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Higher-Order Figure Discrimination in Fly and Human Vision

Minireview

Jacob W. Aptekar and Mark A. Frye

Visually-guided animals rely on their ability to stabilize the panorama and simultaneously track salient objects, or figures, that are distinct from the background in order to avoid predators, pursue food resources and mates, and navigate spatially. Visual figures are distinguished by luminance signals that produce coherent motion cues as well as more enigmatic 'higher-order' statistical features. Figure discrimination is thus a complex form of motion vision requiring specialized neural processing. In this minireview, we will highlight recent advances in understanding the perceptual, behavioral, and neurophysiological basis of higher-order figure detection in flies, much of which is grounded in the historical perspective and mechanistic underpinnings of human psychophysics.

Our most conspicuous sensory modality is vision. As visual animals, we spend our days looking at features in the world, be they the words on this page or a Frisbee intercepted at a full sprint. We do not generally think about the physical properties of the visual world, we just see it. Yet the properties of the things we see are complex and ever changing. A Frisbee in flight has texture and color properties that contrast it against the sky. Some of its properties, like the rotation of the disk, do not themselves predict its trajectory, nor do they remain constant as it passes through shadows cast by background foliage. Yet we never lose sight of it, as our brain has combined these properties to classify it as a stable figure. Flies pursue visual figures such as gaps in the foliage, potential landing sites or conspecifics. How a figure is identified and tracked by flies is the subject of this minireview; we shall aim to highlight the ways in which this research is intimately connected with human visual psychophysics, and how the collective discoveries in flies and humans advance our understanding of the perceptual and computational properties of figure detection in general. We will not discuss one specialized form of figure detection, small target tracking [1–3], although some of the principles discussed here apply.

A figure is a spatially restricted visual object that is defined by difference in one or several *features* from the surround or ground. Thus, figure detection rests on the concept of *sensory discrimination*, one of the oldest areas of inquiry in neuroscience. In the 1830s, Ernst Weber and Gustav Fechner, who are credited with the invention of modern human psychophysics, performed the first quantitative studies of how humans encode sensory information by measuring subjects' ability to discriminate the relative weight of two objects. This task formed the basis of Weber's Law, which states that during discrimination, sensory systems encode a proportionate difference between two intensities rather than an absolute one.

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This class of Weber-like psychophysical laws effectively describes how two stimuli can be discriminated by a single measure, such as the intensity of illumination, which substantiates a quantitative difference. But Weber's law cannot explain discrimination when two stimuli are qualitatively different, such as a bright green figure compared to a dark red ground. Here, discrimination could be achieved either on the basis of any single difference, such as color, contrast or shape, by a Weber-like mechanism, or on an abstract, categorical basis incorporating all of these direct, sensory comparisons. In response to the insufficiency of Weber's law to explain categorical discrimination, Stanley Smith Stevens and H. Richard Blackwell argued for two fundamentally different paradigms: a *prothetic* intensity-based mechanism that discriminated sensory inputs on the basis of a single physically measurable difference, like luminance, and a *metathetic* mechanism that discriminates sensory inputs on the basis of abstract categorization, rather than physical signal strength [4,5].

Because figures must differ from the ground in at least one perceptible feature, but, in practice, often differ in several, figure-detection falls under the metathetic category of sensory discrimination tasks. This classification also implies a parallelization of the underlying neural mechanisms, whereby multiple detectable features are encoded simultaneously by the nervous system and are compared combinatorially to distinguish figures [6,7]. Behavioral examination of this type of perceptual network continues to be a central aim of human psychophysics research.

This metathetic schema is also congruent with neurophysiology. At the time it was conceived, metathetic discrimination resurrected the earliest theories of the nervous system as a parallel network of neural quanta, each tuned to different aspects of sensory stimuli and compared to reach a decision threshold. In modern terms, we use figure-detection as a way to interrogate the neurophysiological basis of sensory coding. The challenge now, as then, remains finding where the separable neural quanta exist at the subcellular, cellular, and cell circuit levels of organization. It has turned out that the complexity of visual feature detection ascribed to multiple streams of processing in the human cortex is also seen in the fly.

Translating from Model Systems

Human psychophysics contributed a strong theoretical foundation to the study of figure-detection, yet studying the cellular basis of perceptual networks required model systems. Fortuitously, while psychologists were developing their theories in human subjects, a group of German physicists had taken a different tack to understanding sensory coding. They reasoned that the optical properties of the world imposed fundamental constraints upon the visual systems of all animals. Therefore, they undertook a comparative cybernetic approach to study vision in insects as a model for discovering basic mechanisms of visual perception.

In 1956, Bernhard Hassenstein and Werner Reichardt [8] demonstrated that a walking beetle would turn to compensate an illusory motion stimulus consisting of paired light flashes delivered to neighboring ommatidial facets of its compound eye with a time delay. With this experiment,

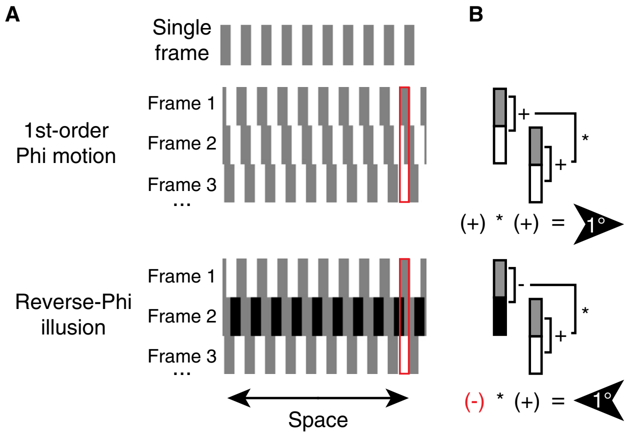

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Figure 1. Reverse-Phi illusion.

(A) Three movie frames showing a square-wave grating that is displaced one fixed step to the right per frame in a sequence that generates a first-order motion percept. In the lower panel, each frame inverts the contrast polarity of the grating, generating reverse-Phi motion. While the flickering bars move right, the first-order motion component of the reverse Phi illusion appears to move to the left. (B) At a sample spatial location, a frame-by-frame spatial shift of one half of the grating pattern is highlighted by the red box in (A). The contrast changes are compared by multiplication. A contrast transition that increments darker-to-brighter (+) is multiplied with a following one that also increments brighter (+), and the resultant EMD-based directional perception reveals the true direction of translation to the right (first-order motion direction, black arrowhead). For the reverse-Phi stimulus, the frame-by-frame displacement of the grating is the same, but background flicker interferes with the motion-detection operation of the EMD. At the same spatial location, contrast transition to darker (–) is multiplied by an increment brighter (+), inverting the perceived direction of motion toward the left (first-order motion direction, arrowhead). This demonstrates how contrast inversion can interfere with first-order motion detection by an EMD mechanism.

they developed the lasting theory of an ‘elementary motion detector’ (EMD). An EMD temporally correlates the luminance signal traversing two spatially separate inputs. In the classical formulation of the difference across mirror-symmetric subunits, this mechanism gives a positive response to luminance-defined motion in one direction and a negative response to such motion in the opposite direction.

Remarkably, the theoretical EMD model, derived from an insect, can also account for a phenomenon first described for human subjects in 1912 and codified thereafter [9,10]: when a bar with alternating contrast is moved through the visual field of human subjects under certain conditions, it elicits a percept of motion in the direction opposite its actual direction of movement (Figure 1A). Reichardt’s EMD model explains this phenomenon, called reverse Phi motion, as resulting from the absence of a rectification stage in the EMD, without which the contrast inversions lead to a corresponding directionally-reversed output of the EMD, and correspondingly inverted percept of motion (Figure 1B). Even with 600 million years of evolution separating insects and humans, the explanatory efficacy of the EMD demonstrates that the perceptual networks of these organisms can be studied to mutual benefit.

The Optomotor Assay

The perceptual decision tasks that psychophysicists rely on are not easily translated to non-primates. There is a useful alternative available, however: the optomotor response, or reflex. These reflexes, analogous to the optokinetic responses in animals with articulated eyes, are compensatory turning movements to minimize the image slip associated with motion perturbations on the retina. Karl Götz developed a durable paradigm for studying the optomotor response in flying insects when he tethered a fruit fly between a pair of programmable projection screens to demonstrate that sequences of static images strung together to form a movie (Phi motion) evoked robust flight optomotor steering maneuvers [11]. This optomotor assay is robust, repeatable, and can demonstrate the formulation of complex visual motion percepts, transduced through the steering system of the fly.

Reichardt and Poggio [12,13] adapted a similar paradigm in large flies to demonstrate that the sensitivity to a figure varies as a function not only of its motion velocity relative to the visual ground, but also upon its position on the retina. Their colleague Pick [14] took this idea one step further by simply placing a static flickering bar at various locations in the arena and showing that the fly’s steering slowly became biased towards the stationary figure. Henceforth, the optomotor flight assay entered the canon of neuroscientific tools with which to study figure-detection.

Higher Order Motion Percepts

The importance of higher order motion detection to figure-tracking is manifest in the abstract nature of figures. Whereas the EMD explains how figures painted with rigid textures can be tracked, it fails with figures defined by any other variation in spatiotemporal statistics. As Götz argued his case for the optomotor response as a method for interrogating fly motion perception, the human psychophysics community, led by George Sperling, was extending the study of motion perception beyond the EMD. Whereas Stevens had recognized the insufficiency of Weber’s law to explain complex discrimination tasks like figure detection, Sperling [15,16] had recognized the insufficiency of the EMD to explain higher-order percepts of motion. In particular, to generate a motion percept the EMD encoded coherent modulation of mean intensity over space and time within a region of the visual field (Figure 2A).

This construction of the EMD was insufficient, however, to explain how human subjects can readily perceive and track a figure defined, for example, by a difference in the luminance envelope of a sinusoidal grating, with no difference in mean luminance between the figure and ground (Figure 2B). This amounts to a modulation of the second moment of the grating. For this reason, Sperling called this *second-order* motion and EMD-detectable motion *first-order* motion.

The identification of two mechanisms within motion vision explained a key aspect of the reverse Phi illusion: subjects perceive the illusory regressive motion most strongly when they are viewed in the periphery. When viewed in the fovea, the illusion fails and subjects instead perceive that the pattern is composed of flickering components moving in the true progressive direction. Sperling’s theory argued that both first-order and second-order motion features are being computed in parallel and compared, on a spatial receptive-field, or more generally a ‘perceptive-field’, basis. The failure of the reverse Phi illusion in the fovea argues that the second-order system dominates in the foveal field, whereas the first-order system dominates in the periphery [17,18].

Sperling studied motion signals defined rigorously by the first and second moments of luminance, but his work also

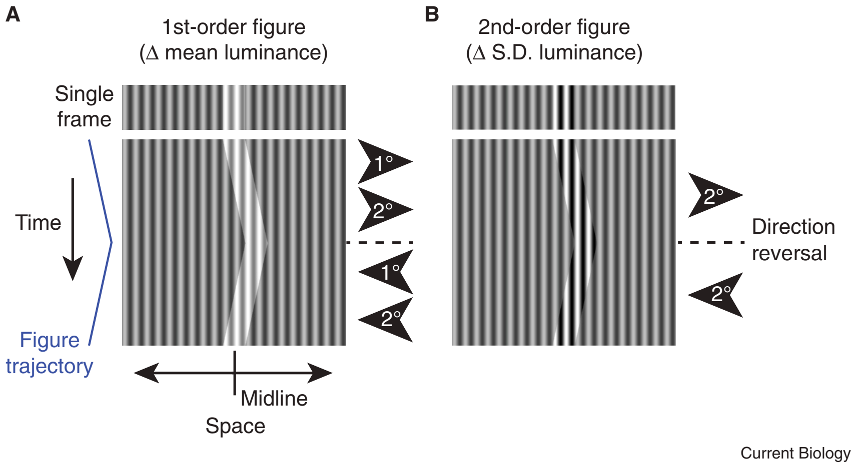


Figure 2. First-order and second-order motion cues.

(A) A stationary, contrast-modulated sinusoidal grating pattern contains a narrow region with increased first-moment or mean luminance (first-order). Note that the stationary single frame contains no variation in the vertical dimension. Therefore, instead of displaying each full frame (as in Figure 1), the space-time graph represents each full frame with a single row of pixels. The stack of rows, one for each frame of the movie, compactly shows how the display changes over time. Oscillating the luminance figure back and forth across the visual midline produces first-order motion signals signaled by an EMD. (B) A stationary sinusoidal grating pattern has a fixed mean luminance, but contains a narrow region of increased second central moment or standard deviation of luminance (second-order). Oscillating the second-order figure is invisible to a standard EMD, yet is readily perceptible to humans and flies. Arrowheads indicate the direction of first-order and second-order motion components.

opened the field more generally to classes of *higher-order* motion that cannot be defined simply by taking more moments of the signal distribution. Adelson and Movshon [19] and Zanker [20] pioneered the use of two classes of stimuli, plaids and theta motion, to investigate the separability of first- and higher-order perceptual streams. Higher-order figures contain pattern features that are not detected by directionally selective first-order or second-order mechanisms.

Plaids

Plaids are an extension of the sinusoidal gratings used to study spatial frequency tuning in motion vision. The sum of two drifting gratings that differ in speed, period, or orientation, produces a 'plaid' (Figure 3A). Plaids have two natural orientations of motion: first, there is a single motion direction defined by the vector sum of the first-order motion cues arising from the offset gratings (Figure 3B, $\Sigma 1^{st}$ order). And, second, there is a single 'rigid direction,' which is formulated by an 'intersection of constraints' originating from the motion vectors of the two sinusoidal components [19]. Abstractly, the rigid direction is the vector along which a picture of the plaid printed on a sheet of paper would have to be moved in order to reproduce the movie generated by the superposed gratings (Figure 3B, pattern motion, red arrowhead). Importantly, the rigid direction cannot be computed locally by an EMD-based mechanism, but instead requires sensitivity to pattern features within the plaid.

This phenomenon has recently been applied to studying visual processing in the blowfly. Measurements of both the optomotor response and spiking responses of several large interneurons (lobula plate tangential cells, LPTCs) to panoramic wide-field translation of a plaid pattern were made at various angular orientations [21]. These LPTCs had historically been interrogated with first-order gratings showing they are directionally tuned with approximately cosine precision. The optomotor responses of flies presented with these stimuli showed a bimodal distribution over the angular orientations of the plaid, which is evidence that the animals are insensitive to motion in the higher-order rigid or pattern motion direction (Figure 3C). However, recordings from LPTCs revealed that, while several have the bimodal tuning profile that indicates sensitivity to only the first-order components of the plaid, at least one cell showed the unimodal tuning to the orientation of the higher-order rigid direction. Thus, Saleem *et al.* [21] found at least a trace of higher-order pattern motion sensitivity in this lobula plate circuitry.

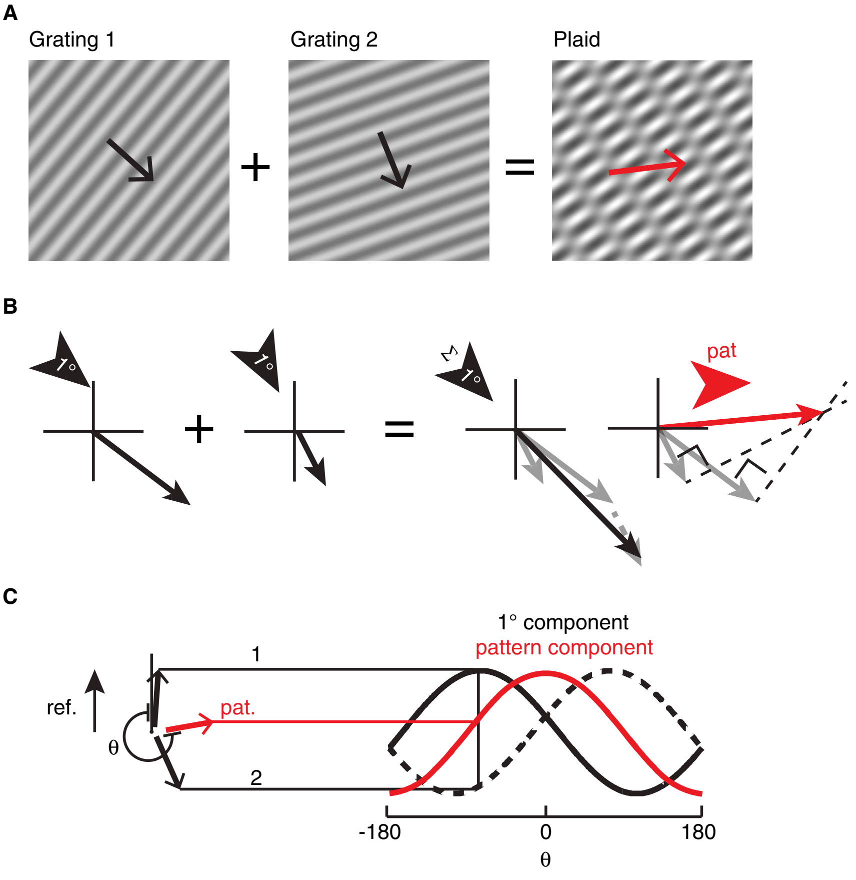
Theta Motion

A figure composed of a random pattern texture moving against the similarly textured stationary ground generates first-order motion (Figure 4A, left). A theta figure is one in which the surface texture generates a directional first-order motion percept that exactly opposes the direction of the figure itself: for example, every rightward increment of first-order motion is matched by a leftward increment of higher-order motion (Figure 4A, right). For this reason, tracking of a theta object is necessarily achieved combinatorially from first-order, second-order and higher-order motion detection mechanisms. The phenomenology of theta object tracking was explored first in humans, but building upon the now well-established optomotor assay, it has subsequently been extended to flies [20,22–26].

As a stimulus class, theta motion shares some similarity with plaids, because it presents the observer with an entangled pair of motion percepts that can be used to experimentally isolate the relative contribution of two processing streams. Theta stimuli are substantially more flexible than plaids, however, because the degree of anti-correlation between the first-order and higher-order components can be varied parametrically by the experimenter. In our lab, we recently exploited this flexibility to demonstrate that, when presented with a vertical bar where the relative gain between the surface texture and the figure motion is varied systematically between –1 (a higher-order theta figure) and +1 (a solid first-order figure), *Drosophila* show composite tracking of both the first-order and higher-order motion components in nearly linear superposition [27]. This insight pointed a way towards separating perceptual streams in a behavioral assay. While decision-theory in humans had argued that figure-*discrimination* arose from a winner-take-all voting between parallelized visual percepts, this work in flies showed that the multiple tracking mechanisms might operate simultaneously and nonexclusively.

Figure 3. Plaids.

(A) Two sinusoidal gratings generate motion cues along their wave vector (black arrows) to produce first-order motion. Superimposing the gratings produces a plaid pattern that contains an emergent higher-order pattern orientation (red arrow). (B) The higher-order vector (red arrowhead) is the direction of pattern translation that produces each first-order motion component simultaneously (black arrowheads). This is determined geometrically as shown. (C) For a specific separation angle between the first-order components (θ =150 deg), systematically rotating the grating vectors together produces a bimodal tuning of perceived first-order components, and a unimodal tuning of the second-order pattern vector. Only the bimodal first-order component (C) is detectable by a standard EMD.



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Spatial and Dynamical Separation of Parallel Motion Streams

In order to measure the simultaneous influence of several perceptual streams on figure-tracking, our group developed a white noise stimulus in which the temporal modulation of the first- and higher-order motion components — referred to as ‘elementary motion’ (EM) and ‘figure motion’ (FM) — is orthogonal or independent under the conditions of impulse response calculation (Figure 4B). In this set-up, involving what is essentially a decoupled theta bar, the first-order velocity of the figure’s surface texture (EM) moves independently from the position of the figure itself (FM). This approach has two advantages: first, having dynamically separable stimuli, which are linearly decorrelated from one another, allows the influence of each stimulus stream to be measured simultaneously. Second, because a figure is by definition spatially-restricted (it is small), the variations of EM and FM responses are measured at each spatial location across the retina (Figure 4C). The resultant spatial maps of temporal impulse responses are termed spatio-temporal action fields (STAFs), and highlight the distinct processing streams for first-order elementary motion and higher-order figure motion [28].

The STAFs we measured on behaving flies share a conceptual basis with the spatio-temporal receptive fields widely used in electrophysiology, and also with the *perceptive fields* used by psychophysicists from the mid-20th century. The idea of a perceptive field is simply that, within a region of the visual world, a particular feature is not only neurally encoded, but behaviorally salient. The term was coined by Lothar Spillmann who, in the 1970s, used a perceptive field mapping task — which relied on a subjective reporting of discrimination thresholds — to define the center-surround geometry of simple cells in humans nearly two decades before that geometry was corroborated by electrophysiology in monkeys [29,30] and recently for their analogous prerequisites in flies [31]. By analogy, STAFs define regionally specific sensitivities to various aspects of motion perception — perceptive fields — and thereby can predict characteristics of the underlying neural coding mechanisms.

The Computational Characteristics of Figure Coding

Recent work continues with this approach of using higher-order motion stimuli to interrogate the coding properties of motion-sensitive neurons in the fly. Calcium imaging from the horizontally-sensitive (HS) class of LPTCs has revealed a correlate in flies of the human reverse Phi illusion, with excitation to preferred-direction motion yet inhibition to reverse Phi motion in the same preferred direction [32]. While this is strong evidence that the motion inputs to HS cells are based in large part on the EMD, some enigmatic properties indicative of parallel higher-order processes have been recently reported for this cell type. In *Drosophila*, the reverse Phi sensitivity of HS cells is not identically inverted from the Phi responses [32], and whereas genetically silencing the cellular inputs believed to carry elementary motion signals to LPTCs indeed abolishes first-order optomotor responses to gratings [33], doing so does not abolish sensitivity to luminance flicker within the LPTCs themselves [34].

Are first and higher-order signals interacting within the same visual ganglion? In hoverflies, one newly discovered cell type of the lobula plate functions outside of the first-order motion stream. This novel cell type is exceptionally sensitive to wide-field flicker generated by high speed motion in any direction; it has the captivating property of being inhibited by a static grating and a receptive field that

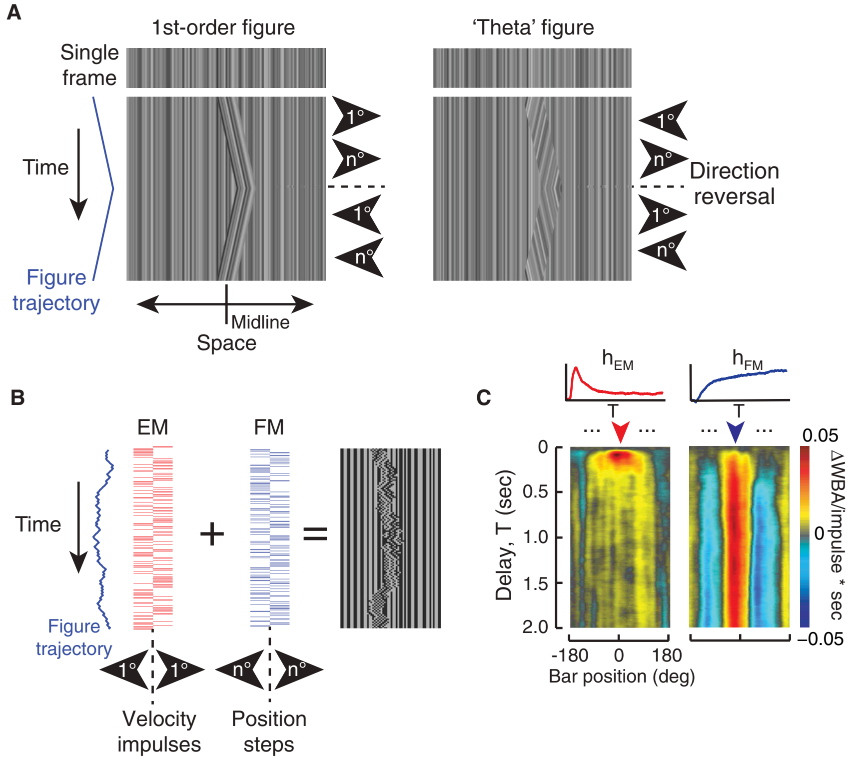

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Figure 4. Theta figures.

(A) An image composed of randomly assigned bright and dark vertical bars contains a figure composed of the same random pattern (and hence is indistinguishable in the static image). Oscillating the figure back and forth across the visual midline produces first-order motion signals detected by an EMD (left panel). A theta figure reverses the direction of first-order internal motion from the direction of the figure itself (right panel). The figure now contains opposing first-order and higher-order components. In practice, the first-order and higher-order components can be moved along independent arbitrary trajectories. (B) A random sequence of left and right motion impulses commands the first-order elementary motion (EM) of the internal figure surface. A second uncorrelated random sequence of left and right motion impulses (equivalent to position steps) commands the second-order figure motion (FM) to produce a compound stimulus. Note that the velocity impulses of the surface of the figure are independent from the position steps of the figure itself. (C) A fly's time-varying optomotor steering response to this compound stimulus is cross-correlated to each of the two input sequences to compute two linear temporal filters (impulse responses, h_{EM}, h_{FM}) with units wing beat amplitude (ΔWBA) per motion impulse seconds. These filters are computed for figure motion centered at each azimuthal position of a panoramic flight arena, color coded for amplitude, and plotted as a spatio-temporal action field (STAF). The STAFs highlight the spatial tuning, temporal dynamics, and independence of the subsystems serving FM and EM optomotor figure tracking, respectively [28].

abuts the visual midline; and it projects its axon terminals into the contralateral lobula plate. These properties make it well-suited to modulate the response properties of other LPTCs and, possibly, to augment higher-order motion sensitivity [35].

Indeed, this cell type seems to directly influence its neighbor, a member of the HS class (HSN), which spatially integrates local EMD input over much of the eye and, in hoverflies, has an uncharacteristically narrow receptive field that imparts remarkably strong sensitivity to the heavy contours present in natural scenes [36]. The directionally-selective HSN responds to the higher-order FM component of a theta figure crossing the center of its receptive field with an excitation that, paradoxically, is transiently equivalent to the response to EM in the same direction [37]. In this instance, the theta figure excites the cell despite containing EM only in the cell's inhibitory anti-preferred direction. Thus, the HSN encodes FM independently from first order signals. A linear model superimposing the cell's sensitivity to first-order EM and higher-order FM captures responses to theta figures containing both signals [37] in a manner consistent with flight optomotor responses by *Drosophila* to similar stimuli [28]. This cross-sensitivity to multiple visual features within the coding properties of even a single LPTC highlights the metathetic coding problem that Blackwell and Stevens had predicted: that perception of qualitatively different stimuli is instantiated neurally through a mixing of quantitatively separable motion processing streams.

The third optic ganglion of the fly visual pathway, the lobula plate, has been compared *sensu lato* with the motion-processing optic tectum of vertebrates (the superior colliculus in mammals), and the fourth visual ganglion, the lobula, with the visual cortex [38]. Lobula circuits show high-order feature extraction in dragonflies and fruit flies [3,38]. Advances in genetic techniques, such as the use of Gal4 lines and their derivatives in flies, and Thy1 and Cre lines and their derivatives in mice, has expanded the utility of these genetic model systems for studying high-order visual processing by advancing our ability to selectively image and inactivate small sub-populations of neurons. In one recent study [39], genetic silencing of neurons projecting from the lobula into the central protocerebrum of *Drosophila* compromised the animal's ability to behaviorally track theta figures, but did not affect the responses to first-order figures, hinting that circuits of the lobula represent focal points for higher-order feature processing, but are dispensable for computing first-order motion. However, extensive connectivity between the two ganglia complicates matters [40], and provides anatomical and conceptual scaffolding for the metathetic figure-coding framework.

The Way Forward

Due to the parallel metathetic processing of figures, improved genetic targeting tools have added experimental power but have also complicated efforts to determine the cellular mechanism of higher-order motion vision. For a system comprising many thousands of neurons, activity silencing that affects few or one of them may have only subtle effects on behavior, so that while the physiology of the ablated cells can be well-determined with imaging or electrophysiology, a behavioral phenotype for those cells may remain enigmatic. This limit is imposed in part by function; although there are satisfying examples in which a single cell may have a specific behavioral correlate — a 'labeled-line' [41] — this cannot be the case in general and one must be aware of the limitations of interpreting structure-function relationships using techniques that manipulate individual neuronal connections embedded within complex networks.

A second challenge is that there have been few concrete examples of how complex coding properties of many of the neuron subtypes classically implicated in figure detection and target tracking — in privet moth [42], blowfly, dragonfly and hoverfly (reviewed in [1]), and more recently in mouse models [43–46] — affect figure–ground discrimination in behavior [47,48]. Thus, correlative evidence of cellular mechanisms underlying perceptually-guided behaviors for higher-order motion and figure-tracking is emerging [28,37], yet remains sparse. New genetically-encoded fluorescent indicators of cellular activity, as well as optogenetic activators and inactivators, have extended the physiological paradigm to include both subcellular compartments and network-level activity. This expansion of technical scope introduces another axis of conceptual complexity, and associated challenges, for understanding how information is encoded spatially within a brain region or even a single cell.

In light of these challenges, a return to our psychophysical roots provides a robust organizational framework to interpret this complexity. We have argued here that, in work on vision, stimulus and experimental design should attempt to interrogate the minimal behavioral effects of a fundamental, indivisible perceptual stream within the most spatially-restricted region of the visual field possible. Ultimately, our aspiration is not only to identify neurons or networks with interesting coding properties, but to demonstrate the necessity of that coding to some observable behavior. The pitfall is that these coding motifs are embedded within a highly parallelized perceptual network. Finally, we have learned with these recent advances that the natural world imposes physical constraints such that, despite massive evolutionary distance, we find converging computational requirements for high performance motion vision across taxa. The parallelized structure of visual centers in flies and mammals [49] provide an anatomical substrate for the metathetic processing required to extract combinatorial features of visual figure motion. There are likely many parallel and interconnected pathways for motion vision. The collaborative history of psychophysics, since Weber, and insect cybernetics, since Reichardt, shows us a way forward.

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