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faces - whereby individual features are integrated into a coherent unified whole - compromising the accuracy and efficiency of their face recognition. Neuroimaging studies have revealed subtle neuroanatomical differences that accompany the condition. Several regions of the visual brain known to play an important role in face recognition, including the fusiform and occipital face areas, appear to be under-connected in developmental prosopagnosia, possibly impairing information exchange within this network. In particular, the integrity of the inferior longitudinal fasciculus, a white matter tract connecting the occipital and temporal lobes, is reduced in many developmental prosopagnosics (Figure 1).

ls developmental prosopagnosia

related to autism? Developmental prosopagnosia may be more common in individuals with autism spectrum disorder than in the general population. Importantly, however, the two conditions are independent; many individuals develop autism spectrum disorder in the absence of face recognition difficulties, and many prosopagnosics exhibit no signs of autistic symptomology. Developmental prosopagnosia is an example of a 'neurodevelopmental' condition, similar to dyslexia, dyspraxia, dyscalculia, and autism spectrum disorder. Many neurodevelopmental disorders are known to co-occur. Genetic or environmental factors that cause an individual to develop a neurodevelopmental condition, such as developmental prosopagnosia, appear to increase their chances of developing others.

Where can I find out more?

- Behrmann, M., and Avidan, G. (2005). Congenital prosopagnosia: face-blind from birth. Trends Cogn. Sci. 9, 180–187.
- Shah, P., Gaule, A., Sowden, S., Bird, G., and Cook, R. (2015). The 20-item prosopagnosia index (PI20): a self-report instrument for identifying developmental prosopagnosia. R. Soc. Open Sci. 2, 140343.
- Susilo, T., and Duchaine, B. (2013). Advances in developmental prosopagnosia research. Curr Opin. Neurobiol. 23, 423–429.
- Thomas, C., Avidan, G., Humphreys, K., Jung, K.J., Gao, F., and Behrmann, M. (2009). Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. Nat. Neurosci. 12, 29–31.

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Quick guide Bioluminescence

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What is bioluminescence?

Bioluminescence is the emission of light by an organism as a result of a biochemical reaction. In contrast to fluorescence and phosphorescence, bioluminescence reactions do not require the initial absorption of sunlight or other electromagnetic radiation by a molecule or pigment to emit light. Bioluminescent systems produce light through the oxygenation of a substrate, generically called luciferin (lat. lucifer, the lightbringer), and an enzyme, luciferase. Bioluminescent reactions vary greatly among organisms but can generally be described as a luciferase catalyzed production of an excited intermediate from oxygen and luciferin that emits light when returning to its ground state. Additionally, many bioluminescence systems involve cofactors such as FMNH, ATP, additional enzymes and intermediate steps for the light production (Figure 1E). In some bioluminescence systems special types of luciferases, photoproteins, bind and stabilize the oxygenated luciferin and emit light only in the presence of cations, such as Mg²⁺ or Ca²⁺, which acts as a mechanism for the host to precisely control the timing of the light emission.

How does bioluminescent light differ among organisms? Light

production in bioluminescence has a remarkable range of emission patterns such as continuous glow (Figure 1A,C), single flashes of light, e.g. in dinoflagellates, or repetitive pulse patterns that are often speciesspecific (Figure 1B). Bioluminescent light is emitted in wavelengths between 400 and 720 nm, from violet into the near-infrared. The majority of bioluminescent marine organisms emit blue light (410-550 nm), which correlates with the peak sensitivities of the opsins of many marine organisms. Interestingly, wavelengths of bioluminescent light seem to shift based on the habitat of the organism:

from violet and blue (420-500 nm) in the deep sea to blue-green (460-520 nm) in shallow waters to green-yellow (520-580 nm) on land, and its hue is often correlated with the optical characteristics of the environment (Figure 1D). The color of the bioluminescent light is dependent on multiple factors such as the luciferins and luciferases that are involved in the bioluminescent reaction or the conformation of the luciferase. In some bioluminescent systems fluorescent pigments, e.g. the green fluorescent protein (GFP), act as secondary emitters that affect the emitted color of the light. In addition to variations of the light-emitting molecules some organisms alter the original color of the bioluminescence through anatomical structures that act as biological filters and can refract or reflect the emitted light.

How is bioluminescence

distributed among taxa? To date, bioluminescence has been reported in nearly 700 prokaryotic and eukaryotic genera. The majority of bioluminescent organisms inhabit marine environments including bacteria, dinoflagellates (the well-known ocean glow), molluscs, crustaceans, bony fish and sharks. In contrast to marine species, bioluminescence has not been confirmed in any fresh water organisms. On land, bioluminescence is less common and almost exclusively found in fungi and animals. Approximately 70 species of fungi in four lineages of the order Agaricales are bioluminescent. In animals, bioluminescence has been reported in two phyla, Nematoda and Arthropoda. Phylum Arthropoda includes one of the best-known groups of terrestrial bioluminescent organisms, the fireflies (order: Coleoptera).

How diverse are bioluminescence systems and what are their

evolutionary origins? Bioluminescent systems are as diverse as their host organisms. Few bioluminescence systems are conserved among related taxa with the exception of fungi which are thought to share one conserved bioluminescence system. Generally, luciferins are more widely conserved than luciferases. For example, the







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Figure 1. Bioluminescence patterns and distribution among different species.

(A) Continuously green (λ_{max} 530 nm) glowing fungus *Neonothopanus gardneri*. Photo from http://www.cell.com/current-biology/fulltext/S0960-9822%2815%2900160-8. (B) Greenyellow (λ_{max} ~550 nm) pulsing light organ of the common glowworm (*Lampyris noctiluca*). Image: wikimedia commons. (C) Glowing light organ of a dragonfish *Photostomias guernei* continuously emitting blue (λ_{max} 530 nm) light. Image: wikimedia commons. (D) Wavelengths of bioluminescent organisms in different habitats. Number of species are approximated for intervals of 20 nm. Redrawn from Widder E.A. (2010). Bioluminescence in the ocean: origins of biological, chemical and ecological diversity. Science *328*, 704–708, and Hastings, J.W. (1996). Chemistries and colors of bioluminescent reactions: a review. Gene *173*, 5–11. (E) Schematic of the fungal bioluminescence reaction as proposed by Oliveira *et al.* (2012). Evidence that a single bioluminescent system is shared by all known bioluminescent fungal lineages. Photochem. Photobiol Sci. *11*, 848.

luciferin coelenterazine is found in the bioluminescent systems of at least nine different marine phyla. In contrast, the luciferases used are highly diverse and often species specific. It is currently estimated that bioluminescence has independently evolved more than 30 times, which suggests that the molecular building blocks of bioluminescence systems are ubiquitous. Nevertheless, their evolutionary origins remain mysterious. One hypothesis is that bioluminescence evolved from detoxification systems as some luciferins show characteristics of strong antioxidants. Additional

hypotheses propose mixed-function oxygenases or, in case of the beetle luciferase, certain types of ligases as the origins of luciferases.

What are the ecological functions of bioluminescence? Despite

the ubiquity of bioluminescence and the fact that early reports of bioluminescence date back to ancient Greece (Aristotle, 384–322 BC and Pliny the Elder, 23–79 AC), evidence for its ecological functions is scarce. Suggested functions of bioluminescence in organisms are diverse and include camouflage via counter-illumination, escapemechanisms through dazzling predators, aposematism (warning colouration), prey luring and courtship. However, outside of animal taxa, the possible functions of bioluminescence are less clear, e.g. in bioluminescent bacteria, or in fungi that only possess luminescent mycelium. For bacteria one hypothesis is that bioluminescence promotes beneficial interactions with host organisms as several bioluminescent bacteria are found as symbionts in the light organs of organisms that lack the ability to emit light themselves. For example, the Hawaiian bobtail squid Euprymnia scolopes has a symbiotic relationship with the bioluminescent bacterium Vibrio fischerii, which populates the squid's light organ. Another hypothesis is that bioluminescence may be incidental in some organisms and that the emission of light is merely a byproduct of another essential metabolic function. However, the repeated evolution of bioluminescence suggests that it may directly or indirectly provide its producer with a selective advantage over its non-luminescent counterparts.

Where can I find out more?

- Day, J.C., Tisi, L.C., and Bailey, M.J. (2004). Evolution of beetle bioluminescence: the origin of beetle luciferin. Luminescence 19, 8–20.
- Desjardin, D.E., Oliveira, A.G., and Stevani, C.V. (2008). Fungi bioluminescence revisited. Photochem. Photobiol. Sci. 7, 170.
- Dubuisson, M., Marchand, C., and Rees, J.-F. (2004). Firefly luciferin as antioxidant and light emitter: the evolution of insect bioluminescence. Luminescence 19, 339–344.
- Haddock, S.H.D., Moline, M.A., and Case, J.F. (2010). Bioluminescence in the sea. Annu. Rev. Mar. Sci. 2, 443–493.
- Hastings, J.W. (1996). Chemistries and colors of bioluminescent reactions: a review. Gene 173, 5–11.
- Stevani, C.V., Oliveira, A.G., Mendes, L.F., Ventura, F.F., Waldenmaier, H.E., Carvalho, R.P., and Pereira, T.A. (2013). Current status of research on fungal bioluminescence: biochemistry and prospects for ecotoxicological application. Photochem. Photobiol. 89, 1318–1326.
- Viviani, V.R. (2002). The origin, diversity, and structure function relationships of insect luciferases. Cell. Mol. Life Sci. CMLS 59, 1833–1850.
- Widder, E.A. (2010). Bioluminescence in the ocean: origins of biological, chemical and ecological diversity. Science 328, 704–708.

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