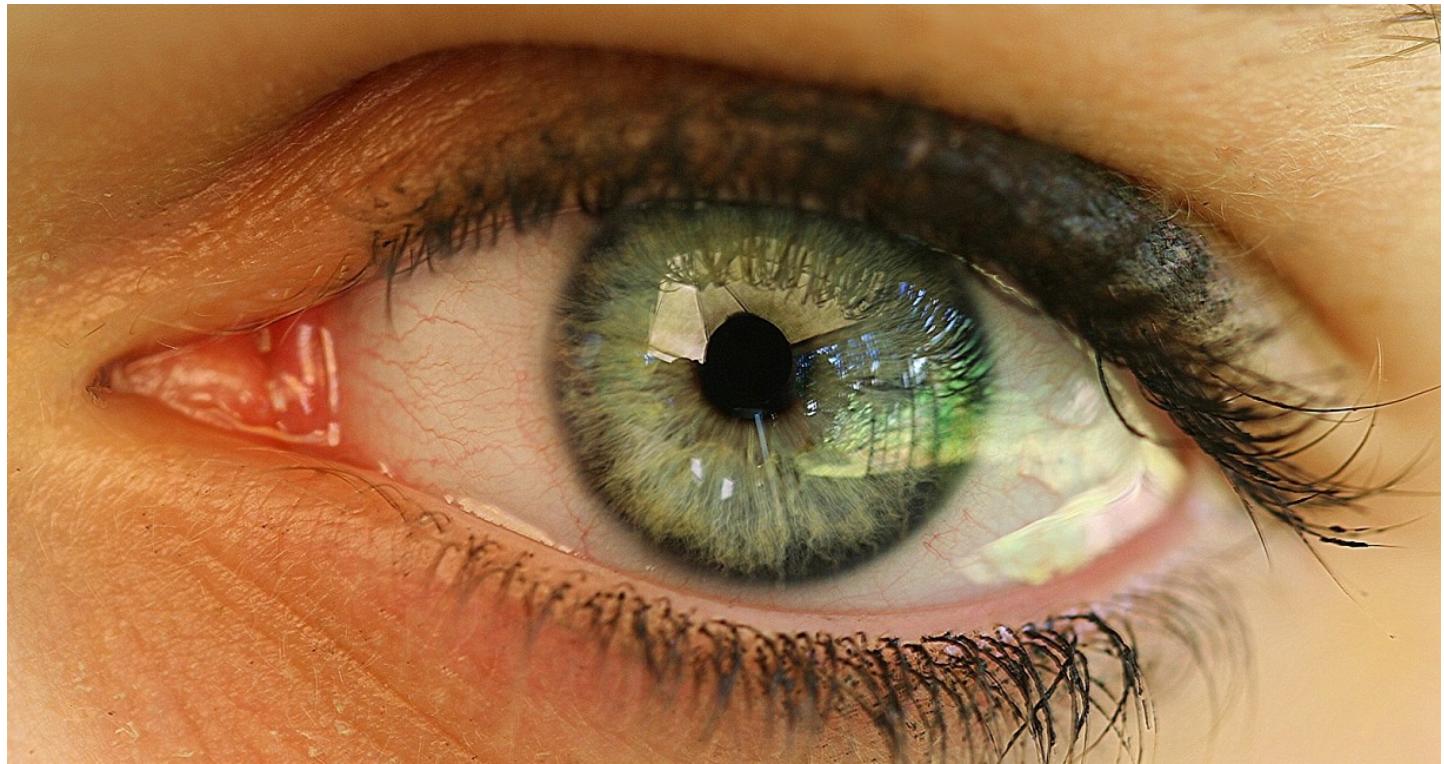


Light, vision and biological clocks

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Since life appeared on Earth, various selection forces have influenced the evolution of living organisms. Among these forces, light generated by our sun probably had the most significant influence. In particular, light and its natural cycles – daily and seasonal – have led living organisms to represent their environment in space and time. This has allowed them to adapt to this environment. How? What visual and non-visual photoreceptor systems have emerged in the animal kingdom? How have the benefits provided by these systems, vision and biological clocks, enabled organisms to control their environment and anticipate its changes?

Our star, the Sun, is 4.6 billion years old. It is a real nuclear reactor: every second, at its heart, 620 million tonnes of hydrogen are converted into 616 million tonnes of helium. The missing four million tonnes are converted into energy radiated outwards, *i.e.* photons, in other words light. Every second, after an 8-minute journey at a speed of 300,000 km per second, 6400 thousands billions photons per square millimeter enter the Earth's atmosphere. A part of them is absorbed or reflected towards space by the atoms and molecules that compose it. The other part reaches the earth's surface and illuminates our planet.

Since life appeared on Earth nearly 3.8 billion years ago, there have been 1,400 billion day/night cycles and 3.8 billion seasonal cycles (see Focus [Light cycles and living organisms](#)). Light has thus strongly influenced the evolution of the living world with the appearance of **photosensitive systems**, **visual or non-visual**, and **biological clocks**. In other words, light and its cycles have allowed living organisms to represent and adapt to space and time [\[1\]](#).

1. Evolutionary history of photoreception

1.1. Photoreceptor proteins

Different steps have marked the evolution of light-sensitive systems, from the appearance of the first photosensitive proteins to

the current complex visual systems. An important class of **photosensitive proteins** is at the origin of **photoreception**: the **opsin** class. There are two super-families of them, the opsins of type I and II [2]. Type I opsins, also called microbial opsins, are found in the three domains of living organisms (*Archae*, *Bacteria* and *Eukarya*). They mainly regulate the orientation reactions of free organisms with respect to light, or **photo-taxia**, as well as the **production of energy**. When did these type I opsins appear? Their general distribution in all organisms suggests that their precursor already existed before the separation of the three domains of living organisms. This distant origin demonstrates the fundamental importance of light for life. Type II opsins, also known as animal opsins, are found only in higher eukaryotic organisms. They mainly regulate **visual photoreception** and **biological clocks**. The precursor of this type of opsin appeared 700 million years ago in primitive metazoans, the first mobile and heterotrophic multicellular organisms. The structure of these two types of opsins is similar, yet there is no phylogenetic link between these two super-families. On the contrary, they would have evolved independently of each other [2].

1.2. The photoreceptor cells

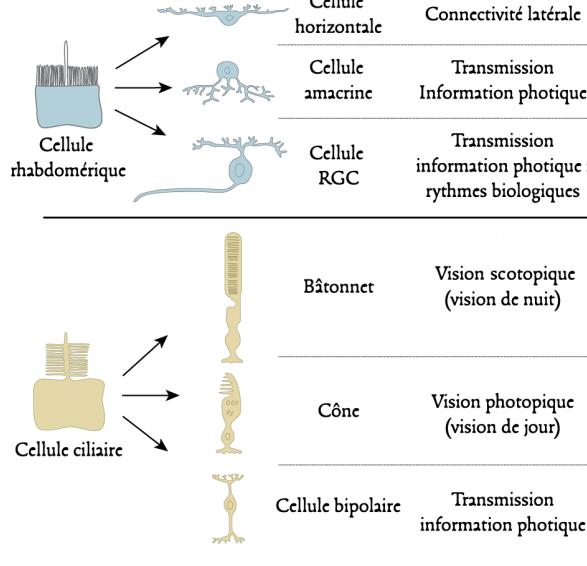


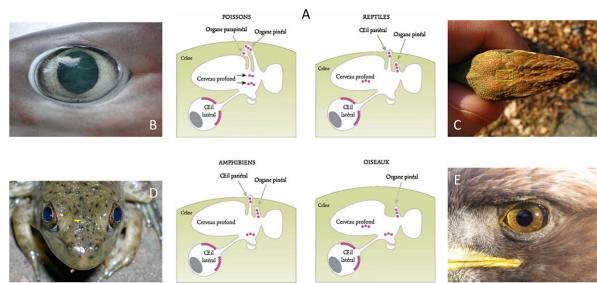
Figure 1. Fate of the two types of rhabdomeric and ciliary photoreceptive cells. [Source: Figure modified (See ref. [4]) after Arendt (See ref. [3])].

Following the appearance of the first **metazoans** and first type II opsins, specialized photoreceptor cells appeared 600 million years ago. However, it was only with the very strong evolutionary radiation{ind-text}Fast evolution, from a common ancestor, of a set of species characterized by great ecological and morphological diversity.{end-tooltip} in the Cambrian, 540 million years ago, that the first complex visual and non-visual systems emerged. In invertebrate and vertebrate animals, there are two types of specialized photoreceptor cells called **rhabdomeric** and **ciliary** cells. They are characterized by a microvilliated apical surface and a ciliated apical surface respectively (Figure 1). In vertebrates, rhabdomeric cells are at the origin of photosensitive ganglion cells involved in the control of biological clocks. Ciliary cells are at the origin of the cones and rods respectively involved in **photopic** (day) and **scotopic** (night) **vision** [3] (Figure 1).

1.3. Non-visual and visual systems

Nowadays, most animals have complex **non-visual** and **visual systems**. Among the non-visual systems, we can distinguish various structures:

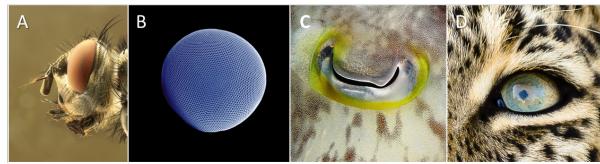
- an organ located inside the skull, in the shape of a small apple: the pineal organ; it is photosensitive in all vertebrates except mammals;
- an organ associated with the **pineal organ**, hence its name as a parapineal organ, intracranial in fish;
- a **frontal organ** or **parietal eye** in amphibians and reptiles;
- **deep brain photoreceptors** in all vertebrates except mammals;
- **dermal photoreceptors**, present on the skin in several vertebrate and invertebrate species, particularly amphibians and cephalopods.



*Figure 2. Visual systems in fish, reptiles, amphibians and birds. A: Sectional schematic representations. The photoreceptor cells are represented by red circles. Modified figure (see ref. [4]) after Foster and Soni (see ref.[5]). B: Lateral eye of a shark (*Hexanchus nakamurai*) [© Photo Jean-Lou Justine (via Wikicommons)]; C: Parietal eye (in the center of the rectangle) on the head of a snake (*Anolis carolinensis*) [©Photo TheAlphaWolf (via Wikicommons)]; D: the lateral eyes and the parietal eye (small grey circle between the two eyes, indicated by a yellow arrow) in the bull frog (*Rana catesbeiana*) [© Photo TheAlphaWolf (via Wikicommons)]; D: golden eagle lateral eye (*Aquila chrysaetos*) [Source: © Photo Peter Kaminski (via Wikicommons)].*

In all these organisms, the lateral eyes provide visual information and are therefore involved in vision: perception of contrasts and colours. In mammals, the lateral eyes are also involved in receiving non-visual information and play an important role in regulating biological clocks [5].

All these organs are involved in non-visual photoreception and play an important role in the regulation and control of biological clocks (Figure 2).



*Figure 3. Some examples of eyes. Compound eyes (A, *Caliphrodae* fly head with compound eye [© Photo Richard Bartz, Munich aka Makro Freak, via Wikicommons]; B, compound eye of Krill, *Euphausia superba* [© Photo Gerd Alberti & Uwe Kils, via Wikicommons]) and single lens eyes (C, cuttlefish, *Sepia* sp © photo Alexander Vasenin, via Wikicommons]; D, leopard's eye, *Panthera pardus* [Source: © Photo Jacques Joyard].*

Visual systems refer to the **lateral eyes** and are found in most invertebrates and all vertebrates. There are ten structurally different categories. Among the most notable are the compound eyes of insects and the single lens eyes of vertebrates and molluscs (Figure 3).

2. The vision

In all vertebrates, the lateral eyes have a common structure. It is similar to that of a single lens camera: the light passing through the pupil (lens) forms an inverted image on the retina (the sensitive surface) that lines the posterior surface of the eye. The retina is a tissue sheet composed of five types of connected **neurons**: visual photoreceptors, horizontal cells, bipolar cells, amacrine cells (without axons) and ganglion cells (Figure 4). A common distinction is between an inner and an outer part [5] (Figure 4).

There are two forms of visual photoreceptors, **cones** and **rods**. The former are sensitive to high light intensities and are therefore involved in so-called photopic day vision. The latter only react to low light intensities and are therefore involved in night vision, known as scotopic vision. The diversity of these photoreceptors is very high, both within the same species and between different species. However, each type of cone and rod contains a specific photoreceptor protein that is only sensitive to certain wavelengths of the electromagnetic spectrum. Each animal species therefore has a monochromatic or polychromatic vision that is specific to it (see below). Thus, fish, amphibians, reptiles and birds are, for the most part, **tetrachromates**: they process visual information using four types of photoreceptors. Mammals are generally **dichromates**, most likely because of their evolutionary history associated with nocturnal ecological niches. A number of primates, such as humans, are a notable exception, as they are **trichromate** [3]. This property, new to mammals, appeared following the duplication of a gene (see Focus [Evolution of colour vision in mammals and primates](#)).

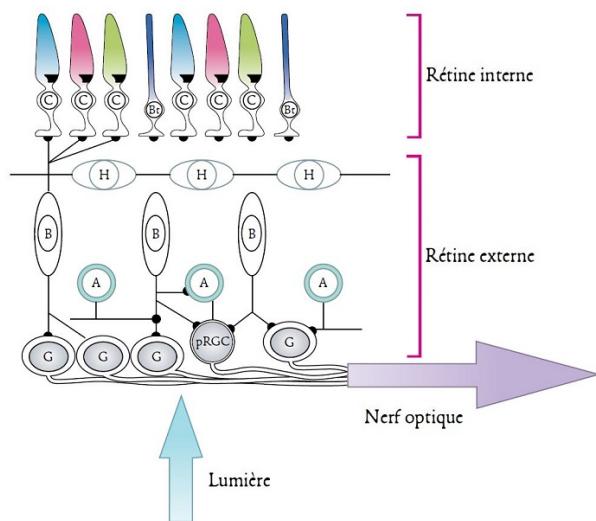


Figure 4. Transmission of photic information. In mammals, the photons that make up light are absorbed by visual photoreceptors, cones (C) and rods (Bt), and non-visual, photosensitive ganglion cells (pRGC). The perceived information is then transmitted, via the optic nerve, to the lateral geniculate body for the treatment of visual photoreception and to the suprachiasmatic nucleus (biological clock) for the treatment of non-visual photoreception. The horizontal (H), bipolar (B), ganglionary (G) and amacrine (A) cells located in the retina participate in the transfer of photic information from the photoreceptors to the optic nerve. [Source: Modified figure [4] from Arendt [3]].

When photons meet visual photoreceptors, they transmit light information - that is, the number of photons - to the ganglion cells of the **retina** through bipolar cells. The **axons of the ganglion cells**, which form the optic nerve, in turn transmit this information to the geniculate (knee-shaped) lateral body, which communicates with the visual cortex where the photic information is interpreted. During information transfer, horizontal cells facilitate lateral connectivity between photoreceptors and regulate their activity to increase the acuity of the photic signal. **Amacrine cells**, on the other hand, allow connections between bipolar and ganglion cells and participate in the transfer of information. It should be noted that there is a subpopulation of photosensitive ganglion cells that directly transfer photic information to the suprachiasmatic nucleus (located above the optical chiasma), the center of the biological clock [6] (Figure 4). This notion is discussed below.

Thus, organisms are able to perceive the visual information emanating from their environment and can therefore make a spatial representation of it.

3. Clocks and biological rhythms

3.1. Biological rhythms and the day/night cycle

The term "**biological rhythm**" refers to a phenomenon that, within a living organism, is repeated over a period and amplitude that is constant over time. For a given species, these rhythms are genetically determined and generated by an internal clock that is active even in the absence of external stimuli. It is possible to distinguish three types of biological rhythms:

- **circadian rhythms**, also called daily rhythms, which have a period close to 24 hours;
- **ultradian rhythms**, which have a period of less than 24 hours;
- **infradian rhythms**, which have a period of more than 24 hours; the **circadian rhythm**, close to a terrestrial year, falls into this last category [6].

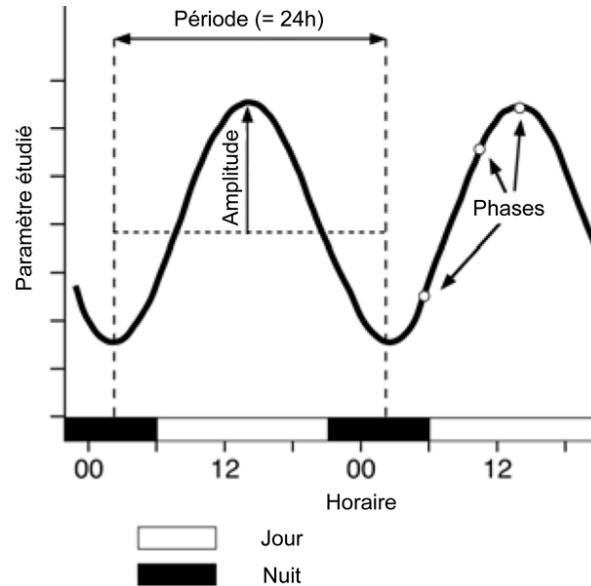


Figure 5. Biological rhythm. Graphical illustration of a biological rhythm synchronized by the day/night cycle over a 24-hour period. The parameter studied may be hormone production or body temperature in a mammal, etc. [Source: Figure modified from Koukkari & Sothern (see ref. [7])]

The internal clock is driven and synchronized by external stimuli. The most important is the day/night cycle. It has several advantages for living organisms. It does not vary from year to year and is correlated to seasonal changes in the environment, unlike other external stimuli such as temperature, humidity or tidal cycles. Thus, driven by the 24-hour day/night cycle, living organisms can anticipate seasonal changes in the environment, express physiological and behavioural characteristics at appropriate times, and thus survive and benefit from their environment [7] (Figure 5).

3.2. Central and peripheral clocks

In mammals, the main internal clock resides in the **suprachiasmatic** nucleus of the **hypothalamus**. This nucleus is composed of about 20,000 neurons capable of spontaneously and cyclically activating "clock" genes. Without external stimuli, and depending on the species, the expression of these genes oscillates over an endogenous period between 23h and 25h. Once activated, these clock genes in turn control the expression of other genes. In total, in mammals, nearly 20% of the genome is under the control of the main internal clock [7].

There are also secondary peripheral clocks. Indeed, clock genes are expressed in most peripheral tissues. However, without the main internal clock, the expression cycles of the clock genes differ from one peripheral tissue to another. The suprachiasmatic nucleus is therefore necessary to synchronize these secondary clocks.

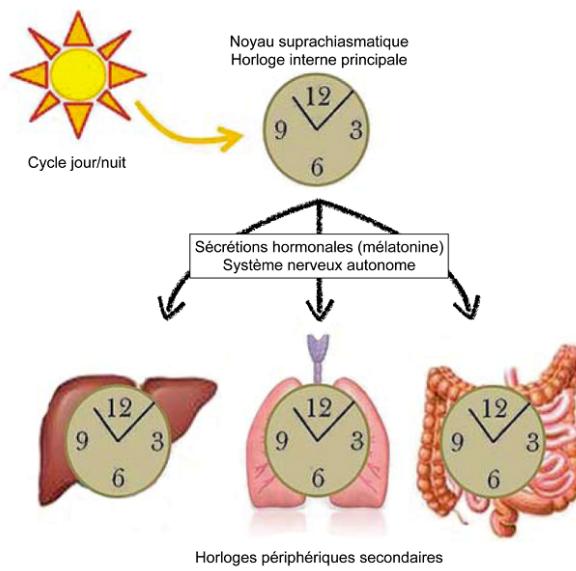


Figure 6. Biological clock. In mammals, the day/night cycle synchronizes the main internal clock over a 24-hour period. This clock, in turn and via hormonal secretions and the activation of the autonomic nervous system, synchronizes the body's peripheral secondary clocks. [Source: Figure modified from ref. [9]].

Thanks to the day/night alternation, the main internal clock is strictly synchronized over a 24-hour period. In mammals, photic information is perceived by the internal retina of the lateral eyes. As we have already seen, it is composed of several families of photoreceptor cells, including photosensitive ganglion cells at wavelengths between 460 and 480 nm (blue) involved in the transmission of non-visual information. It is these cells that transmit, *via* the retino-hypothalamic pathway, the photic information to the suprachiasmatic nucleus. This information activates or inhibits the expression of the clock genes of the neurons that make up the nucleus. From then on, it is synchronized by the day/night cycle [18].

Once synchronized, the suprachiasmatic nucleus imposes its rhythm on brain structures and secondary peripheral clocks *via* hormonal secretions and activation of the autonomic nervous system. In particular, the suprachiasmatic nucleus modulates the activity of the **pineal gland**. During the day, it inhibits the activity of the cells of this gland: the **pinealocytes**. At night, it stimulates them. Pinealocytes produce and secrete the sleep hormone **melatonin**. Once secreted and released, melatonin binds to specific receptors located on the cell membrane of secondary peripheral clock cells, indicating to the body that it is dark. The suprachiasmatic nucleus thus imposes its rhythm on the whole organism [19] (Figure 6).

4. Natural light and its roles in life

4.1. Natural light and ecosystems

During a 24-hour day, the light intensity perceived by living organisms varies by several magnitudes. In other words, there is a specific light intensity for each hour of the day: the day/night cycle thus splits the environment. This is why, in animal species, there are different profiles of daily activities: daytime, nocturnal, twilight and cathedral activities (both day and night). This fractionation therefore has strong ecological and evolutionary implications [10]. It should be noted that the cycle of seasons and the lunar cycle also participate (see Focus [Light cycles and living organisms](#)).

The temporal fractionation of the environment favours the coexistence of competing species and the prey/predator balance. If several competing species do not have access to the same resource at the same time, direct confrontations between these species are limited. Similarly, if the resource has time to renew itself between two periods of predation, the resource remains available for several species. In this way, coexistence between competitors is ensured. The prey/predator balance is subject to temporal and predictable fluctuations in the risk of predation. The various species involved will then adopt an activity profile that will reduce the risk of predation while promoting access to environmental resources [11]. For example, small mammals with limited defences have adopted a nocturnal activity profile during evolution that limits the risk of predation. Here too, coexistence between prey and predators is ensured.

The temporal fractionation of the environment and the adoption of different activity profiles have imposed different anatomical, physiological or behavioural constraints on species. Thus, day species use vision for communication and predation and their retinas are rich in cones. In contrast, nocturnal species use smell, hearing and touch for communication and predation. Their eyes have large pupils, sometimes even a membrane capable of reflecting light (*tapetum lucidum*) and their retina is rich in rods. Thus, due to the differences in light intensity between day and night, complex adaptations have evolved and emerged to accompany the different activity profiles [11].

4.2. Natural light and individuals

Light and its cycles, because they provide non-visual and visual information, are essential to living organisms. For a given species, the non-visual information provided by light, such as light intensity or photoperiod, allows individuals to orient themselves in their environment, follow a light gradient and synchronize their biological rhythms to anticipate seasonal changes in the environment. Anticipation is essential to take advantage of favourable seasons and protect against unfavourable ones. To anticipate seasonal changes in the environment, organisms must put in place physiological and behavioural characteristics, specific and adapted to the situation: migration, accumulation of nutritional reserves, hibernation and reproduction. To this end, it is essential for them to synchronize their biological rhythms with a geophysical indicator that can serve as a "calendar". This is the role played by light and its cycles [11],[11].

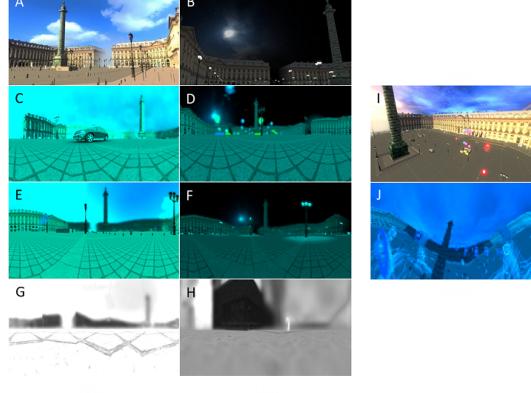


Figure 7. Theoretical representation of the human vision and that of different animals. A & B, Human vision, day & night (very good day vision, precise, trichromate i. e. perceiving blue, green and red); C & D, Cat vision, day and night (poor visual acuity, but good night vision adapted to movements in an angle of 280°, dichromate animal not perceiving red) ; E & F, Human vision, day & night (very good day vision, precise, trichromate i. e. perceiving blue, green and red) F, Vision of the dog, day and night (vision fairly close to that of the cat, but with a more restricted angle); G & H, Vision of the rat (adapted to the night, sharp up to about fifteen centimetres only); I, Vision of the falcon (very good daytime vision, very precise in flight, trichromate animal); J, Vision of the bee (compound eyes allow a very good precision in flight, excellent vision of movement). These images are reproduced from the "All Eyes on Paris" project, which proposes a simulation of animal vision during the flight over Place Vendôme [Source: Current Productions, Dassault, Ile de France Region].

Finally, for a given species, visual information provided by light, such as contrasts and colours, allows individuals to detect objects on the visual background, navigate in their environment in relation to inanimate or living elements (Figure 7) and express coloured characters that are used for camouflage, mimetism or are associated with sexual dimorphism. The visual information provided by light is therefore essential for navigation, food research, predation, communication and reproduction [11].

In conclusion, light and its natural cycles therefore represent an important selection force which, through evolution, has conditioned the appearance of visual and non-visual systems and biological clocks in living organisms. At the individual level, light and its natural cycles have enabled organisms to develop a spatial and temporal representation of their environment, enabling them to control, exploit and anticipate changes in the environment. At the ecosystem level, light and its natural cycles also ensure the fragmentation of habitats over time and space, which is a key factor in inter- and intra-specific balances.

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