Flies see second-order motion

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Motion detection is nearly ubiquitous among visual animals. Simple ‘first-order’ motion in an image is defined by spatiotemporal correlations in luminance, and is useful for tasks such as identifying a bright butterfly crawling on a tree. Humans additionally perceive ‘second-order’ motion [1], defined by spatiotemporal correlations in higher-order image statistics, such as local contrast or texture. Detecting second-order motion is useful, for example, in identifying a butterfly in flight, because fluttering wings produce a flickering brightness with weak luminance correlations. Second-order motion detection in humans involves sophisticated cortical processing [2]; however, these signals are also extracted by lower vertebrates such as fish [3], suggesting this is not a recent specialization within higher vertebrates. Motivated by this idea, we tested flies, and found their steering reflexes during flight robustly track second-order motion, even in the presence of conflicting first-order motion cues. Second-order motion processing, known in primates, fish, and now invertebrates, reveals convergent evolution of a specific neural computation.

We flew animals in two different flight simulators, each equipped with a cylindrical high-performance computer-animated display [4]. Visual motion stimuli consisted of a 30° vertical bar that oscillated horizontally against a randomly patterned stationary background (see Supplemental movie available on-line). Each stimulus was presented for two consecutive oscillation cycles, which were averaged. The sequence of stimuli was randomized for each fly, which received each stimulus once and only once. Taking advantage of a powerful reflex in which a fly actively tracks a moving vertical bar, we measured motion responses by: (i) optically tracking wing motions of rigidly tethered flies since the difference in wing beat amplitude across the two wings is proportional to yaw torque (Figure 1A); and (ii) video tracking flies, suspended within a magnetic field, that rotate on a near frictionless pivot (Figure 1B). For the first experiment, the fly was stationary, and a vertical bar swept back and forth across the retina eliciting measurable wing kinematics. For the second experiment, the fly was free to rotate and the moving bar elicited active tracking. The stimulus cycle for the fixed tether was 0.5 Hz, but the magnetic tracking behavior required a slightly slower, 0.2 Hz, presentation. We compared fly behavioral responses to the prediction of the classical elementary motion detector (EMD) model [5] (see Supplemental Experimental Procedures in the Supplemental data available on-line).

Neither the EMD model nor the flies showed measurable responses to a flickering control stimulus (Figure 2, first row). In response to a first-order motion stimulus (also called Fourier motion) composed of a randomly textured bar moving against the stationary background, flies bilaterally modulate wing beat amplitude and actively steer to track the position of the bar (Figure 2, second row). These responses are due to the strong spatiotemporal correlation in luminance and are consistent with the prediction of the EMD model. By contrast, a second-order object that merely inverts the sign of the background pattern (also referred to as a drift-balanced stimulus) generates no correlated luminance signals and so elicits no net output from the EMD model. As with the first-order stimulus, however, flies on the fixed tether modulate their wing kinematics in proportion to the azimuthal position of the second-order bar, and flies on the free-yaw magnetic tether actively track the bar’s position (Figure 2, third row).

Finally, we tested flies’ responses to a stimulus with conflicting motion information: a bar within which a textured pattern drifted in one direction, generating first-order motion, while the bar itself moved in the opposite direction, generating opposing second-order motion (also called theta motion [6]). The output of the EMD model tracks only the first-order component of theta motion, and as such the mean integrated output is 180° out of phase with the bar’s position (Figure 2, fourth row). Surprisingly,
the flies apparently ignored the first-order motion signal and instead they robustly tracked the moving bar within both immobilized and freely-pivoting preparations. We note that the amplitude of steering responses is comparable across all stimulus conditions. During flight, the mean wing beat amplitude and wing beat frequency vary considerably according to the type of visual stimulus [7]. Therefore, to confirm that the different visual treatments here did not result in qualitative changes in flight motor output, we compared the measurements for the fixed tether experimental treatments. We found that the mean uncalibrated wing beat amplitude (1.6 V) and mean wing beat frequency (182 Hz) did not significantly vary across treatments.

In flies, the third optic ganglion houses a population of directionally selective neurons that retinotopically integrate local motion signals [5]. One such neuron (H1) is somewhat sensitive to drift-balanced motion, although it does not respond robustly to theta motion [8]. However, we have shown in this study that fruit flies are sensitive to second-order stimuli, including both drift-balanced and theta motion, implying a visual channel beyond what has been previously described. Elaborations on the classical luminance based EMD, such as front-end nonlinearities, are sufficient to produce a system sensitive to some forms of second-order motion [8, 9], but not necessarily theta motion [6]. Flies could potentially be tracking the flickering stimulus, a simpler second-order component of theta motion, but our results indicate otherwise as the flies failed to track a pure flickering stimulus of the same parameters. Taken together our results indicate that complex motion processing is not the sole purview of vertebrates, but rather may be shared among animal groups displaying high-performance visual behavior. The genetic and quantitative behavioral tools available in Drosophila shall make it possible to investigate the structural circuits and functional algorithms by which a compact brain achieves great computational sophistication.

Supplemental data
Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/11/R464/DC1

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References

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