Luminance-dependent visual processing enables moth flight in low light

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Animals must operate under an enormous range of light intensities. Nocturnal and twilight flying insects are hypothesized to compensate for dim conditions by integrating light over longer times. This slowing of visual processing would increase light sensitivity but should also reduce movement response times. Using freely hovering moths tracking robotic moving flowers, we showed that the moth’s visual processing does slow in dim light. These longer response times are consistent with models of how visual neurons enhance sensitivity at low light intensities, but they could pose a challenge for moths feeding from swaying flowers. Dusk-foraging moths avoid this sensorimotor tradeoff; their nervous systems slow down but not so much as to interfere with their ability to track the movements of real wind-blown flowers.

To quantify the change in processing time, we can estimate a single time constant from the phase response at each light level (Fig. 2B). Overall, the moth’s tracking response is 17% slower in dim moonlight than at early dusk: 83.3 ± 2.4 ms as compared to 71.5 ± 3.5 ms, respectively (mean ± SEM; Fig. 2B and C; t = 2.82; df = 21; P = 0.01). We obtained similar results when we considered only frequencies below 10 Hz, which was the highest frequency that all individual moths could track (67.2 ± 3.1 and 80.6 ± 3.3 ms; Fig. 2D).

Next we tested whether the slower tracking responses were consistent with a luminance-dependent delay within the moth’s visual system. Moths track flowers in closed loop, meaning that their visual input is the difference between their own motion and the flower’s (visual “error”; fig. S3) (13, 15). We applied a luminance-dependent delay to the visual response within this closed feedback loop (fig. S3) (15). From this, we predicted the moth’s response in low light, \( \hat{L}(s) \), for each frequency component of the flower’s movement (defined by the Laplace variable \( s \)). This prediction (Fig. 2, light blue lines) depends only on the measured high-luminance response, \( H(s) \), and a single parameter \( \tau \), representing the difference in processing time (delay) between the two light levels

\[
\hat{L}(s) = \frac{e^{-\tau s}H(s)/(1 - H(s))}{1 + e^{-\tau s}H(s)/(1 - H(s))}
\]

A delay (\( \tau \)) of 10.4 ms best fits the change in response from the bright to dim light levels. This single parameter captures the empirical phase differences as well as the overshooting that occurs under low light (Fig. 2, E and F). Hence, the hypothesized luminance-dependent visual processing in the moth’s nervous system can account for the differences in the closed-loop tracking response at different light intensities.

The above model treats the change in processing as a single time delay. Changes in spatial processing are likely to help shape the moth’s tracking response, especially the gain (10, 19). Temporal processing might also be distributed across multiple regions of the visual system, including in the photoreceptors and motion detection circuits (1, 10, 19). Most importantly, insect motion detection itself is thought to arise by the correlation of adjacent photoreceptors (20, 22), and the process of correlation is non-linear. What remains unclear is how these more complicated processes would affect moth motion lag if their time constants were luminance-dependent. To be consistent with our simplified models, a more detailed model would need to produce a lag in its input-output relationship that increases linearly with the time constant inside the model. To test for this relationship, we implemented a longstanding model proposed for visual motion detection, the elaborated Hassenstein-Reichardt (HR) correlator (see the supplementary text). We simulated this model’s response to an oscillating visual input and explored how this response depends on the

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M ost animals rely on vision to maneuver through complex environments. Similarly, many engineered systems use machine vision to sense their surroundings. Yet all biological or synthetic visual systems operating in natural environments must deal with high variability in ambient light intensity. Animals can encounter light intensities that vary over 10 billion-fold within a single day (1-3). Low-light specializations can extend an animal’s sensory capabilities but frequently produce tradeoffs, (such as increased sensitivity but reduced resolution) (4-6). Revealing the mechanisms that enable nervous systems to adapt to this vast range of light, as well as their functional tradeoffs, are fundamental to understanding the versatility of vision.

We investigated visual processing in dim light—and its functional consequences—in the hawkmoth Manduca sexta, an agile flyer that extracts nectar from moving flowers while hovering even in very dim light (Fig. 1A) (7-9). The moth’s compound eye has an adjustable pseudo-pupil that allows a large number of the highly refractive eye facets (ommatidia) to deliver light to a single photoreceptor in low light, thereby increasing sensitivity (1, 2). Early in visual processing, neurons may also pool inputs from multiple photoreceptors providing spatial summation of light (1, 10). These spatial adjustments improve sensitivity, but they are insufficient to account for the range of low-light sensitivity exhibited by moths in the moth’s visual system (10). A hypothesized complementary mechanism is that moths may progressively slow their visual processing as light intensity (luminance) decreases (1, 10, 12). In effect, as light diminishes, moths might temporarily integrate light for a longer period of time, in addition to summing over larger spatial regions (Fig. 1B) (10, 12). This luminance-dependent neural processing predicts a tradeoff: The increased sensitivity that comes with increased processing time should also slow motion detection. This predicts that moths should lag behind the motion of objects that they are visually tracking. Because moths track and feed from moving flowers (7-9), we can test not only whether the moth’s motion response is slowed, but also what potential tradeoffs this poses for tracking natural flower movements.

We used robotic artificial flowers to explore the moth’s behavior under different light levels (Fig. 1, A and C, and movies S1 and S2) (13). Moths tracked flowers moving side-to-side with a linear combination of sinusoidal trajectories with frequencies spanning two orders of magnitude (0.2 to 20 Hz, Fig. 1, D to F) (14, 15). Hovering and maneuvering in midair is demanding, inherently unstable, and energetically costly (9, 16, 17). Nonetheless, moths are able to track and feed from moving flowers even at 14 Hz (Figs. 1E and 2A). In contrast to tethered moths (open-loop) tracking visual images (18), flower tracking by freely flying (closed-loop) moths is highly linear (coherence in Fig. 1E; explicit test in fig. S2).

Moths lag farther behind flower movement in dim moonlight (0.3 lux) than in the brighter light of early dusk (300 lx), as predicted for a slowing visual system (Fig. 2B; F = 46.3, df = 349, P < 0.0001). At both light levels, moths produce the largest motions (highest gain) to flower movements at intermediate frequencies (1- to 2-Hz bandwidth, Fig. 2A and fig. S1). However, in low light they begin overshooting the flower (gain > 1, which is 0 dB) (all frequencies: F = 16.4, df = 349, P < 0.0001; at 1.7 Hz: t = 4.5, df = 20.5, P = 0.0002). Because the mechanics of flight are the same at both light levels, the differences in tracking must arise because the moth relies on a luminance-dependent neural processing model.

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model’s time constants. (10, 12, 20, 21). These simulations show that the phase shifts we observed in experiments are consistent with the HR model of insect visual processing, as well as with simple closed-loop delay models (fig. S5).

In all these analyses, a simple luminance delay term accounts for the closed-loop response (Fig. 2, E and F). The increased phase lag in low light supports the hypothesized luminance-dependent visual processing. However, in order to consider overall tracking performance, we cannot consider phase lags and gain separately, because they each describe only one aspect of the response. To accomplish our second aim of assessing a potential performance tradeoff, we combined gain and phase into one metric of tracking error (e).

Specifically, we used the distance in the complex plane between the moth’s responses and the ideal tracking conditions (gain = 1, phase = 0°; fig. S4) (13, 14)

$$e = \| H(s) - (1 + 0i) \|$$

where $i = \sqrt{-1}$.

Although tracking performance depends on light intensity, the effect is frequency-dependent and separates into three distinct frequency bands (Fig. 3A). Below 1.7 Hz, tracking error is relatively low ($e < 1$) and does not differ between high- and low-luminance conditions ($F = 0.49$, df = 137, $P = 0.48$). However, tracking error increases rapidly at higher frequencies, even when gain remains high. This is because the moth is more than 90° out of phase with the flower between 1.7 and 8 Hz. In this frequency band, moths track significantly worse in low light ($F = 17.6$, df = 137, $P < 0.0001$). However, at the very highest frequencies (>8 Hz), tracking error reverts toward unity because the gain is very small.

Counterintuitively, moths are still much more likely to forage and track moving flowers in dim light levels, despite poorer tracking performance (higher e; Fig. 3B). This suggests that moths incur worse performance in order to obtain the increased sensitivity afforded by luminance-dependent neural processing. However, moths might avoid this

Fig. 1. The effect of light intensity on moths tracking robotic flowers. (A) Human photoreceptors, like those of all animals, are capable of detecting even single photons (28). However, human color vision (colored arc), as well as our ability to resolve motion and spatial detail, deteriorates below the photopic visual threshold (1 to 10 cd m$^{-2}$) corresponding to light levels at dusk (11, 29). This is also true for diurnal insects such as the blowfly Calliphora (30). Human scotopic vision (gray arc) is strictly monochromatic (29). The hawkmoth Deilephila is truly nocturnal, with color vision throughout much of the scotopic range (2). [In (A), “*” indicates experimental light levels. “?” indicates that data are not available.] Manduca is crepuscular and is hypothesized to adjust its visual processing (B) in order to visually track flowers over its large range of light intensity (>10$^6$ cd m$^{-2}$) (10, 27). CNS, central nervous system.) Robotic, three-dimensional printed flowers generated repeatable moth flight maneuvers (C) (movies S1 and S2). We moved the flowers with a trajectory of many superimposed sinewaves to sample many of the frequencies of movement simultaneously (D). Fourier transformations (E and F) of the flower’s (green) and moth’s (blue) movements show high coherence [(E), gray line], which is the normalized cross-power spectral density (18, 24). Flower movements were prescribed to have equal peak velocities at each frequency (F), which helps avoid saturation in the moth’s ability to track.
tradeoff if the flowers they track only move at frequencies below ~2 Hz, below where the performance tradeoff occurs.

We filmed five species of hawkmoth-pollinated flowers in natural wind (see the supplementary text, fig. S6, and movie S3) and found that these flowers move at frequencies where the moth does not suffer a performance cost for tracking in dim moonlight conditions. The vast majority (94%) of moth movements were below 1.7 Hz (Fig. 3, C and D, and fig. S6). So whereas moths benefit from the increased sensitivity of slower visual processing in low light, they also avoid negative consequences, because natural flowers usually oscillate in the wind at speeds below those that incur a performance tradeoff.

This matching of frequencies between pollinator vision and flower movement indicates that the relationship between the two organisms probably constrains the slowing of neural processing in variable light conditions. Notably, moths’ tracking error increases dramatically above the frequencies of normal flower motion, regardless of light level (Fig. 3C). When the robotic flower moved at frequencies above 2 Hz, the moth would have tracked better by remaining stationary (ε > 1; Fig. 3, A and D). If moths’ visual processing was even slower, they would begin to experience adverse tracking performance in dim light.

**Fig. 2. Visual processing slows in low light.** The relative amplitudes of moth and flower give the tracking gain (A), and their relative timing gives the phase difference (B) with means ± 95% confidence intervals (CIs). The qualitative shape of the response is consistent with the drift-compensation response in the diurnal hawkmoth Macroglossum (θ). Regressing phase onto frequency [(B), dash-dotted lines] estimates the best-fit time constant across all frequencies (C) or just those <10 Hz (D). We created a prediction for the low-luminance response (light blue) from a closed-loop model of the high-luminance response (orange) with a delayed sensory gain (fig. S3). This prediction successfully captures the overshooting (E) and phase shift (F) evident in the actual low-light response (dark blue) replotted from (A) and (B) on a log axis.

**Fig. 3. Tracking performance and real flower movements.** Tracking error (ε, mean ± 95% CI) is a function of frequency for both luminance conditions. Three distinct frequency bands result, denoted by dashed lines. Behavioral performance of moths (B) was scored as no flight (~F); flight, but not tracking (F, ~T); or flight and tracking (T). The power spectra (C) of hawkmoth-pollinated flowers blowing in breezes from 0.1 to 2.7 m/s are normalized to the total power. 94% of the cumulative power in the flower’s movement (black: mean) occurs in frequencies below 1.7 Hz, where ε = 0.2 to 0.4 (D).
the frequency band where natural flowers move. One reason moths might rely on both temporal and spatial adjustments to deal with low light (10) is to limit the costs to both motion-tracking performance and spatial resolution.

The frequencies with which a moth can maneuver could provide a selective pressure on the biomechanics of flowers to avoid producing floral movements faster than those that the moth can track in low light (22). The converse interaction—flower movements selecting on the moth—could also be important, suggesting a coevolutionary relationship between pollinator and plant that extends beyond color, odor, and spatial features (23) to include dynamic motions.

The emerging use of system identification to connect open- and closed-loop experiments (6, 14, 15, 18, 24, 25) provides a useful paradigm for exploring sensorimotor strategies in many systems. Robotic models enable rapid, repeatable experiments that extract critical features of the biological system (26) and extend the physical modeling toolkit that has been useful for easing apart pollinator-plant interactions (7, 9, 23). Here the robotic flower enabled us to test predictions about closed-loop behavior from open-loop electrophysiological results and models of neural processing (6, 15).

The dual demands of acquiring reliable sensory information and maintaining motor performance are a general challenge, especially for animals such as Manduca, which operate in impoverished sensory environments (4–6, 27) and on the edge of flight instability (6, 25). Matching the requirements of the motor system to constraints imposed by the dynamics of the environment can provide strategies that enable more extreme sensory performance while averting tradeoffs in motor performance.

REFERENCES AND NOTES

13. See the supplementary materials and methods.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

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BIOGEOGRAPHY

The dispersal of alien species redefines biogeography in the Anthropocene

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It has been argued that globalization in human-mediated dispersal of species breaks down biogeographic boundaries, yet empirical tests are still missing. We used data on native and alien ranges of terrestrial gastropods to analyze dissimilarities in species composition among 56 globally distributed regions. We found that native ranges confirm the traditional biogeographic realms, reflecting natural dispersal limitations. However, the distributions of gastropods after human transport are primarily explained by the prevailing climate and, to a smaller extent, by distance and trade relationships. Our findings show that human-mediated dispersal is causing a breakdown of biogeographic barriers, and that climate and to some extent socioeconomic relationships will define biogeography in an era of global change.

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The reduced similarity in species composition between distant locations is one of the most noticeable patterns in nature (1–3). Dispersal limitation is at the heart of this pattern, either simply because of the accessibility of nearby locations or because environmental factors of ecophysiological importance tend to be spatially autocorrelated within the range of natural dispersal (4). Notwithstanding, human trade and travel have been transgressing natural barriers to dispersal (5), and increasing numbers of species are becoming established in places far away from their native range (6, 7). Ultimately, this may cause the breakdown of the “classical” biogeographic regions (8)—mainly determined by dispersal barriers and historical factors such as continental drift or palaeoclimates—and the emergence of new biogeographic arrangements determined primarily by environmental requirements and by geographic patterns in human transport pathways.

In recent centuries, and particularly during the past few decades, transport pathways have intensified in frequency and extended worldwide (5, 9). This accelerates the speed at which species colonize suitable areas across the globe and inherently contributes to the homogenization of species assemblages at a global scale (10–12). Niche theory and metacommunity theory suggest that the
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