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Report

Sensor Fusion in Identified Visual Interneurons

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Summary

Animal locomotion often depends upon stabilization reflexes that use sensory feedback to maintain trajectories and orientation [1–4]. Such stabilizing reflexes are critically important for the blowfly, whose aerodynamic instability permits outstanding maneuverability but increases the demands placed on flight control [5]. Flies use several sensory systems to drive reflex responses [6–9], and recent studies have provided access to the circuitry responsible for combining and employing these sensory inputs [10–13]. We report that lobula plate VS neurons combine inputs from two optical sensors, the ocelli and the compound eyes. Both systems deliver essential information on in-flight rotations, but our neuronal recordings reveal that the ocelli encode this information in three axes, whereas the compound eyes encode in nine. The difference in dimensionality is reconciled by tuning each VS neuron to the ocellar axis closest to its compound eye axis. We suggest that this simple projection combines the speed of the ocelli with the accuracy of the compound eyes without compromising either. Our findings also support the suggestion that the coordinates of sensory information processing are aligned with axes controlling the natural modes of the fly's flight to improve the efficiency with which sensory signals are transformed into appropriate motor commands [5].

Results

Flies employ several specialized sensors to measure their rotation in space [7]. We investigated how signals from the fly's two visual systems—the compound eyes and ocelli—are integrated during sensory processing. Both of these sensors obtain information on the fly's head rotation but differ in their optics and neural circuitry. The compound eyes use approximately 10,000 optical units (ommatidia) to sample the visual field with relatively high spatial resolution [14]. This image is processed retinotopically in two layers of small neurons before wide-field patterns of optic flow—corresponding to head rotations—are extracted by tangential neurons in the lobula plate and then projected to the posterior slope of the brain for distribution to descending interneurons and neck motor neurons [15]. By comparison, the three ocelli have poor spatial resolution but deliver their signals directly, without passing through several layers of processing. Large caliber L neurons sum the synaptic outputs of ocellar photoreceptors over wide visual fields and conduct a transient graded signal also to the posterior slope [16, 17]. Behavioral studies show that flying insects benefit from the advantages of both systems [18, 19], but our knowledge of how neurons extract rotation signals from the ocelli and combine these with rotation signals from the compound eyes is rudimentary. Fortunately, we know a great deal about the neurons, circuits, and algorithms that extract body rotations from the compound eyes [20–22]. Elementary motion detectors (EMDs) compare neighboring image pixels to extract information [23] on the direction and relative velocity of motion (Figure 1A). In the fly lobula plate, an ensemble of ten VS neurons integrates local motion signals from many EMDs in a particular pattern that corresponds to the optic flow produced during a rotation [24] (Figure 1B). Each VS neuron is highly sensitive to rotations about a particular preferred axis (Figure 1C); however, their response latency is limited by the number of processing stages and the time delay that EMDs use to signal directional motion.

The ocelli compute rotation information directly by simply monitoring the light intensity at three large and slightly overlapping areas in the dorsal visual hemisphere (see Figure S2 available online). The ocelli are situated on top of the head (Figure 2A), and each consists of a highly convex lens, with the retina fused to the curved rear surface, 50–100 μm in front of the focal plane [25]. Consequently, the ocelli (Figure 2B) form blurred images on their retinae, containing little spatial detail. These adaptations enable the ocelli to exploit the high contrast between sky and ground to monitor changes in attitude [26]. As the head rotates, the horizon moves across the visual fields of the three ocelli to produce correlated changes in light level (Figure 2C). Light signals in ocellar interneurons are generally found to develop around two times faster than the equivalent signals in VS neurons mediated by the compound eye [16, 27]. Despite the apparent simplicity of the functional organization of the ocelli, it has not yet been shown how ocellar signals are processed to extract information on rotations. We recently discovered that one lobula plate interneuron, V1—which receives monosynaptic input from VS neurons—responds directionally to stimulation of the ocelli [11]. Here we show that VS neurons—known to be involved in compound eye-mediated stabilization reflexes—also extract rotation information from ocellar input according to a cosine tuning function.

We first established that VS neurons are driven by the ocelli. Through intracellular sharp-electrode recording, we measured the membrane potential response amplitude of 12 cells and, by dye injection, found that we had sampled 7 of the 10 VS neurons, namely VS1–3, VS6, VS7, VS9, and VS10. We used three fiber-optic micro light guides to stimulate the ocelli with 10 Hz triangular waveforms of light intensity [11]. In every cell, we observed clear hyper- and depolarizations about the resting potential of the neuron, phase locked to the stimulus. The mean latency of ocellar-evoked activity in the recorded VS neurons (obtained via temporal cross-correlation) was 5.7 ± 2.0 ms (2333 repetitions across all stimulus protocols). This latency is consistent with the short neuronal pathway between ocellar interneurons and VS neurons [10] and compares with a response latency for compound eye stimulation

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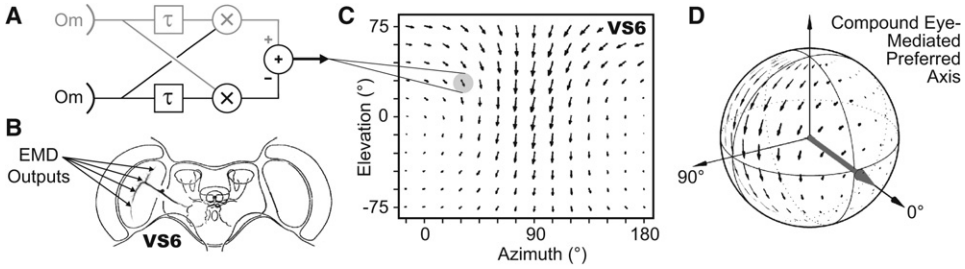

Figure 1. Compound Eye Rotation Detection Is Based on Optic Flow Processing

(A) Elementary motion detectors (EMDs) compute direction and rate of motion by multiplication of signals with a delay (τ) in neighboring ommatidia (Om).
(B) VS neurons in the lobula plate selectively integrate many EMD outputs across a large dendritic tree. The lobula plate is a retinotopically organized neuropil that maps the entire visual field of a compound eye.
(C) Because of the selective integration of directional motion signals, the receptive field organization of each VS neuron closely resembles the pattern of optic flow generated by rotation about a particular axis.
(D) The VS6 preferred axis lies at 0°: a roll rotation.

in the spiking tangential neuron H1, which is generally 20–30 ms for both step motion response measures [27] and for temporal cross-correlation [28].

Knowing that VS neurons receive fast inputs from the ocelli, are these inputs processed to extract rotations about specific axes? If so, are these ocellar axes aligned with the preferred axes established by input from the compound eyes? To answer these questions, we devised optical stimuli that mimic the inputs generated by head rotation. We modeled how the visual fields of the three ocelli sample the visual environment while the head of the fly rotates about a given horizontal axis (Figure 2C). Despite the apparent simplicity of the visual environment in our model, it is actually a surprisingly realistic stimulation for the ocellar system (Figures S2 and S3). The model incorporates data on ocellar optics [25], including spectral sensitivity [29], the intensity and spectral composition of ground-reflected light [30], and the intensity distribution of the sky [31]. We used the model to calculate the light intensities experienced by the three ocelli as the head rotated about a given axis (Figure 2C) and then delivered these stimuli to the ocelli with three fiber-optic light guides (Figure 3A). Previous experiments have shown that these light guides do not evoke neuronal responses via the compound eyes through light leakage [11].

We stimulated the ocelli with a set of mimicked rotations that covered the horizontal plane in 20° increments while recording intracellularly from identified VS neurons (Figure 3B). By measuring the response amplitude (see Supplemental Experimental Procedures) of each neuron to 20–30 stimulus repetitions at different rotation axes, we obtained a well-defined tuning curve (Figure 3C) that could be fitted by a cosine function with a high (>0.9) coefficient of determination. The position of the maxima of the cosine fit specified each VS neuron's ocellar preferred axis (Figure 3D). To our knowledge, these are the first data showing that information from insect ocelli is processed neurally to extract rotations about specific axes. Furthermore, we have measured this rotation specificity in cells that already encode rotations from the compound eyes and which are separated by only 2–3 synapses from the muscles controlling stabilizing behavior [32].

We then compared the ocellar-mediated rotation axes of our identified VS neurons with previously published measurements of their compound eye-mediated rotation axes [24] and found that for several VS neurons the two axes are misaligned (Figure 4A). For example, VS1 has a compound eye-mediated preferred axis at 90°, but our measurements place the ocellar-mediated preferred axis at 47°, a misalignment, δ, of −43°. The overall distribution of δ (Figure 4B) is broad, certainly more so than would be expected by random interindividual differences [24]. Such large random misalignments would also contradict the precision with which VS neuron receptive fields are matched to rotational patterns of

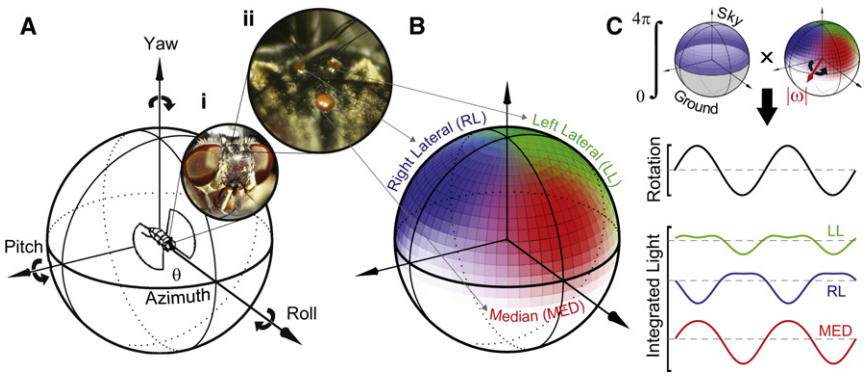

Figure 2. The Ocelli Exploit the Light Intensity Difference between the Sky and Ground to Detect Rotations

(A) In level flight, the ocelli point directly upwards. I: front of the head of a female *Calliphora vicina*; scale: inset diameter is 3 mm. II: the area between the compound eyes containing the ocelli; scale: inset diameter is 600 μm.
(B) Visual fields of the ocelli: each covers almost one-fourth of the visual sphere, so there is some overlap.
(C) During a rotation about a particular horizontal axis (|ω|), the visual fields move past the horizon, changing the total integrated light in each ocellus. We modeled this system and reconstructed the integrated light signals experienced during a rotation. Here, a large-amplitude sinusoidal rotation about a horizontal axis (red vector) generates the light signals shown below (red, green, and blue traces).

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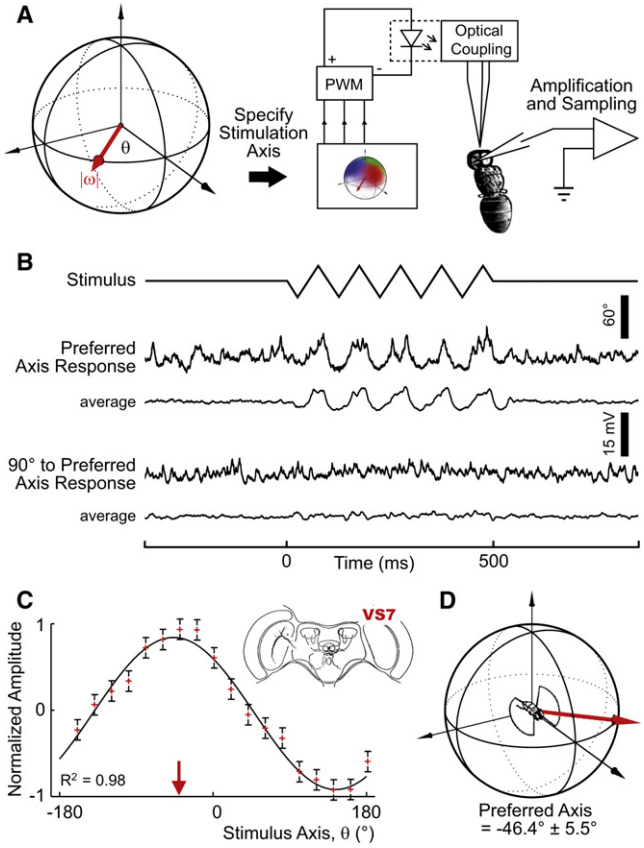

Figure 3. Measuring the Ocellar Rotation Tuning of VS Neurons

(A) Our ocellar illumination model allows us to specify a stimulation axis and convert a model rotation signal into three light signals. These were used to drive three LEDs, coupled to optical fibers positioned 100 μm above the ocelli of an intact, restrained fly.

(B) We made intracellular recordings from VS neurons while stimulating the ocelli with 10 Hz, 500 ms segments of mimicked triangle-wave rotation. VS neurons responded with robust hyper- and depolarizations about their resting potential, in phase with the rotation stimuli. The neurons displayed cosine-like rotation tuning. Maximum response amplitudes (see Figure S1 and Supplemental Experimental Procedures) occurred at the preferred rotation axis, whereas zero response was observed at 90° to this axis. Top and bottom scale bars represent 60° and 15 mV, respectively.

(C) A complete set of axis-response data from a VS7 neuron: data are normalized to the maximum response. A least-squares cosine fit gives a preferred axis of 46.4° ± 5.5°, with a coefficient of determination (R^2) of 0.98.

(D) A vector indicating the position of the ocellar-mediated preferred axis of this cell.

optic flow in the compound eyes [33]. In fact, we found that the ocellar-mediated axes are narrowly distributed about −45° and +45°, with another observed at 0° (Figure 4C). By comparison, the equivalent preferred axes of the VS neurons mediated by the compound eyes are approximately evenly distributed (Figure 4D).

Though we did not sample from all ten VS neurons, the tightness of the clustering about [−45°, 0°, +45°] (Figure 4E) strongly suggests that the ocelli encode rotations in only three axes. However, the compound eye-mediated tuning of the ten VS neurons defines a neuronal coordinate system with nine axes (VS1 and VS2 have the same azimuthal tuning). This difference in dimensionality is commensurate with the spatial resolution of each system: the ocelli have three lenses, with broad visual fields, whereas the greater number of preferred rotation axes mediated by the compound eyes is based on the selective input from thousands of small field elements.

Discussion

We have shown that VS neurons in the blowfly lobula plate receive short latency ocellar signals that code rotations of the head about horizontal axes. Though behavioral studies of stabilization reflexes suggest that it is advantageous to combine signals from the ocelli and the compound eyes [18, 19, 25], our study identifies a set of neurons in which we can actually observe this sensory integration. Full characterization of the fusion of compound eye and ocellar information still requires further studies involving combined naturalistic stimulation of the two systems. However, our measurements of the ocellar rotation tuning suggest a tradeoff between spatial precision and speed of action. Ocellar-mediated responses reveal coding of rotations about three horizontal axes, whereas nine axes of rotation are extracted from motion signals from the compound eyes. Inversely, we know from previous studies performed under similar laboratory conditions that compound eye signals are transmitted with latencies close to 20–30 ms [27, 28]. We measured an ocellar latency of 6 ms, a significant reduction compared to behavioral responses that are of the order of 40 ms [7, 34].

Our discovery that the ocellar inputs to VS neurons specify three horizontal axes of rotation raises certain questions. In particular, why do the ocelli code rotations about only three axes, how problematic is the inevitable spatial misalignment that occurs in the rotation tuning of VS neurons, and to what extent will signals gathered by the poorly focused ocelli detract from the superior spatial resolution of the compound eye? First, the positions of the ocelli should promote high sensitivity to rotations approximately about these axes (see Figures 2A and 2B); indeed, our model of the ocellar visual fields predicts axes of maximal sensitivity within 20° of the coordinates [−45°, 0°, +45°] (see Figure S4). It would also be counterintuitive to expect the ocelli, with only three points of measurement, to utilize a nine-axis coordinate system. Second, because the compound eye preferred axes range from +90° (VS1) to −69° (VS10) across the ensemble and the ocellar-mediated preferred axes are positioned at [−45°, 0°, +45°], the average misalignment should be smaller than 45°. Our measurements of δ support this: the mean value of |δ| was +13°, and the maximum was 59°. Consequently, the two inputs to the VS neurons are always additive, and the errors introduced by misalignment will be relatively small because the tuning curves are described by broad cosine functions (Figure 3C). Furthermore, because the ocellar input has a lower latency and is transient, much of it has been and gone before the more finely tuned compound eye inputs are fully developed [16]. This temporal segregation will be particularly effective for sudden stepwise rotations that are commonly produced by saccadic body movements in flies [35]. Finally, turning to the possibility that signals from the poorly focused ocelli could degrade signals from the more acute compound eyes, this does not appear to be a serious problem. When the ocelli fail to detect a rotation because they lack the necessary resolution, there is no degradation because there is no ocellar input, and when the ocelli do detect the rotation, their signals augment the compound eyes' because they are correlated.

What is the significance of the correlation between the principal axes defined by the anatomy and optics of the ocelli and the rotational tuning observed in VS neurons? A close analog

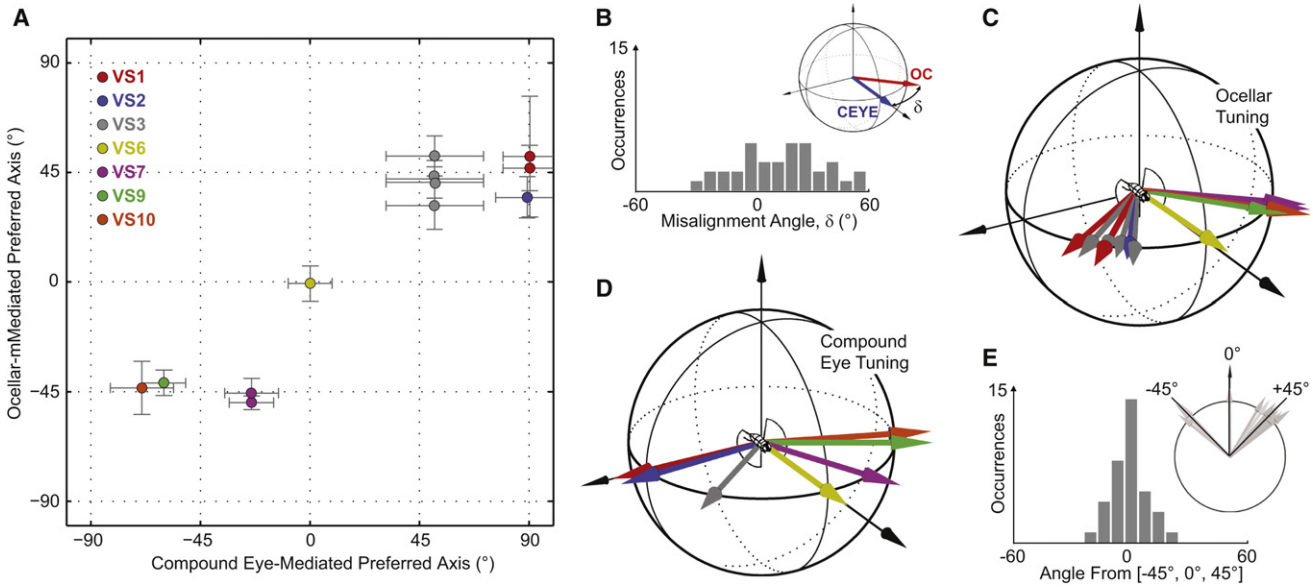

Figure 4. Comparison of the Ocellar Rotation Tuning with the Compound Eye Rotation Tuning

(A) For each intracellular recording, we measured the ocellar preferred axis (vertical graph axis) and plotted versus the compound eye preferred axis (horizontal graph axis) (data from [24]). Each VS neuron is assigned a different color (e.g., VS1 is red).

(B) We calculated the angle, δ, between the ocellar preferred axis (OC, red vector) and the compound eye preferred axis (CEYE, blue vector) for each recording and constructed a frequency histogram (see Figure S1 and Supplemental Experimental Procedures).

(C) The ocellar preferred axes, plotted as 3D vectors.

(D) The compound eye preferred axes, plotted as 3D vectors.

(E) Frequency histogram of the angle between each ocellar preferred axes and the nearest of the three angles, −45°, +45°, and 0°.

to this can be found in the pigeon, where the planes of the semicircular canals—which sense head rotations—are aligned with the preferred directions of optic flow processing neurons [36]. Sensory coordinates can also be aligned with the motor system: in mammals and amphibians, there is coalignment of the muscles involved in the vestibulo-ocular reflex (VOR) and the semicircular canals [37]. This matching of the coding properties of neurons to the anatomy of sensors and effectors is thought to increase processing efficiency, but why are particular spatial coordinates "chosen" over others? Recently it has been suggested that an insect's flight control system gathers and processes sensory information according to the demands made by its aerodynamics [5]. One of the key hypotheses generated by this suggestion is that information is collected in coordinates closely related to the axes of flight instability. This brings two advantages: it applies the limited information capacity of the nervous system to the most important regions of input space, and it generates output vectors whose axes are most effective for control. In the blowfly, two recent studies have revealed the rotation tuning of neck motor neurons and descending neurons, which mediate stabilizing reflexes and receive synaptic input from VS neurons [10, 12]. These downstream neurons show a strong preference for rotations about two symmetric axes either side of pure roll, close to the ocellar preferred axes we have identified. We suggest that these axes are correlated with the axes of instability, or "flight modes," of the insect and that the use of these axes throughout the sensorimotor loops used for flight control promotes efficient processing.

Experimental Procedures

Female *Calliphora vicina*, aged 3–10 days, were taken from a managed colony and mounted onto a copper holder. A small piece of cuticle was removed from the rear of the head capsule to expose the lefthand lobula plate. Electrodes were filled with 0.5 M LiCl (shaft) and 0.5 M LiCl + lucifer yellow dye (tip), which gave a range of electrode resistance from 40–120 MΩ. Cells were impaled, and the membrane potential was recorded with an Axoclamp 2B intracellular amplifier (Axon Instruments) and a National Instruments DAQ card.

Stimuli were delivered to each of the ocelli with fine optical fibers, 62.5 μm in diameter. The light source for each optical fiber was a blue LED (Lumiled Luxeon III – λ_{max} = 455 nm) that produced a maximum irradiance at each ocellus of approximately 15 W/m^2. The LED output was controlled via pulse width modulation at a base frequency of 4 kHz. Experiments were conducted at approximately 20°C.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at doi:10.1016/j.cub.2010.01.064.

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