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[REVIEW]

Guiding Light: Mechanisms and Adjustments of Environmental Light Interpretation With Insights From *Platynereis dumerilii* and Other Selected Examples

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Animals possess many light-sensitive molecules. They exist as dedicated photoreceptors, or as byproducts of biochemical reactions. Their numbers are often high even in species that live in environments that humans would consider dark, as well as in species that are considered comparably simple (e.g., worms, cnidarians).

But why are there so many photoreceptors? We provide some considerations on this question. Light conveys a significant amount of information to animals, through complex spectral and intensity changes, often specific to the spatial and temporal ecological niches a species inhabits. We discuss that the large number of opsins and cryptochromes, often also present outside the eyes and partially co-expressed, represent adaptation mechanisms to the highly complex light environment within a given niche. While theoretical, it is a plausible hypothesis given that most experimentally tested opsins and cryptochromes have been shown to be functional photoreceptors. The example of lunar and solar timing of the marine annelid *Platynereis dumerilii* provides insight on how animals use the biochemical and cellular properties of different photoreceptors to decode solar versus lunar light, and their different adaptations in *Drosophila melanogaster*. We suggest that the future understanding of biological processes will strongly benefit from comparative lab and field work on the same species, and provide a first example for such work in *P. dumerilii*. Finally, we point out that work on animal light detection systems and their adaptability is crucial to understand the impact of anthropogenic changes on species and ecosystems.

Key words: light receptors, opsin, cryptochrome, lunar timing, solar timing, *Platynereis dumerilii*

INTRODUCTION: THE HIGH COMPLEXITY OF LIGHT INFORMATION

Regular changes to light intensity and spectrum have occurred ever since the dawn of life. These changes harbor critical (and often regular) information about an organism's location and the state of the environment (e.g., extent of vegetation, weather conditions, passing of potential prey or predators) and time (from tidal to annual). Light of biological origin (bioluminescence and fluorescence), serves as communication signals (e.g., Sarfati et al., 2021, 2023; Hensley et al., 2023), but can also be used to optimize physiological processes by serving as a wavelength converter (Bollati et al., 2022). Given that light can thus provide plenty of information, whose correct interpretation can be highly advantageous, this provides a likely explanation for the presence of the large number and diversity of animal light receptors. Light can be measured by light-sensitive processes (i.e., light-sensitive biochemical reactions, such as vitamin D synthesis or the production of urocanic acid in mammalian skin) or by dedicated receptors (i.e., opsins and cryptochromes);

both types of processes have been shown to impact animal physiology and behavior (reviewed in Mat et al., 2024). Given the multitude of processes that can be affected by light, but should be affected only by the "right" light changes, it also implies that visual and non-visual photoreceptors have to be properly adapted to the specific spatial and temporal ecological light niches a species inhabits (Carothers and Jaksić, 1984; Hut et al., 2012; Menchetti et al., 2019; Häfker et al., 2022b).

One particularly complex cue highly influential for animal behavior and physiology consists of the changes in light spectrum and intensity over time (Fig. 1). Probably most obvious and best known to humans are the daily and annual (i.e., daylength in the temperate zones, monsoon/non-monsoon in the subtropical/tropical zones) changes of the solar cycle (Fig. 1B–E). Many animals use this information for daily and annual timing, but although much focus had been on light intensity and photoperiod (i.e., daylength), evidence for the importance of relative spectral changes for precise timing is increasing (Walmsley et al., 2015; Veedin Rajan et al., 2021). The latter requires an ability of the light sensory systems to decode such relative spectral shifts. The exact spectral shifts depend on the respective ecological niches and hence the decoding is expected to be optimized by species-specific adaption mechanisms. Another impor-

tant, yet often less regarded, temporal cue is moonlight (Fig. 1A, C–E). Its duration and timing relative to the daily solar light cycle provides animals with information on the month, but also time of day relative to the month (Fig. 1C–E). When taking dusk and dawn into consideration, this results in highly complex, seasonally changing light spectra and intensity changes (Fig. 1) (Nordtug and Melø, 1988; Veedin Rajan et al., 2021), again also ecological-niche dependent, because the light conditions themselves will be influenced by plant or algal growth and the animals' behaviors. In the marine environment, the aspect of temporal timing cues gets even more complicated by the in-parallel-occurring tidal water depths changes (Fig. 2). While some coastal regions, such as the Island of Ischia, Italy in the Mediterranean experience water depth changes only in the range of 10–50 cm and are hence within the range of waves, other places, such as Roscoff, France on the Atlantic Coast of Britany experience tidal changes in the range of several meters, while others, like Osaka, Japan facing the Seto Inland Sea are in between (Fig. 2A–C). Whether or not there are several meters of water above organisms has again significant consequences for the light intensity and spectrum that can reach them from both sun- and moonlight due to the light scattering and absorbance properties of the water, which will also differ depending on turbidity from organic and inor-
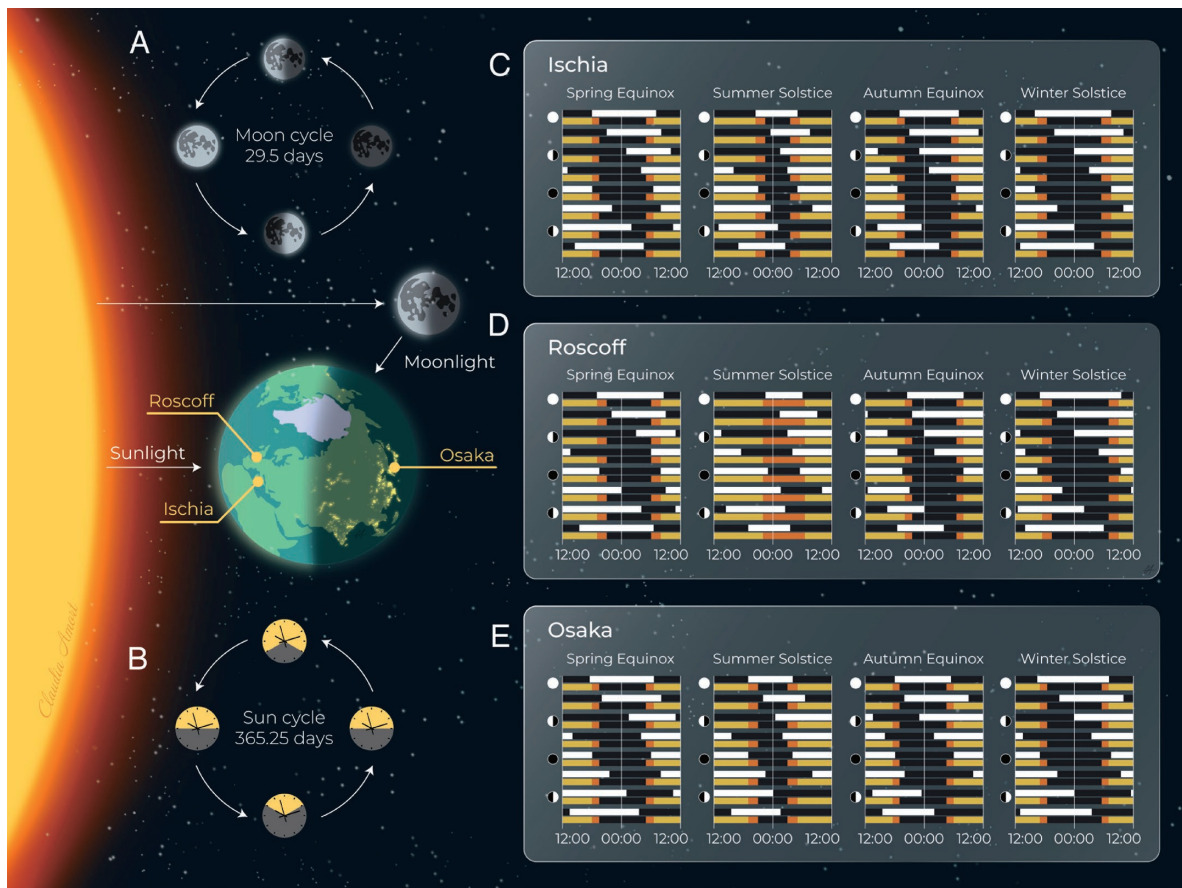
Fig. 1. Complex natural light cues with much temporal information for animals. **(A, B)** schematized lunar and solar cycle. For **(B)**, the yellow/gray pie chart pieces indicate day and night length, respectively. **(C–E)** Typical solar/lunar light regimes at different marine locations. Lunar cycle across the annual equinoxes and solstices are shown. White: lunar light, yellow: solar light, orange astronomical dusk/dawn periods, black: no natural sun or moonlight visible at location. Figure from C. Amort under CC-BY license.

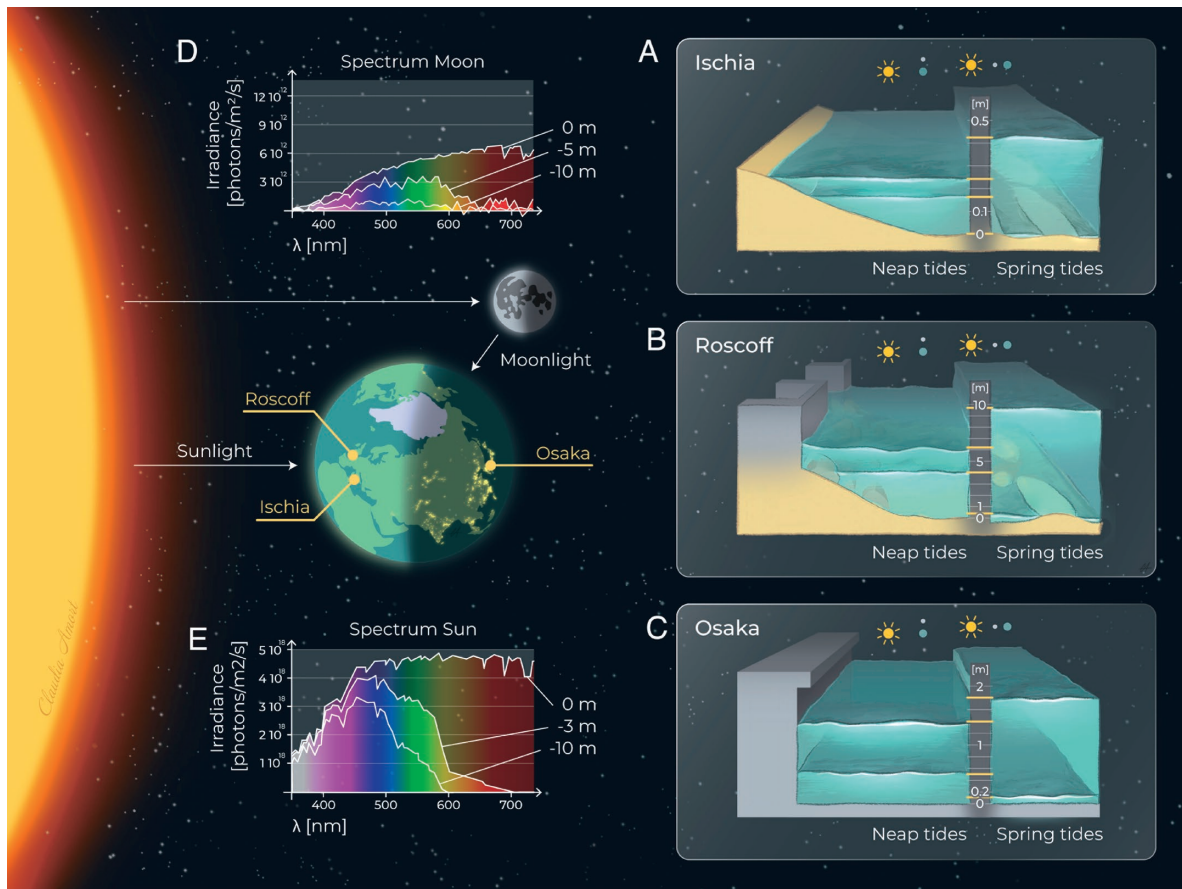**Fig. 2.** Influence of light spectrum and intensity by tides. **(A–C)** Tidal changes at marine locations known to harbor animals with complex light-dependent chronobiology. **(D, E)** Light changes depending on water depth, redrawn from Mat et al. (2024). Figure from C. Amort under CC-BY license.

ganic material (Fig. 2D, E) (Speight and Henderson, 2010; Depauw et al., 2012; Veedin Rajan et al., 2021).

DECODING THE LIGHT INFORMATION

How can organisms decode the relevant light information from the complex spatially and temporally changing signals that reach them? As mentioned above, the number of animal genes encoding proteins that belong to the known photoreceptor classes of opsins and cryptochromes is – at first glance – unexpectedly high and diverse (Mat et al., 2024). The frequently occurring argument that likely many of those may not function as actual light receptors is ad hoc difficult to prove or disprove. While loss of sensitivity to photons has certainly happened under some circumstances, such as the mechanosenory function of opsins in the Johnston organ of the fly antenna (Senthilan et al., 2012; Katana et al., 2019), even in this case it likely represents an evolutionary derivation rather than the original functionality of the opsin, as comparative functional analyses in annelids suggest (Revilla et al., 2021). A more extended discussion on this topic is present elsewhere (Mat et al., 2024). Interestingly, it is at present even unclear if a non-photon-dependent function is evolutionarily ancient for the cryptochrome type-II class, best studied in mammals, where they function as light-independent transcriptional repressors (Michael et al., 2017). In contrast to their mammalian light-independent

function, the teleost CRYII-class member, cry1a, is light-sensitive (Tamai et al., 2007), suggesting specific mammalian adaptations, possibly during the nocturnal bottleneck period Cretaceous–Paleogene extinction event (Gerkema et al., 2013). This is consistent with the idea that cryptochromes are originally light-sensitive, given their evolutionary close relatedness to light-dependent DNA repair enzymes, the photolyases (Gehring and Rosbash, 2003; Oliveri et al., 2014). In summary, it can be stated that the evidence for a generalization of presumptive non-photon-dependent functions of opsins is low. Thus, the many animal photoreceptors likely represent adaptations to the species-specific light niches. These adaptations can be on several levels, most obvious is the maximal spectral sensitivity and the spectral sensitivity range, which cannot be predicted from the amino acid sequence and structure. Noteworthy examples for this are the two ciliary-type opsins in the marine bristle worm *Platynereis dumerilii*, both close in sequence, but differing significantly in the spectral sensitivity properties (activating light range: U-VA/deep violet for c-opsin1, blue/green for c-opsin2; Tsukamoto et al., 2017; Ayers et al., 2018; Veedin Rajan et al., 2021).

Bistability versus monostability of opsins, and differing downstream signaling cascades provide additional features that can be used by organisms to optimize their photoreceptors' functions to a given environment. It is important to note

that bistability, the ability of opsins to change the state of its co-factor (typically between 11-cis and all-trans retinal) back and forth by the absorption of different wavelengths makes them "evaluators" of the respective environmental spectra, because the speed and level of re-activation depend on the available wavelength (Zhong et al., 2012; Tsukamoto, 2014). In contrast, monostable opsins need a catalyzing photoisomerase to return retinal to the (typically) 11-cis state and hence depend on the kinetics of this enzyme for their re-activation (Zhong et al., 2012; Tsukamoto, 2014). From the signaling perspective, a single monostable opsin acts more like a switch, rather than the more constant signaling bistable opsins can perform. Again, examples of likely specific environmental adaptations exist. In medaka fish, the opsins *tmt-opsin1b* and *tmt-opsin2* are co-expressed in several brain regions, in addition to another opsin family, the *val-opsins* (Fischer et al., 2013). While tmt-opsin1 is bistable, tmt-opsin2 is monostable (Sakai et al., 2015), likely contributing to differential environmental signal interpretation. Of note, the signaling properties of medaka val opsins are still unclear. Truly understanding the combined functions of such non-visual opsins in an environmental context will certainly be challenging future endeavors, as mutants in just two of these opsins exhibit age- and temperature-dependent synergistic effects (Fontinha et al., 2021; Zekoll et al., 2021).

Yet, it is important to tackle these challenges, because such co-expression of photoreceptors, both opsins and cryptochromes, may turn out to be the rule rather than the exception in invertebrates and vertebrates. A notable example in an environmental context is the regulation of growth and feeding in echinoderms (Liu et al., 2025), where larvae can regulate such intricate processes as the pyloric (lower stomach) opening in response to light (Yaguchi and Yaguchi, 2021), likely tuning digestive processes to time and position in the water.

Similarly, the study of eyes in the diversity of animal species has revealed a complexity of photoreceptors, their wavelength, and downstream signaling that show how different from "conventional" molecular text book model systems other animals can function. The rhabdomeric photoreceptors of the terrestrial slug *Limax* co-express at least three functional opsins and one retinochrome with different cellular signaling features (Matsuo et al., 2023). Similarly, single cell sequencing revealed the co-expression of several *opsins* and the light-receptive cryptochrome *l-cry* in the rhabdomeric eyes of *Platynereis*, at least partially co-expressed in the same cells. While several of them function in the differentiated photoreceptors, one of them, *c-opsin1*, is present in the neurogenic precursor cells in the eyes prior to photoreceptor differentiation. In *c-opsin1* loss-of-function mutants, combined single-cell RNA sequencing and labeling of actively dividing cells by EdU suggest that *c-opsin1* regulates divisions and differentiation of these neural stem cells in the eye, separate from its function in the differentiated ciliary photoreceptors in the worm's median brain (Milivojev et al., 2024 preprint). This leads to the intricate question of why these bristle worms would adjust their eye growth based on light conditions? We hypothesize that this may allow them to adjust to the different depths the species has been reported to inhabit, given that *Platynereis* has been documented for coastal habitats across a range of depths from 1–5 m, but also at 10 m and below (Gambi et al., 1992; Somaschini et al., 1998; Galparsoro et al., 2012; Özpolat et al., 2021). Individuals settling at these different depths' light conditions will significantly differ (Fig. 2, also see discussion in Häfker et al., 2024). Another reason for the likely light-dependent adjustment of eye growth could be the seasonal changes in the light conditions these worms also experience (Veedin Rajan et al., 2021). In either case, the actual meaning of larger eyes for behavior and/or physiology of the animals remains a yet unresolved puzzle.

Another example of the astonishing complexity and sophisticated environmental adaptation to light are the various opsins present in sea urchins (Raible et al., 2006), which appear to render the adult animals into whole visual systems, i.e., the animal functions as an eye (Kirwan et al., 2024 preprint). This again raises many fascinating questions, especially in the context of the different environments sea urchins inhabit.

Most of the above-mentioned light-sensory systems likely represent adaptation to light environments under daylight. However, lunar light also provides a significant amount of information to animals, which can be used for orientation (Foster et al., 2019) or timing (Kronfeld-Schor et al., 2013; Last et al., 2016; Andreatta and Tessmar-Raible, 2020). At least under some instances, this requires animals to distinguish lunar and solar light and – in order to phase synchronize their inner timing systems – even moon phase.

How animals adapted to decode moon phase: the *Platynereis* example

The marine bristle worm *Platynereis dumerilii* exhibits a reproductive strategy tightly linked to the lunar cycle. By timing their sexual maturation and synchronized swarming events through an endogenous oscillator, aka inner calendar or circalunar clock, which is entrained by nocturnal light of full moon duration, these worms enhance fertilization success. This synchronization ensures simultaneous maturation, a strategy also observed in many other externally fertilizing marine species, but even increasingly documented for terrestrial animals (reviewed in Ritter and Tessmar-Raible, 2024).

Accurate interpretation of moonlight against other light stimuli is crucial for synchronizing the circalunar clock among individuals. The cryptochrome L-Cry plays a key role in this differentiation. Loss-of-function mutants of *l-cry* adjust their circalunar clocks more quickly to shifts in moon phase under artificial light, but do not show significant disadvantages under naturalistic light stimuli (Poehn et al., 2022). This suggests that correctly identifying the full moon requires molecular collaboration between L-Cry and at least one other photoreceptor.

To correctly identify the full moon, photoreceptors must detect both the intensity and the duration of the moonlight stimulus. Intensity alone is insufficient because – dependent on weather and other environmental conditions – different moon phases can produce similar light levels, making it difficult to distinguish the full moon based solely on brightness. Likewise, duration of a light stimulus alone cannot be relied upon because sunlight would be confusing to animals (Fig. 1C–E). Therefore, combining information about both the intensity and duration of moonlight allows for a determina-

tion of moon phases, including the full moon.

Biochemically, L-Cry forms a homodimer that predominantly resides in the nucleus under dark conditions (Poehn et al., 2022; Vu et al., 2023). This dimer state serves as a prerequisite for its ability to distinguish between the vastly different light intensities of moonlight and sunlight, which amount to 10^5–10^6 orders of magnitude difference (Posch et al., 2010; Poehn and Tessmar-Raible, 2022). Each monomer within the dimer contains the cofactor flavin adenine dinucleotide (FAD), which is sensitive to light. When exposed to light mimicking moonlight intensities and spectra for an extended period of several hours, only one of the two FAD molecules within the dimer becomes photoreduced, supposedly resulting in an asymmetric dimer: one L-Cry in the dimer has its FAD photoreduced. Protein structural changes cause the oxidized FAD in the second L-Cry of the dimer to require more energy for the photoreduction process. This results in a scenario under which the two FADs in the L-Cry dimer have different sensitivities to light. Notably, even prolonged moonlight exposure of up to 12 hours does not lead to the reduction of this second FAD (Poehn et al., 2022).

In contrast, under the much more intense illumination of sunlight, both FADs in the dimer are rapidly photoreduced within minutes. Sunlight provides enough photons to overcome the lower quantum efficiency of the second L-Cry-bound FAD within minutes (Fig. 3A) (Poehn et al., 2022). This full activation induces a conformational change in L-Cry, leading to the dissociation of the dimer into monomers (Vu et al., 2023). The monomers are then exported from the nucleus, where they can still be detected for 30–60 min. Subsequently they are degraded in the cytoplasm (Poehn et al., 2022; Vu et al., 2023). However, analyses of L-Cry protein levels under continuous sunlight exposure reveal that apparently this is certainly not capturing the entire complexity of the process, because L-Cry can be re-detected after 8 hrs, but the exact level may depend itself on the phase of the circalunar clock (Zurl et al., 2022; Coric, Orel, and Tessmar-Raible, unpublished).

The differential sensitivity of the two L-Crys within a dimer allows L-Cry to act both as a highly sensitive moonlight detector and as a sunlight sensor, but importantly, due to its kinetics under moonlight, it provides the animals with information on moon phase, which is crucial for setting their inner calendars to the same phase across the population. Moonlight needs several hours to photoreduce the first FAD in the L-Cry dimer, a duration of moonlight that in the natural habitat of *Platynereis dumerilii* in the Bay of Naples is only reached by the times around full moon.

While the inner monthly oscillator thus requires a detection of moon phase, classical work has shown for species as diverse as humans and algae that light intensity also impacts the period length of the ~24-hr circadian oscillators (Aschoff, 1960, 1965). This means that the exposure to moonlight could also influence the daily timing. Comparative work on the bristle worm *Platynereis* versus *Drosophila* suggests that such influences can be tuned depending on the temporal niches of the species. *Platynereis*, as nocturnal animal, uses the exposure to moonlight (together with influences by its circalunar oscillator) to change the period length of its plastic ~24-hr circadian-circalunidian oscillator to tune the onset of the population-synchronized swarming to the hour just before the rise of the moon (Zurl et al., 2022). *Drosophila melanogaster* as a crepuscular animal should avoid shifting its daily timing in response to moonlight, as dusk and dawn times are independent of this. Consistently, whereas *Platynereis* uses its moonlight detection system to tune its ~24-hr clock, *Drosophila* uses such a system to prevent large effects of moonlight. While both animals use their cry-I type system in combination with rhabdomeric opsins, the systems function mechanistically differently (Zurl et al., 2022). In contrast to the L-Cry of *Platynereis*, the fly's ortholog dCry does not respond to moonlight as a purified protein. The nevertheless high sensitivity suggested by functional genetic analyses (Vinayak et al., 2013) may thus be a property enhanced by endogenous cellular processes.
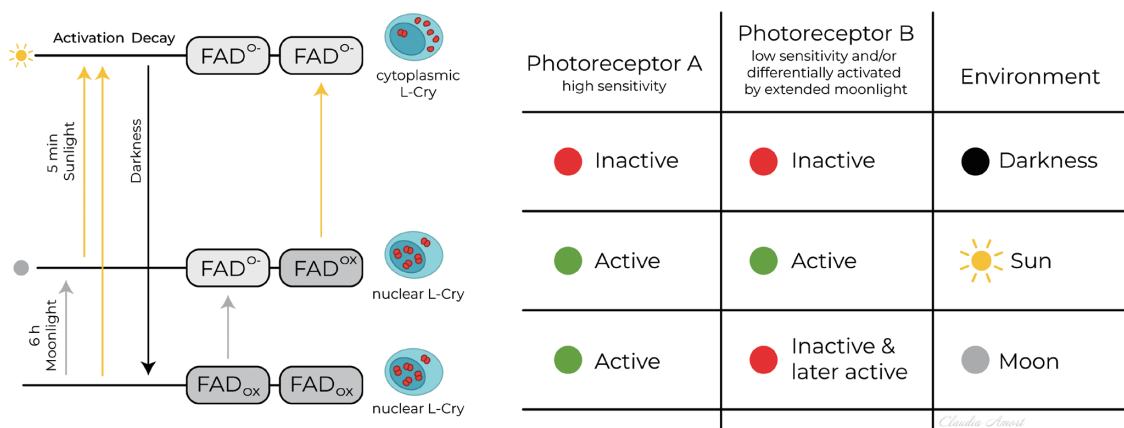
Both *Platynereis* and *Drosophila* can then use a combi-

Photoreceptor A high sensitivity	Photoreceptor B low sensitivity and/or differentially activated by extended moonlight	Environment
🔴 Inactive	🔴 Inactive	⚫ Darkness
🟢 Active	🟢 Active	☀️ Sun
🟢 Active	🔴 Inactive & later active	⚪ Moon

Fig. 3. Concepts for decoding complex natural light information by different photoreceptors. **(A)** Model of an L-Cry dimer, which shows differential quantum efficiency depending on the states of its FAD co-factors. In dark state, both FADs are oxidized and photon capture results in photoreduction of the first FAD with high quantum efficiency, which can be achieved by extended moonlight illumination. The FAD photoreduction results in a presumptive structural change of the L-Cry protein dimer. A subsequent photoreduction of the second FAD is now much less quantum efficient and can only be reached by the high energy of sunlight. Hypothesis and figure modified from Poehn et al. (2022). **(B)** Hypothesis about how the combination of photoreceptors with different light sensitivities and/or biochemical light activation properties can in its combinatoric decode complex natural light information. Figure from C. Amort under CC-BY license.

natorial code of photoreceptors to detect moonlight due to the differential response properties of their photoreceptors to sun- versus moonlight (Fig. 3B). Such combinatorics allow for the identification of the type of natural light, but not the duration of moon phase, which for *Drosophila* (or other diurnal animals) is, however, likely not relevant, as they mainly aim to protect their endogenous circadian oscillators from being impacted by this type of dim nocturnal light irrespective of the specific moon phase. This comparison illustrates how similar proteins can diverge in function based on the ecological requirements of different species.

ANIMAL ADAPTATIONS TO THEIR NATURAL LIGHT NICHE IN A HUMAN-LIT WORLD

The intricate and specifically tuned light sensory mechanisms present in animals are nowadays challenged by the changes humans are making to the light environment. For scientists, this is relevant from at least two different perspectives: first, there are the direct environmental interferences that humans do by artificial illumination, typically referred to as artificial light at night (ALAN) (Davies et al., 2014; Kronfeld-Schor et al., 2017; Walker II et al., 2019). Humans directly (by artificial light sources) and indirectly (e.g., by sky glow) light up the night and illuminate places, such as the oceans' dark/twilight zones that naturally have no or much less light. On the other end, solar panels and other devices are put in places on land and water and block out light that

would normally shine on the organisms underneath. There are even discussions about artificially reducing the amount of light that reaches the earth's surface to reduce global warming. While the latter is targeting the sun, it will certainly also affect lunar light. Furthermore, natural light intensity and spectrum can be affected by snow and ice loss, increase in algal growth or vegetation, etc. (e.g., Häfker et al., 2022a, b). Given the complexity and importance that natural light has for animals it can certainly be stated that the effects of such geoengineering proposals and interventions on complex environmental balances can at present not be realistically estimated and would be likely to unhinge long-evolved systems we may not have even discovered yet. Thus, research into the functions and adaptations of light sensing systems in animals is highly relevant not just for the understanding of biological mechanisms, but to also educate the general public and political decision makers about the consequences human interference with natural sun- and moonlight can have.

Second, when performing lab experiments, we as scientists typically work with animals raised and tested under lab conditions, i.e., artificial illumination. While the lights may appear similarly white to us, their spectrum and intensity differs significantly from natural light (e.g., Dekens et al., 2017), with consequences for the results of experiments.

This calls for a consequent reporting of the experimentally used light conditions, but also for comparative analyses
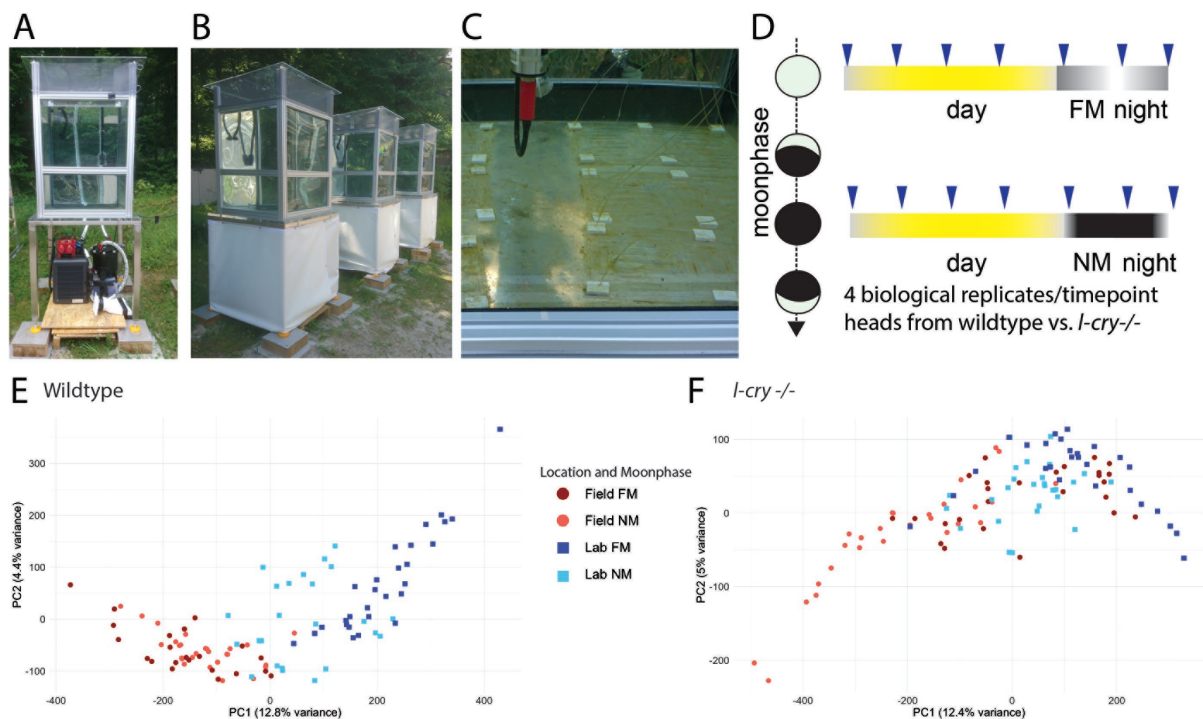

Fig. 4. Comparative diel and lunar transcriptomic analyses of worms under lab vs. field conditions. **(A–C)** Experimental setup in the field. The worms were kept in UV-transparent plexiglass containers at Haidlhof, Austria, an area without artificial light sources. Tanks contained a filtering and temperature control system (visible in **[A]**), to ensure water quality and minimize the impact of temperature. For sampling, worms were allowed to pre-settle on plexiglass squares with glued glass slides that were easily harvested at time of sampling (visible in **[C]**). **(D)** Temporal sampling scheme. Worms were sampled every 4 hours over a 24 h period in four biological replicates (4–5 heads pooled) and analyzed by Illumina-sequencing. **(E, F)** Initial Principal Component Analysis (PCA) of RNA-Seq data for wildtype and *l-cry* mutants (–/–) samples across lab and field conditions. Each biological replicate is shown as an individual data point, color-coded according to the corresponding moon phase and the environment where sampled. Details on the experimental set-up are available from the authors upon request.

of experiments under lab versus more natural (light) conditions.

Driven by these considerations, we designed tanks for outside maintenance of *Platynereis dumerilii* worms (Fig. 4A–C), maintained them under these conditions for several months and subsequently sampled their heads for transcriptomic analyses over the 24 h cycle and at two different lunar phases (new moon: NM and full moon: FM, Fig. 4D). The tanks were designed such that the temperature was regulated and thus constant over the course of the experiment, to focus on the effects of illumination.

The same sampling scheme was in parallel mimicked in the lab, allowing us to assess the specific effects of natural versus artificial light conditions. The amount of data resulting from this approach was large and will require more long-term dedicated analyses beyond the scope of this article. However, initial principal component analyses (PCAs) for the data structure already reveal two interesting aspects. First, for wild-type animals, the difference between lab versus field tank animals is significant for transcript level, exceeding the difference between moon phases and time of day (Fig. 4E). Second, this is different for mutants of the light-interpreter *l-cry*. These mutant worms show fewer differences between lab and field tanks, being overall closer to lab counterparts than are the lab and field wild-type worms (Fig. 4E, F). While PCAs represent differences caused by several variables, these plots are consistent with our interpretation of the lab experiments under artificial versus naturalistic light that *l-cry* mutants are less able to discriminate between the different types of light (Poehn et al., 2022; Zurl et al., 2022).

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COMPETING INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Conceptualization: POW, NSH, KT-R. Methodology: NSH, KH, KT-R. Investigation: POW, NSH, KH, KT-R. Funding acquisition: KT-R. Project administration: KT-R. Supervision: NSH, KT-R. Writing – original draft: POW, KT-R. Writing – review and editing: POW, NSH, KH, KT-R.

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