the understanding of how the animal's central nervous system (CNS) integrates the processing of sensory information to control motor behavior. Scientists working in artificial intelligence and robotics use functional principles generated in the study of living animals (e.g., amphibians) as models to build computer systems to control automata that display complex sensorimotor behaviors (see article by Arkin in Ewert and Arbib, 1989; NEUROETHOLOGY, COMPUTATIONAL, and REACTIVE ROBOTIC SYSTEMS).

Although anuran amphibians (frogs and toads) live in a three-dimensional world rich in multiple modes of sensory signals (e.g., visual, tactile, and olfactory), their behavior is guided primarily by visual information. Therefore, they have been studied mostly under visuomotor coordination paradigms. In these animals, visuomotor integration implies a complex transformation of sensory data, since the same locus of retinal activation might release different types of behavior, some directed toward the stimulus (e.g., prey catching) and others directed to an opposite part of the visual field (e.g., predator avoidance). Furthermore, the efficacy of visual stimuli to release a response (i.e., type of behavior, intensity, and frequency) is determined by many factors: (1) the stimulus situation (e.g., form, size, velocity, geometric configuration with respect to the direction of motion, spatiotemporal relationship with the animal); (2) the current state of internal variables of the organism, especially those related to motivational changes (e.g., season of the year, food deprivation); (3) previous experience with the stimulus (e.g., learning, conditioning, habituation); and (4) the physical condition of the animal's CNS (e.g., brain lesions). Thus, to define the next behavior required to interact with a specific external situation, other sensory signals (e.g., kinesthetic information about the muscles and joints intervening in the execution of the behavior), as well as signals indicating the state of motivational variables and of learning processes, must be integrated with those signals encoded in the locus and level of retinal activation.

In searching for the neural mechanisms responsible for connecting the presentation of a visual stimulus with the elicitation of a specific behavior, experimental and theoretical studies have generated and analyzed a series of hypotheses pointing at the interactions among neural elements of the retina, the optic tectum, and the thalamic-pretectal region, or *pretectum*, as the underlying mechanisms. For example, it has been proposed that the locus of activity within the optic tectum and pretectum

defines the spatial location of visual stimuli and the direction of prey-catching and predator-avoidance behaviors (see Lara, Cromarty, and Arbib, 1982; Cervantes-Pérez, Lara, and Arbib, 1985; Liaw and Arbib, 1993; articles by Ewert and Grobstein in Ewert and Arbib, 1989; article by Cobas and Arbib in Arbib and Ewert, 1991).

Visually Guided Behaviors in Amphibians

Ethological results show that amphibians are capable of interacting with a wide variety of moving and nonmoving visual stimuli by presenting motor actions that can be classified into different behavioral patterns.

Responses to nonmoving stimuli. Diverse stationary objects may influence the animal's next action. In general, frogs move toward zones in the visual field where blue is preponderant, probably because this situation might be associated with the location of a pond (a proper habitat) and other stimuli whose presence is important for the frog's survival (e.g., prey to eat, water to maintain its body humidity) (see article by Grüsser and Grüsser-Cornhels in Llinás and Precht, 1976). When an obstacle, such as a barrier or chasm, is placed between the amphibian and potential prey, toads display *detour behavior*, following predictable routes to avoid the obstacle and catch the prey (see article by Arbib in Ewert and Arbib, 1989).

Mating. During the spring mating season, the presence of a female in a male's visual field may elicit: (1) an *orienting* response toward the female if she appears in the peripheral part of the visual field; (2) an *approaching* action to reduce the distance to the female when she is far afield in the binocular field; and (3) a *clasp* behavior if the female is within reaching distance in the frontal part of the visual field (Kondrashev, 1987).

Predator avoidance. Large stimuli at close distances may yield one of several avoidance behaviors in the frog and toad, depending on its parametric composition. A flying stimulus close to a frog releases a *ducking* behavior, but when it is far afield, the frog *orients* toward the opposite direction and *jumps* or *runs away*. In the presence of a ground predator, toads display a stiff-legged posture, puffing up and *orienting* toward the predator, and *tilting* the body. Then, they *sidestep* or *jump away* from the predator's location (see Liaw and Arbib, 1993; articles by Ingle and Ewert in Fite, 1976; Ewert in Vanegas, 1984; Cobas and Arbib in Arbib and Ewert, 1991).

Prey acquisition. The presence of potential prey may elicit an action from the following repertoire: (1) amphibians *orient* the head and body toward prey appearing in the peripheral part of