FN-Merge-Augen-EN-v0.1-2026-05-17

Research Note — Eyes in the Animal Kingdom

Author: Thomas Schüller · forschung@tschueller.com · ORCID 0009-0003-9799-6747 **Affiliation:** privately funded, no institutional affiliation **Licence:** CC BY 4.0 · **Version:** 0.1 · **Date:** 2026-05-17 **Strand:** FORSCHUNG / Merge / N2 Eyes in the Animal Kingdom **Tool:** OCULI · **Document type:** Research note (Template v1.0) **Status:** completed test with documented assessment **Special feature:** third **merge module** — connects optics, perception and evolutionary biology

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1. Thesis

Module N1 (CAMERA COMPARATA) advanced the **objective-function thesis**: camera and eye are not differently good but designed for different tasks. This module tests the thesis on a broader base — not technology against biology, but **biology against biology**.

The tested baseline model M1 reads: *“There is a ranking of eyes. They can be ordered by performance; the human eye stands high, simpler designs are precursors or leftovers.”*

This notion is widespread and seems obvious — a fly’s compound eye appears primitive, the vertebrate eye highly developed. This module’s claim: **the ranking does not exist**, because there is no common target quantity. Every design is a compromise between physically coupled quantities, cut to an ecological task and constrained by a developmental legacy.

2. Assumptions

1. The resolution of a compound eye is physically limited by diffraction and sampling, and is calculable.
2. Resolution, temporal resolution and low-light performance can be quantified for different species.
3. These three quantities are coupled through the photon budget.
4. Convergent development (independent emergence of similar solutions) is demonstrable.
5. Comparisons between designs require specifying a **task** — without one, “better” is undefined.

3. Mathematical model

M1 — “ranking of eyes”: There exists an ordering relation over eyes that represents their performance.

M2 — size limit of the compound eye. In a compound eye two effects compete: smaller facets permit narrower angular spacing (better sampling) but worsen the diffraction limit λ/D. The optimum lies at (Kirschfeld 1976, Snyder 1977): $$\Delta\varphi = \sqrt{\frac{\lambda}{2R}} \qquad\Longleftrightarrow\qquad R = \frac{\lambda}{2\,\Delta\varphi^{2}}.$$

Resolution thus grows only with the **square root** of the radius: doubling resolution requires four times the radius.

M3 — trade-offs. Photon flux per channel scales with collecting area A and integration time t. High temporal resolution (t small) and high spatial resolution (A small) both reduce photon count and hence low-light performance. The three quantities are **not independent**.

M4 — convergence and contingency. Two designs are convergent if they arose independently; contingent if their structure is explained by developmental history rather than function.

Symbol	Meaning	Unit
$\Delta\varphi$	interommatidial angle	rad
R	eye radius	m
λ	wavelength	m
A	collecting area per channel	m^2
t	integration time	s

4. Parameters

Scenario	Setup
A compound eye	$\lambda = 500$ nm; target resolutions 1.5° to 0.5 arcmin; real eyes (fruit fly, bee, dragonfly)
B trade-offs	five species with resolution (cpd), flicker fusion (Hz), minimum luminance (cd/m^2)
C convergence	vertebrate versus cephalopod eye; blind spot 5.5°

Tolerance: $\varepsilon = 0$ — one case where the ordering fails suffices for refutation.

5. Prediction

Scenario	Expectation
A	human resolution requires a compound eye of metre scale
B	no species leads in all three criteria
C	cephalopod eye without blind spot, vertebrate eye with

6. Falsification criterion

M1 is refuted as soon as (a) one design is superior under certain conditions, (b) no species leads in all criteria, or (c) a group regarded as “lower” possesses a technically cleaner design.

7. Competing models

- **K1 — ranking (M1):** tested baseline; implicit in phrases like “more highly developed”.
- **K2 — scale dependence:** which design is superior depends on body size.
- **K3 — Pareto optimality:** eyes lie on a front where no quantity can be improved without worsening another.
- **K4 — ecological adaptation:** design follows task (Land & Nilsson).
- **K5 — developmental constraint:** design follows legacy, not function (Gould & Lewontin, spandrel argument).
- **K6 — compensation argument:** the inverted retina is largely offset by Müller cells acting as light guides (Franze et al. 2007) — after the fact, not by design.

8. Domain of failure

- **Species-specific values scatter considerably.** Resolution, flicker fusion and low-light thresholds depend on measurement method, adaptation state and individual. The figures are **orders of magnitude**, not precision values.
- **The Kirschfeld formula is an approximation.** It assumes diffraction-limited ommatidia and uniform eye curvature. Real compound eyes have local regions of increased resolution (acute zones) that the simple calculation does not capture.
- **Only three criteria.** Colour vision (mantis shrimp with more than twelve receptor types), polarisation vision (bees, cephalopods) and UV vision are missing — they would support the thesis but are not computed.
- **No efficiency comparison.** Energy consumption per unit of information would be a further criterion and would reorder the ranking again.
- **The compensation of the inverted retina is contested.** How completely Müller cells offset the scattering loss is not conclusively settled.
- **No inference to optimality.** That no ranking exists does not mean every design is optimal. These are different claims.

9. Simulation

Numerical evaluation in `augen_simulation.py`:

1. Scenario A: Kirschfeld scaling for four target resolutions; comparison with real compound eyes; back-calculation of the literature figure.
2. Scenario B: five species across three criteria; test for an all-rounder; ranking of the human.
3. Scenario C: juxtaposition inverted/everted; area fraction of the blind spot.

Results in `augen_results.json`, plot as `augen_szenen.svg` (four subplots).

10. Result

10.1 A — size limit of the compound eye

Target resolution	required eye radius
fly (~1.5°)	0.0004 m

good dragonfly (~0.4°)	0.0051 m
human, coarse (1 arcmin)	2.95 m
human, fovea (0.5 arcmin)	**11.82 m**

That is **5372 times** the eye radius of a large dragonfly (2.2 mm).

Reconciliation with the literature: The frequently cited figure “about 1 m” (Kirschfeld 1976) corresponds, back-calculated, to \(\Delta\varphi = 1.72\) arcmin, that is roughly one third of human foveal resolution. Cross-check: 1.72 arcmin yields 0.999 m. The discrepancy is thus a question of **target resolution**, not of the formula.

Assessment M1: refuted.

10.2 B — trade-offs

Species	Resolution (cpd)	Flicker fusion (Hz)	min. luminance (cd/m²)
human	60	60	10^{-6}
housefly	0.5	**300**	10^{-2}
tawny owl	8	50	10^{-8}
eagle	**140**	100	10^{-3}
deep-sea fish	2	5	**10^{-10}**

All-rounder present: **no**. Human’s rank: resolution 2nd, temporal resolution 3rd, low light 3rd — **leading in no category.**

Assessment M1: refuted.

10.3 C — convergence and contingency

Feature	Vertebrate	Cephalopod
retina	inverted	**everted**
receptors	facing away from light	facing the light
blind spot	**yes** (5.5°, 0.093 % of the visual field)	no
optic nerve	pierces the retina	approaches from behind
origin	evagination of the diencephalon	invagination of the body surface

Assessment M1: refuted.

11. Assessment

M1 (“there is a ranking of eyes”) is refuted in all three scenarios — and the three refutations operate at different levels: physical, ecological, developmental.

Scenario A shows a physical limit — and its reversal. A compound eye with human foveal resolution would need almost twelve metres of radius. At first this sounds like a confirmation of M1: the design evidently cannot keep up. But the inference is wrong, for two reasons.

First, the limit is a **scaling law**, not a deficiency. Resolution grows with the square root of the radius; doubling resolution requires four times the radius. This holds for every compound eye, regardless of its quality.

Second — and more importantly — **the comparison reverses at small body sizes**. A lens eye of 0.2 mm diameter would be nearly blind from diffraction: the aperture is too small to form a usable image at all. At this scale the compound eye delivers a wide field of view and high temporal resolution. **For a fruit fly the compound eye is the superior solution, for a human the lens eye.** The question “which design is better” has no answer without specifying body size — just as the dynamic-range question in N1 had no answer without a time specification.

Scenario B delivers the most direct blow. The eagle resolves more than twice as finely as the human, the housefly processes five times faster, the deep-sea fish sees at ten thousand times less light. **The human leads in none of the three categories.**

Crucially this is not an artefact of selection but **physically enforced**. All three quantities hang on the photon budget: high temporal resolution means short integration time and hence fewer photons per measurement; high spatial resolution means small collecting area per channel and likewise fewer photons. An eye leading simultaneously in all three criteria would have to circumvent photon count — which is impossible. The eyes lie on a **Pareto front** (K3): no quantity can be improved without worsening another. A ranking presupposes a total ordering; on a Pareto front there is none.

Scenario C is the strongest argument because it strikes the premise. Vertebrates and cephalopods developed the camera eye **independently**. Both arrived at lens, iris, vitreous body and retina — the physics of image formation permits few solutions (convergence). But in one point they differ: the vertebrate retina is **inverted**, the receptors face away from the light, light must first cross the nerve layer and blood vessels, and the optic nerve pierces the retina, creating a blind spot. The cephalopod eye is **everted**: receptors facing the light, optic nerve from behind, **no blind spot**.

Were the human eye the result of an optimisation, it would be built everted. It is not, because it arose from an evagination of the diencephalon, while the cephalopod eye arose from an invagination of the body surface. Structure follows **developmental history**, not function (K5).

The counterargument belongs here and must be taken seriously: the inverted arrangement is not dysfunctional. The pigment epithelium behind it supplies the receptors and regenerates visual pigment, and Müller cells act as light guides that largely offset the scattering loss (Franze et al. 2007). But this is an **after-the-fact compensation of a legacy**, not a design. The order matters: first the constraint, then the repair.

The generalisation. N1 showed the objective-function thesis for camera and eye. One might object that this stems from the difference between technology and biology — engineers and evolution simply pursue different goals. Scenarios B and C close this escape: **the eyes among themselves are equally unrankable by quality.** There is no common target quantity, because the relevant quantities are physically coupled and each species sits at a different point on the Pareto front.

This also makes the language questionable. “More highly developed”, “primitive”, “precursor” presuppose an axis along which one can stand higher or lower. For eyes this axis does not exist. **“Best eye”**

presupposes a designer who does not exist — evolution optimises not globally but locally on an existing design, under physical constraints, for a concrete task.

Connection to the perception strand. If every eye is cut to a task, then every perception is task-specific — and that means: **no sense organ delivers "the world", each delivers a section usable for its task.** This is the same finding as in Module 02, L1 and M1, derived here from comparative biology. The fly does not see a poorer version of our world, but a different one.

12. Next test

Module M2 Optical Mechanics (ANALOGON) or **L6 Gestalt Laws (GESTALT)** as continuation.

Possible extension v0.2: colour vision compared (mantis shrimp, birds with four cone types); polarisation vision; energy consumption per unit of information as a fourth criterion; acute zones in compound eyes; mirror eyes (scallop) and pit eyes as further designs.

Appendix A — Cross-references

- Practice explanation: `PRAXIS-Augen-EN.md` · Companion paper: `BEGLEITPAPIER-Augen-EN.md`
- Tool: `OCULI.html`
- Code: `augen_simulation.py` · Plot: `augen_szenen.svg` · Data: `augen_results.json`
- **Modules used:** N1 camera vs. eye (objective-function thesis), M1 signal chain, 03 single slit (diffraction), 12 instruments (diffraction limit), L1–L5
- **Planning document:** `MERGE-ARCHITEKTUR-v0.1-2026-05-17.md`

Appendix B — External stocktaking

- **Kirschfeld (1976)** — size limit of the compound eye.
- **Snyder (1977)** — optimisation of the interommatidial angle.
- **Land & Nilsson (2012)** — *Animal Eyes*, comparative optics.
- **Warrant & Nilsson (2006)** — vision in dim light.
- **Franze et al. (2007)** — Müller cells as light guides.
- **Gould & Lewontin (1979)** — spandrel argument, critique of adaptationism.

What the workshop note adds: the bringing together of these findings into an explicit falsification of the ranking notion; the worked-through scaling including back-calculation of the cited literature figure; the Pareto front as a formal argument against any total ordering; the connection to the objective-function thesis from N1.

Appendix C — Sources

- Kirschfeld, K. (1976). The resolution of lens and compound eyes. In: Zettler, F.; Weiler, R. (eds.), *Neural Principles in Vision*. Springer, Berlin, 354–370.
- Snyder, A. W. (1977). Acuity of compound eyes: physical limitations and design. *J. Comparative Physiology* 116:161–182.
- Land, M. F.; Nilsson, D.-E. (2012). *Animal Eyes*. 2nd ed., Oxford University Press.
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- Franze, K. et al. (2007). Müller cells are living optical fibers in the vertebrate retina. *PNAS* 104:8287–8292.
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