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Shining a light on jellyfish behaviour: Enhanced motor activity and positive phototaxis in *Aurelia coerulea*.

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ABSTRACT

Jellyfish of the genus *Aurelia* possess a decentralized nervous system and rhopalia that contain basic visual structures, providing a unique opportunity to explore light-driven behavior in the absence of a centralized brain. Despite their anatomical simplicity, little is known about how these animals modulate their motor activity in response to light or whether they exhibit consistent preferences for light or dark environments. In this study, we conducted two behavioral experiments to investigate the light-dependent behaviour in juveniles of *Aurelia coerulea*. In Experiment 1, we measured pulsation frequency under light and dark conditions as a proxy for motor activity. In Experiment 2, we adapted a scototaxis-based test to assess phototactic preferences in an environment divided into illuminated and dark compartments. Our results show that jellyfish increased pulsation rates under light conditions and spent significantly more time in the illuminated area, suggesting a consistent positive response to light. These findings provide evidence of light-mediated behavior in *Aurelia coerulea* and contribute to a deeper understanding of how complex sensory-guided behaviors can emerge in organisms without centralized nervous systems.

1. Introduction

Animals as diverse as vertebrates and invertebrates commonly respond to light stimulation. One of the simplest forms of this response is an increase in motor activity in the presence of light (photokinesis). For instance, larval zebrafish sharply increase locomotor activity when exposed to light after a period of dark adaptation; conversely, they show transient hyperactivity upon entering darkness before becoming quiescent (Burgess and Granato, 2007). In vertebrate amphibians, such as *Xenopus laevis* tadpoles, ambient light, even without retinal input, can drive rhythmic swimming activity via deep-brain photoreceptors tuned to ultraviolet light wavelengths (Currie et al., 2016). In invertebrates, mayfly nymphs (*Stenonema modestum*) adjust locomotor and vertical movements in response to simulated light/dark cycles, increasing movement under higher illumination (Schloss, 2002).

A relatively more complex response to light is called 'phototaxis', which is characterized by movement toward (positive phototaxis) or away from (negative phototaxis) a light source (reviewed in Jékely, 2009). Both types of behaviors can offer potential ecological advantages. For example, positive phototaxis may help phototrophic organisms to locate food sources, facilitate larval dispersal, or enhance the likelihood of gamete fusion at the surface (Jékely, 2009). Negative phototaxis, by contrast, is thought to be associated with one of the most critical behaviors for survival: the ability to hide from predators (Eterovick et al., 2018; Lima and Dill, 1990). To assess light/dark preference, animal individuals are often placed in an environment divided into illuminated and dark areas, and their spontaneous preference is recorded. This test is known as the scototaxis test and has been widely used with laboratory animals, such as rodents (Bourin and Hascoët, 2003), amphibians (Guimarães et al., 2021), and fish (Maximino et al., 2010; Pecunioso et al., 2024). Although tests assessing reaction to light are commonly used with bony fish, comparable approaches have also been applied to other aquatic invertebrates, particularly crustaceans such as crayfish (Fossat et al., 2015) and crabs (Hamilton et al., 2016).

Among invertebrates, jellyfish (phylum Cnidaria) have evolved

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sophisticated sensory systems despite their anatomical simplicity and lack of a centralized nervous system (Birch et al., 2023). Within the phylum Cnidaria, the subphylum Medusozoa (four classes, Staurozoa, Cubozoa, Scyphozoa and Hydrozoa) is characterized by the presence of a medusoid stage in their life cycle. Cubozoa and Scyphozoa are grouped into a clade, called Rhopaliophora, which indicates the presence of the rhopalia (4 in Cubozoa, 8 up to 16 in Scyphozoa). Rhopalia are marginal sensory structures of the umbrella which contain a statocyst for spatial orientation, chemo-sensory pits and light-sensitive structures that span from simple eyespots, pigment cups or lensed eyes (Sötje et al., 2011; Nakanishi et al., 2009). Hydrozoa lack rhopalia, but have eyespots or pigment cups; only two orders possess statocysts, Trachylinae and Leptothecata (Avian, Ramšak, 2021). Their visual systems are particularly notable, exhibiting a wide range of complexity, from simple photoreceptors to image-forming eyes (Birch et al., 2023; Garm and Ekström, 2010; Picciani et al., 2018). However, the investigation of light responses in jellyfish is limited to a few species. Some hydromedusae (e.g., *Polyorchis penicillatus, Corymorpha gregaria, Spirocodon saltatrix*), which possess basic sensory structures such as statocysts and simple ocelli, exhibited light-response swimming behaviour that may be related to predator avoidance strategies or diurnal migrations (Arkett, 1985; Arkett and Spencer, 1986a, 1986b; Ohtsu and Yoshida, 1973).

Cubozoans, conversely, represent the upper extreme of cnidarian visual evolution and the complexity of light responses is higher. Species such as *Tripedalia cystophora* possess articulated rhopalia featuring 24 eyes of four morphologically distinct types (upper and lower lens-eye, pit-eye, and slit-eye), enabling behaviors such as obstacle avoidance, spatial navigation, and orientation (Garm et al., 2008; Garm and Ekström, 2010; Nilsson et al., 2005; Petie et al., 2011). Cubozoans also employ multiple photosystems (different eye types and extraocular photoreceptors) that likely subserve different visually guided behaviours (Garm and Ekström, 2010). Box jellyfish seem to be attracted by light objects and avoid darker ones, which suggests a positive phototaxis (Garm et al., 2016, 2011). This behavior is further supported by their preference for foraging in light shafts between the mangrove roots (Buskey, 2003).

Scyphozoans, including the genus *Aurelia* (commonly referred to as moon jellyfish), possess a nervous and visual system of intermediate complexity within Medusozoa (Cunningham et al., 2024; Jarms et al., 2019). These structures are more elaborate than those found in hydromedusae, yet less specialized than those of cubozoans. Their rhopalia contain pigment-spot ocelli for photoreception and statocysts for equilibrium, enabling coordinated responses to environmental light cues (Albert, 2011; Birch et al., 2023). While their visual systems lack image-forming optics, scyphozoans exhibit a range of sophisticated light-mediated behaviors, such as diel vertical migration and sun-compass-based horizontal navigation (Albert, 2011; Hamner et al., 1994). In particular, Hamner et al. (1994) documented the capacity of *Aurelia aurita* to maintain directional swimming relative to solar cues, suggesting a photoreceptive system capable of detecting and processing directional light information. However, this study was conducted under natural conditions, where isolating the specific effect of light from co-varying physiological and environmental variables (e.g., water temperature) remains challenging. Consequently, controlled laboratory experiments are necessary to isolate environmental parameters and rigorously evaluate phototaxis. Horstmann (1934) investigated whether ambient light alters the contraction frequency of *Aurelia aurita*, and sought to isolate the precise anatomical structures responsible for light perception. The author recorded pulsation rates alternating periods of illumination and total darkness in glass containers. The average number of pulsations per minute was significantly higher in enlightened environments than in the dark. Following microchirurgical excision of the pigment spots (ocelli) from the marginal organs, this light-dark frequency differential completely vanished, and the animals ceased to respond to illumination changes. Parallel testing on *Cyanea capillata*, a species naturally lacking ocelli, yielded no behavioral response to light. These findings demonstrated that the ocelli of *Aurelia aurita* function as true photoreceptors, providing sensory inputs that directly accelerate the motor output of the marginal organ ganglia to speed up the animal's swimming pace.

Therefore, while it is established that *Aurelia* jellyfish respond to light stimulation via kinesis (Horstman, 1934), and field observations suggest they orient toward the sun via positive phototaxis (Hamner et al., 1994), empirical evidence remains partially inconclusive regarding their true preference for bright versus dark environments independent of co-varying diurnal factors. The present laboratory study aims to address this gap. Given the ongoing replication crisis in the behavioral sciences (Bogdan, 2025; Locey, 2020), including comparative psychology (Farrar et al., 2020; Agrillo and Miletto Petrazzini, 2012), validating foundational observations has become paramount. Therefore, prior to examining spontaneous preferences for light or dark environments, we preliminarily sought to replicate and verify the kinetic behaviors originally reported by Horstman (1934) within our specific experimental setup. Considering the growing prominence of the moon jellyfish as a model organism in neurobiology (Albert, 2011; Pallasdies et al., 2019), clarifying its behavioral responses to light can offer crucial insights into the evolution and mechanisms of visual systems in decentralized organisms.

In this study, we conducted two experiments to investigate *Aurelia* jellyfish's response to light. Exploiting their spontaneous pulsations, in Experiment 1, we scored whether jellyfish display greater locomotor activity in light conditions relative to darkness; in Experiment 2, we assessed phototactic behavior by adapting the apparatus and procedure for the scototaxis test described above.

2. Experiment 1: motor activity in a dark/light environment

2.1. Experiment 1 - methods

2.1.1. Ethical statements

Jellyfish are not covered by European legislation governing the use of animals in research. Nevertheless, all experiments were conducted in accordance with the principles of the 3Rs, and the number of animals was kept to the minimum necessary. The reporting of this study follows the ARRIVE guidelines for animal research (Du Sert et al., 2020).

2.1.2. Animals

Jellyfish observed in our study were obtained from the PetJellyfishUS© company, and the original population was collected in the Mediterranean Sea, and identified as *Aurelia spp*. The genus *Aurelia* (Lamarck, 1816) comprises a group of morphologically cryptic scyphozoan jellyfish, commonly known as moon jellyfish, whose evolutionary history dates back to 300–400 million years (Fernández-Alías et al., 2023; Khalturin et al., 2019). Recent integrative taxonomic studies combining molecular and morphological evidence have substantially revised the systematics of the genus, leading to the recognition of 27 distinct species (Lawley et al., 2021; World Register of Marine Species WoRMS, 2026). To date, five species of *Aurelia* are currently recognized as occurring in the Mediterranean Sea. Three species are regarded as native to the region: *Aurelia persea* (Forsskål, 1775), *Aurelia pseudosolida* (Garić and Batistić, 2022), and *Aurelia relicta* (Scorrano et al., 2017). *Aurelia coerulea* (von Lendenfeld, 1884), and *Aurelia solida* (Browne, 1905) are considered non-indigenous.

To overcome the issues related to the sibling species inside the *Aurelia* genus in the Mediterranean Sea, molecular analyses were performed to identify the individuals at the species level. DNA was isolated from the margin umbrella of one specimen by E.Z.N.A.® Mollusc & Insect DNA Kit (Bio-tek), following the manufacturer's instructions. A fragment of the cytochrome c oxidase subunit I (COI) gene was amplified using Folmer et al. (1994). PCR, carried out in a final volume of 25 μL, was performed with 1 × AccuStart II PCR ToughMix (Quantabio), 0.3 μM of each primer, and 20 ng of gDNA, following the touch-up

thermal profile: initial denaturation 95 °C for 2 min; 6 cycles with denaturation at 95 °C for 15 s, annealing at 46 °C for 15 s and elongation at 72 °C for 35 s followed by 35 cycles with denaturation at 95 °C for 15 s, annealing at 54 °C for 15 s and elongation at 72 °C for 35 s plus a final extension at 72 °C for 2 min. The PCR was checked using a 1.5% TAE electrophoretic gel, and the PCR was purified with ExoSAP-IT™ PCR Product Cleanup Reagent (Applied Biosystems™). The purified PCRs were sent to an external service to be Sanger sequenced (Eurofins; Hamburg, Germany). The identification of the COI fragment (GenBank ID PX452223) led to the identification of *Aurelia coerulea* (von Lendenfeld, 1884), a cosmopolitan species spread from Japan, California, and the Mediterranean basin.

A total of 16 juvenile jellyfish, approximately 3 cm in diameter, were tested (Fig. 1). Individuals were divided into two groups of eight individuals and housed in two separate stock tanks. The circular stock tanks (Jellyfish Aquarium 'O16', 38 cm diameter, width: 21 cm) were round with an inbuilt biological filtration system and a color-changing LED lighting (15 watts) with a remote control. Jellyfish were fed twice a day with live *Artemia salina* nauplii. Marine water was used with the following parameters: salinity of 30–34 ppt, pH of 8.0–8.3, and a temperature of 20°C.

2.1.3. Apparatus and procedure

The experimental setup was identical to the stock tanks (Fig. 2a). Jellyfish were placed individually into the tank and allowed a 30-second acclimation period under a dim lighting condition, provided solely by the room's ceiling neon lights (two 58-watt tubes). This lighting served as an intermediate level between complete darkness and full illumination. Following acclimation, the experimental procedure commenced. Half of the jellyfish were exposed to the Light Condition, during which the apparatus was illuminated with an LED (15 watts). The other half was placed in the Dark Condition, in which the tank was kept in complete darkness by covering the walls and the bottom of the tank with black plastic sheets (Poliplack©). Each condition lasted 10 min, during which the number of pulsations, as a measure of photokinesis, was recorded as the dependent variable using 'Ciclic Timer' software (University of Padova). A 1-minute transition interval separated the two conditions, during which the experimenter prepared the software for the next phase. During this brief period, the jellyfish remained under the intermediate lighting condition provided by the ceiling neon lights. Statistical analyses were conducted using SPSS version 29.0.2.0.

Fig. 1. A juvenile specimen of *Aurelia coerulea* used in the present study.

2.2. Experiment 1 – results and discussion

Data were normally distributed, as confirmed by the Shapiro-Wilk test ($P = 0.109$); therefore, parametric analyses were applied. A repeated-measures ANOVA was conducted with Condition (Light / Dark) and Time (1–10 min) as within-subjects factors, and Order (Light first / Dark first) as a between-subjects factor. The Condition variable had a significant effect on the number of pulsations (pulsations in the bright environment: 95% CI [21.610, 37.740], pulsation in the dark environment: 95% CI [15.639, 27.345]; $F_{1,14} = 10.104$, $P = 0.007$, partial eta squared $\eta_p^2 = 0.419$), indicating that jellyfish exhibited a higher number of pulsations in the light condition compared to the dark condition. No main effect of Time was found ($F_{9126} = 1.093$, $P = 0.373$, $\eta_p^2 = 0.072$), nor was there a main effect of Order ($F_{1,14} = 0.01$, $P = 0.970$, $\eta_p^2 < 0.001$). Additionally, no interaction effects were significant (Condition × Order: $F_{1,14} = 0.024$, $P = 0.880$, $\eta_p^2 = 0.02$; Time × Order: $F_{9126} = 1.153$, $P = 0.331$, $\eta_p^2 = 0.076$; Condition × Time: $F_{9126} = 1.922$, $P = 0.054$, $\eta_p^2 = 0.121$; Condition × Time × Order: $F_{9126} = 0.525$, $P = 0.854$, $\eta_p^2 = 0.036$; Fig. 3).

This first experiment showed that *Aurelia coerulea* displays greater locomotor activity (i.e., higher pulsation frequency) in a bright environment compared to a dark environment, in line with previous finding in a closely related species (*Aurelia aurita*, Horstmann, 1934). In the second experiment, we assessed whether they actively swim toward a brighter environment.

3. Experiment 2: phototaxis response

3.1. Experiment 2 – methods

3.1.1. Animals

A total of 17 juvenile experimentally naïve jellyfish (*Aurelia coerulea*) were tested; they were reared in the same conditions described in Experiment 1, in two separate groups of 8 and 9 individuals.

3.1.2. Apparatus and procedure

The experimental tank (length × width × height, 39 × 19 × 32 cm) was divided into a bright and a dark compartment using white and black plastic sheets (Poliplack©), which were used to cover the inner walls and the bottom of the tank (Fig. 2b). One half of the tank was covered by white material to create the illuminated area, while the other half was covered by black material to create the dark area. An LED (18 watts) was placed directly above the white compartment to brighten the white area. The tank was filled with 16 cm of seawater, using the same water parameters as those maintained in the stock tanks. Due to the negligible infrared emission characteristic of LED lighting, the 18 W light source suspended 32 cm above the tank did not induce any detectable thermal changes in the water. To ensure the absence of localized temperature gradients between the experimental zones (e.g., radiant heating within the bright area), we recorded five temperature measurements on opposite sides of the apparatus. Water temperature remained consistent across both halves (bright area: 95% CI [19.24, 20.91], mean ± SD = 20.08 ± 0.672 °C; dark area: 95% CI [19.74, 20.30], mean ± SD = 20.02 ± 0.228 °C).

At the beginning of the first trial, the jellyfish were individually transferred from the stock tank to the centre of the experimental tank using a black plastic ladle. In half of the trials, the darker compartment was positioned on the right side of the tank; in the other half, it was on the left. Two independent observers recorded the position of jellyfish in the tank for 30 min. At the end of each trial, each jellyfish was placed in an individual 1-liter tank to allow for identification in the second trial. The second trial was conducted 3 h later and followed the same procedure as the first, with the only difference being that the positions of the light and dark compartments were reversed for each jellyfish (e.g., if the dark compartment was on the left in the first trial, it was on the right in the second). To assess the existence of positive phototaxis, we

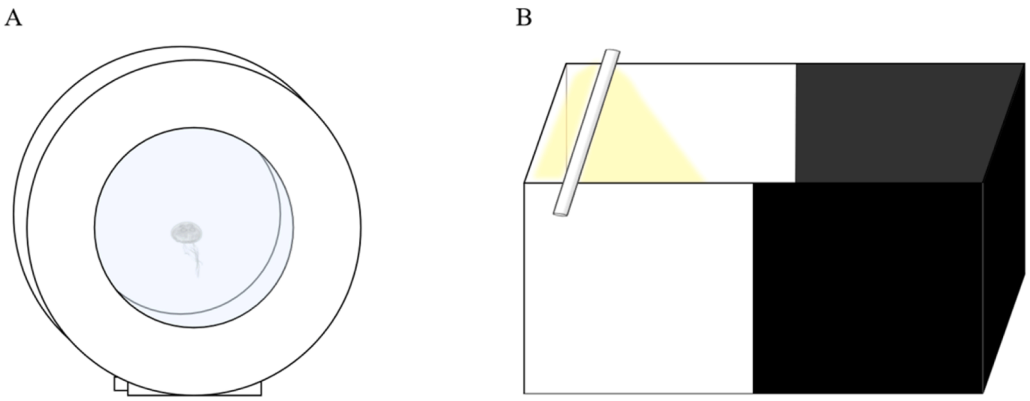

Fig. 2. (A) Experimental tank (38 × 38 × 21 cm) used in experiment 1 with integrated biological filtration and color-changing LED lighting. (B) The experimental tank (39 × 19 × 32 cm) used in experiment 2 was divided into bright and dark compartments using black and white plastic sheets. An LED was placed above the white compartment to illuminate the bright area.

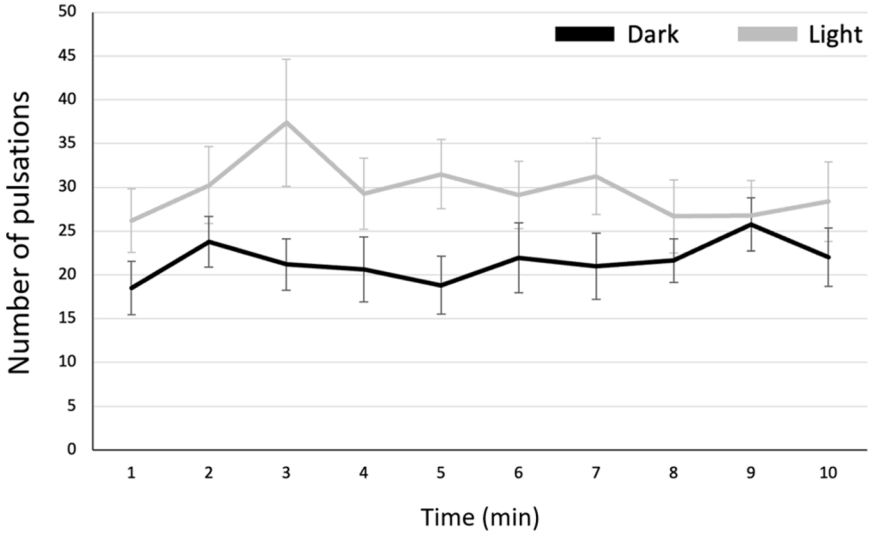

Fig. 3. Number of pulsations as a function of time and light/dark condition. Moon jellyfish were consistently more active in the light condition across the 10-minute observation period. Bars represent standard errors of the mean.

recorded as dependent variable the proportion of time spent in the brighter area [time spent in the brighter area / (time spent in the brighter area + time spent in the darker area)] using the software 'Ciclic Timer'. Statistical analyses were conducted using SPSS version 29.0.2.0.

3.2. Experiment 2 – results and discussion

Data were normally distributed, as confirmed by the Shapiro-Wilk test ($P = 0.393$); therefore, parametric analyses were applied. A repeated-measures ANOVA was conducted with Trial (trial 1 and 2) and Time (five-minute interval, for a total of 6 blocks) as within-subjects factors. No main effect of Trials was found ($F_{1,16} = 0.006$, $P = 0.941$, $\eta_p^2 < 0.001$), nor was there a main effect of Time ($F_{5,80} = 0.259$, $P = 0.934$, $\eta_p^2 = 0.016$), indicating that the proportion of time spent in the brighter area was consistent between the two trials and across time. Additionally, no interaction effect was significant ($F_{5,80} = 0.304$, $P = 0.909$, $\eta_p^2 = 0.019$; Fig. 4).

When the time spent in each half was analyzed, a significant preference for the brighter area was observed (proportion of time in the brighter area, CI [0.515, 0.796], one-sample *t*-test, $t_{16} = 2.340$, $P = 0.033$, Cohen's $d = 0.567$).

4. General discussion

Our laboratory study replicates previous findings regarding the role of light on motor activity in another *Aurelia* species, while providing new insights into how light drives compartmental preference within a light/dark gradient and highlighting the capacity for sensory-guided behavior in this species.

In Experiment 1, jellyfish exhibited a significantly higher pulsation frequency under illuminated conditions compared to darkness. Early studies reported that light may stimulate the ocelli, which in turn stimulates the pacemaker activity located in the rhopalia of *Aurelia* (Horridge, 1956; Horstmann, 1934). Critically, the increase in pulsation rate in our study is independent of both exposure order and test duration, indicating a robust and consistent behavioral response to light. Because this result could be attributed to different reasons, as a stress-like reaction to light or increased arousal, in Experiment 2, we investigated whether moon jellyfish actively search for light in a two-alternative forced choice test, providing them with two adjacent compartments, an illuminated and a dark one, freely explorable. This design was adapted from scototaxis protocols widely applied across animal taxa (Guimarães et al., 2021; Fossat et al., 2015; Hamilton et al., 2016; Pecunioso et al., 2024). Our results showed a clear preference for the illuminated compartment, as moon jellyfish spent significantly more

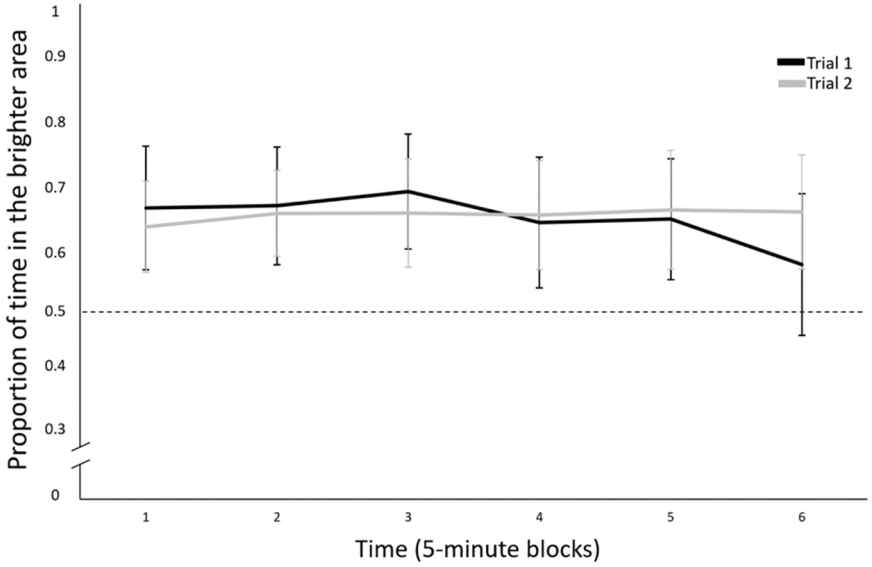

Fig. 4. Proportion of time spent in the brighter area as a function of time across the two trials. Each point on the X-axis represents 5-minute blocks (1−5, 6−10, 11−15, 16−20, 21−25, 26−30). Black lines indicate jellyfish behavior in the first trial; grey line indicates their behavior in the second trial. Bars represent standard errors of the mean.

time in the light area across both trials. It is important to note that water temperature was kept constant between the two halves of the apparatus, thereby excluding a confounding variable often encountered when investigating sun compass orientation or light/dark preference in natural environments (Hamner et al., 1994). Furthermore, unlike natural environments where prey/predator density can also be affected by solar activity, our laboratory setting explicitly excluded the presence of prey or predators in either area. Our results suggest a form of positive phototaxis, echoing similar findings in cubozoans (Garm et al., 2011, 2016), some hydromedusae (Arkett and Spencer, 1986a, 1986b), and extending the tendency to a scyphozoan, *Aurelia coerulea,* never investigated before. The consistency in preference across the two repeated trials, counterbalancing light/dark compartment placement, reinforces the conclusion that the choice reflects a genuine preference for more illuminated areas and is not due to any positional bias.

Taken together, the findings from both experiments suggest that moon jellyfish are not only capable of detecting light but also modulating their motor activity and spatial orientation accordingly. Although the visual system of *Aurelia coerulea* lacks image-forming capacity, the rhopalia contain photoreceptors (Albert, 2011; Birch et al., 2023). It is possible to hypothesize that the ocelli may not merely act as simple metabolic triggers (Horstmann, 1934), but may participate in a more complex spatial processing system capable of comparing light gradients to guide goal-directed orientation. The positive phototactic response observed here could be ecologically relevant. In natural settings, a preference for light may facilitate vertical migration toward the ocean surface, aiding in feeding, dispersal, or synchronization of reproductive activities (Jékely, 2009; Hamner et al., 1994). Alternatively, increased pulsation in response to light might serve as a readiness mechanism for active swimming when visual cues are most informative, such as during daytime (Benhamou and Bovet, 1989).

Interestingly, our results contrast with the negative phototaxis (or scototaxis) behavior observed in many vertebrates, including aquatic ones, in which dark environments are often preferred due to their association with shelter and predator avoidance (Guimarães et al., 2021). The preference for light in moon jellyfish suggests that this environmental cue may signal opportunity rather than threat, a distinction that likely reflects their distinct ecological niche and evolutionary trajectory.

In conclusion, our study contributes to the growing body of evidence that decentralized nervous systems can support flexible, sensory-guided behavior (Agrillo et al., 2025), suggesting an enhanced motor activity in a bright environment and a spontaneous search for brighter areas in a jellyfish. Moon jellyfish are becoming a new model in neurobiology (Albert, 2011); therefore, our research may pave the way for neurobiological investigations of light responses. As we tested juvenile individuals, future studies are necessary to assess whether this preference is consistent across developmental stages (see Arkett, 1985). Additionally, we advocate for further investigation in other scyphozoan species to determine whether our results are specific to *Aurelia* or can be generalized broadly to scyphozoans.

CRediT authorship contribution statement

Alessandra Pecunioso: Writing – original draft, Methodology, Data curation, Conceptualization. **Chiara Manfrin:** Formal analysis, Data curation. **Gregorio Motta:** Writing – original draft, Methodology. **Cinzia Chiandetti:** Writing – original draft, Supervision, Conceptualization. **Massimo Avian:** Writing – original draft, Supervision. **Christian Agrillo:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization.

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