observation learning abilities, it is important to state that being able to learn from others does not necessarily mean that individuals learn from conspecifics. Cephalopods are known to dynamically change their appearance to resemble specific features of their surroundings: e.g., cuttlefish and octopus can change their posture to resemble objects such as sea grass and rocks, as well as other animal species that are either venomous or unpalatable. For instance, cuttlefish can mimic hermit crabs to catch more prey (Figure 3A), and octopus can mimic lionfish, flounder, and banded sea-snakes to avoid being eaten (Figure 3B). Octopus not only physically resemble these animals, but also learn to imitate the way they move or swim. Observational learning abilities in octopuses might not only result from the need to deceive potential predators but also from the fitness advantages potentially provided by learning from other species. For instance, the day octopus (*Octopus cyanea*) hunts with multiple fish species that have complementary hunting techniques (Figure 3C). Learning from others might be paramount for this form of collaborative hunting because it involves complex social interactions that likely require the need to prevent exploitation (one hunter takes all the food) and ensure collaboration.

Conclusions

In summary, knowledge of cephalopod cognition has been propelled forward in recent years. We have learnt a lot from learning and memory experiments couched within foraging contexts (i.e., using food rewards) but more knowledge can be gained about the flexibility of these capacities by investigating such abilities across different contexts (e.g., predator avoidance, mating). Uncovering these cognitive details in cephalopods — an animal lineage far removed from the more traditionally studied species (i.e., social primates and corvids) — has the potential to provide a more comprehensive understanding of the evolutionary patterns of intelligent behaviour. Indeed, these large-brained invertebrates provide a unique opportunity to go further back

in evolutionary time to pinpoint when certain cognitive abilities emerged.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Primer

Neural control of cephalopod camouflage

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In *Die Another Day*, James Bond receives an Aston Martin that can render itself invisible by dynamically reproducing the surroundings on the car's "polymer skin". In what is widely regarded as the worst Bond movie ever, the invisible car scene is cited as the moment the plot plunges into the truly absurd. But what if nature had actually invented such a technology, and did so hundreds of millions of years ago? The coleoid cephalopods — octopus, cuttlefish and squid — are living examples of dynamic camouflage. Their skin is covered with a high-resolution array of 'cellular pixels' (chromatophores) that are controlled by the brain. To disappear into their surroundings, cephalopods recreate an approximation of their environment on their skin by activating different combinations of colored chromatophores. However, unlike the fictional Bond car, whose surface is coated in tiny cameras to detect the environment, cephalopods don't see the world with their skin. Instead, the visual world is detected by the eyes, processed in the brain, and then used to activate motor commands that direct the skin's camouflage pattern. Thus, cephalopod skin patterns are an external manifestation of their internal perception of the world. How do cephalopods approximate the world with their skin? What can this teach us about how brains work? And which neurobiological tools will be needed to uncover the neural basis of camouflage?

The functional units of cephalopod skin

During camouflage, coleoid cephalopods recreate their surroundings by dynamically altering the color, pattern and three-dimensional texture of their skin (Figure 1A,B). Color patterning is created by chromatophores: expandable sacs filled with pigment, surrounded by muscles under the control of motor neurons projecting from the brain
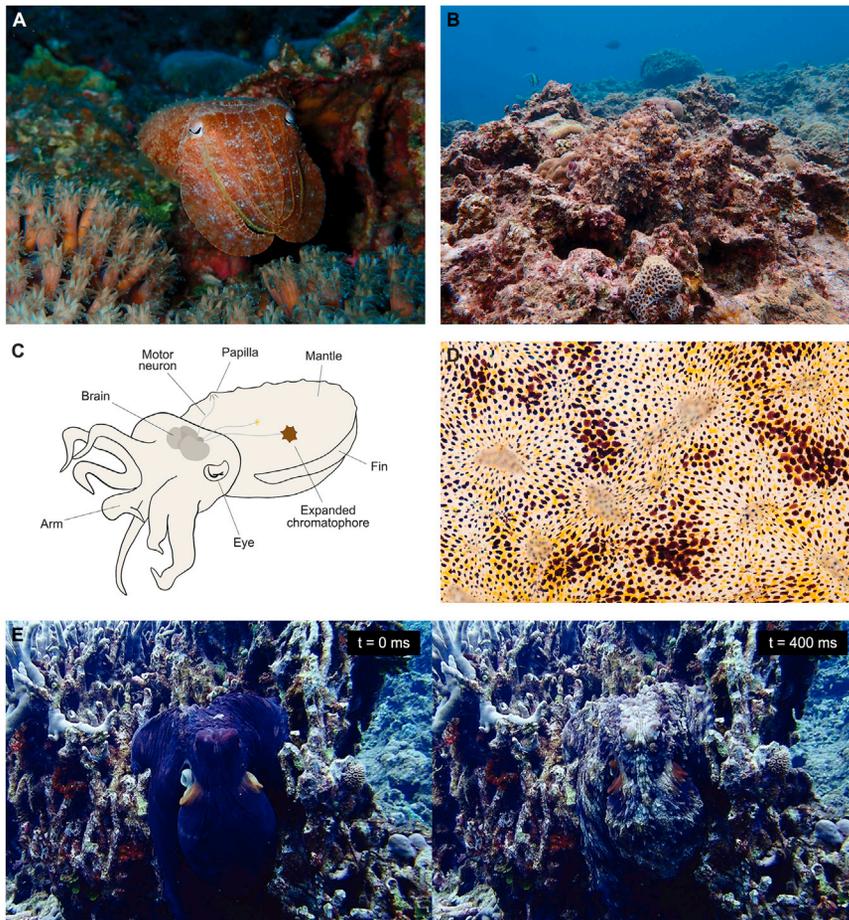
Figure 1. Cephalopod dynamic camouflage.
(A) A broadclub cuttlefish (*Sepia latimanus*) creates a skin pattern by engaging chromatophores and iridophores (photo: Keishu Asada). (B) A day octopus (*Octopus cyanea*) camouflages using chromatophores and papillae (photo: Keishu Asada). (C) Diagram of a cuttlefish. Chromatophores and papillae are controlled by motor neurons projecting from the brain. (D) Skin of a dwarf cuttlefish (*Sepia bandensis*) showing chromatophores and papillae. (E) Two video frames of *Octopus cyanea*, 400 milliseconds apart (video: Keishu Asada).

(Figure 1C,D). Upon neuronal excitation, the radial muscles surrounding the pigment sac contract, expanding the chromatophore to create a visible colored spot on the skin. In the absence of neuronal activation, the chromatophore shrinks to an imperceptible dot, revealing the animal's underlying white skin layer. The pixel resolution of cephalopod skin varies by species, ranging from thousands of chromatophores in squid to millions of chromatophores in cuttlefish and octopus. By expanding combinations of chromatophores of different colors, the animal can create dynamic patterns of stripes and spots. Neuronal control permits chromatophore expansion to occur in ~100 milliseconds, creating the fastest known animal color change on Earth (Figure 1E).

Typically, cephalopods use a limited color palette of yellow, red and brown pigments, but this palette is expanded by a layer of iridophores in the skin that create structural color (Figure 1A). Each iridophore features repeating 'platelets' of the protein reflectin, with the distance between platelets determining the color of reflected light. Remarkably, some cephalopods have evolved tunable iridescence, a rare feature within the animal kingdom. Current evidence suggests that iridophore color is modulated when neurons projecting from the brain activate a cellular cascade within the iridophore that phosphorylates reflectin, drives protein condensation and expels water from the cell. The cellular dehydration shrinks

the distance between the platelets, altering the color of reflected light. This structurally-generated color change is far slower than the expansion of pigment-filled chromatophores, taking around 30 seconds.

How do cephalopods accurately match the color of their environment? One might assume these animals see the world in technicolor. However, with the exception of the firefly squid, cephalopods have only a single opsin photoreceptor gene, rendering them colorblind. Alternative color detection mechanisms have been proposed, such as RNA editing of their opsin gene, or chromatic aberration by their pupil shape, but no evidence has been found to support either model. To add to this enigma, even though most cephalopods have three chromatophore pigments, new chromatophores, which are created throughout the life of the animal, are all born yellow. Over the course of a few days and then weeks, the chromatophore changes from yellow to orange and then to brown. How does the cephalopod keep track of these asynchronous color changes to know which color of chromatophore it is using?

To complete their mimicry of seaweed, sand or coral, octopus and cuttlefish are also able to recreate the 3D texture of their surroundings using papillae — tiny muscular hydrostats that prickle under their skin (Figure 1C,D). Like the chromatophores, skin papillae are controlled by brain motor neurons, allowing the animal to shift from smooth to spiky in less than a second. Behavioral experiments have indicated that cuttlefish use visual rather than tactile cues to detect the textures around them.

Assembling skin patterns
Watch a cuttlefish or octopus explore an environment for a few minutes and it is quickly apparent that they do not match their surroundings pixel-for-pixel. Instead, cephalopods have evolved a more interesting computation than pixel matching. It appears that they match the visual statistics of their skin pattern to the environment in a way that fools the visual systems of both predators and prey. Each motor neuron innervates a cluster of ~5–30 chromatophores, and complex skin patterns are created

through the combined activation of many different clusters. Each species has evolved a different array of skin patterns that reflect the visual statistics of their habitat. Whereas the dwarf cuttlefish (*Sepia bandensis*) has evolved predominantly high frequency pattern components and leafy papillae to mimic the coral reefs of the Indo-Pacific, the repertoire of patterns in the common cuttlefish (*Sepia officinalis*) includes large shapes that blend in with the stony pebbles of coastal Europe.

Traditional approaches to studying cuttlefish camouflage have led to the idea that camouflage patterns are both low-dimensional — featuring three pattern classes generated with ~30 components — and stable. However, more recent imaging approaches have generated a more complex picture of chromatophore dynamics. Using an imaging system to monitor *Sepia officinalis* for weeks while tracking thousands of individual chromatophores across the entire mantle of the animal, cuttlefish skin patterns were found to be high-dimensional and dynamic — they meander over time, accelerating and decelerating, while often engaging different chromatophore components in the construction of similar patterns. There appears to be similar complexity in the dwarf cuttlefish. The patterns are dynamic, they evolve and sometimes stabilize, and then change subtly, reflective of persistent chromatophore activity. Statistical analysis of these skin dynamics may reveal whether these local variations have little impact on the skin pattern's *Gestalt*, or rather represent genuinely new patterns.

If you were tasked with painting a landscape, chances are you would carry out frequent, perhaps near constant comparisons of your brushstrokes with the scene before you. By analogy, you might expect a camouflaging octopus to compare its own 'brushstrokes' with the scene to avoid a potentially fatally flawed piece of art. How does the animal know it has reached a reasonable pattern? Proprioceptive feedback from the skin to the brain could report its current state, but so far no such fibers have been identified. Projections within the brain, from motor to higher brain areas, could provide similar feedback, or the animal may observe its own skin and make visually-driven adjustments. Alternatively, natural selection over millennia may have
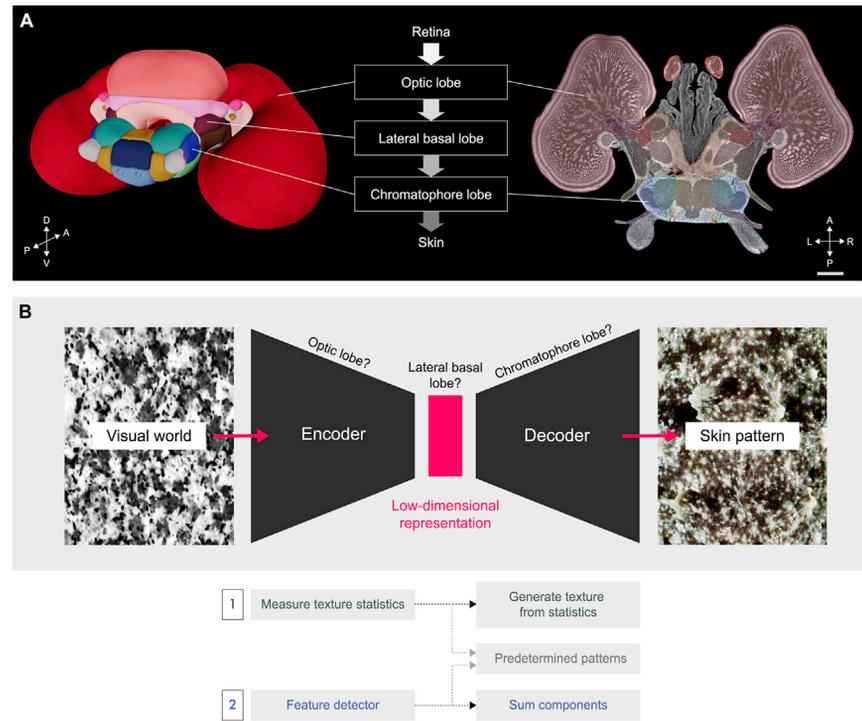

Figure 2. The cephalopod brain and camouflage control.
(A) Brain of the dwarf cuttlefish (*Sepia bandensis*). Left: 3D model. Right: histological slice, stained with NeuroTrace, a Nissl stain that labels neuronal cell bodies. Data from cuttlebase.org. A, anterior; P, posterior; D, dorsal; V, ventral; L, left; R, right. Scale bar, 1 mm. (B) Hypothetical model of the cephalopod camouflage circuit, based on a variational autoencoder. High-dimensional visual information is compressed into a low-dimensional representation and then decompressed to create a high-dimensional approximation of the visual environment on the skin. Model 1: the cephalopod visual system is tuned to visual texture. The encoder measures texture statistics, and the decoder generates a new texture with the same statistics. Model 2: the encoder detects visual features of the visual scene. The decoder maps the features onto skin components and sums them to create appropriate skin patterns. In either model, the visual input could trigger an entire predetermined skin pattern.

afforded effective camouflage without feedback.

The cephalopod brain and camouflage control

How does the cephalopod brain take in the complexities of the visual world, create an internal, abstract representation of that information, and then recreate an approximation of the same visual world on the skin? Scientists have pondered this question (or perhaps a philosophical version of it) since Aristotle. In the early 1900s, Santiago Ramón y Cajal began exploring the neuroanatomy of the cephalopod visual brain areas, and half a century later, John Z. Young, John B. Messenger and Brian B. Boycott investigated the structure and function of each subdivision of the cephalopod brain using neuroanatomy and electrophysiology. Their studies revealed that the cephalopod brain is

structured a little like that of a fruit fly, only thousands of times larger. Two optic lobes (~3/4 of the entire brain volume) straddle a central brain mass through which the esophagus passes (Figure 2A). Exiting the cephalopod brain, nerve bundles project to the eight prehensile arms while others extend to the color- and texture-changing skin. Large nerves that innervate the mantle muscles (the famous 'squid giant axons') allow the animal to produce rapid body contractions, jetting away from trouble. By systematically stimulating each lobe of the brain and observing its effect on behavior, Young and Boycott uncovered the major brain areas involved in camouflage. They found a relatively simple and hierarchical structure: neurons in the retina project to the optic lobe. Optic lobe neurons in turn project to the lateral basal lobe, and finally lateral basal lobe neurons project to the
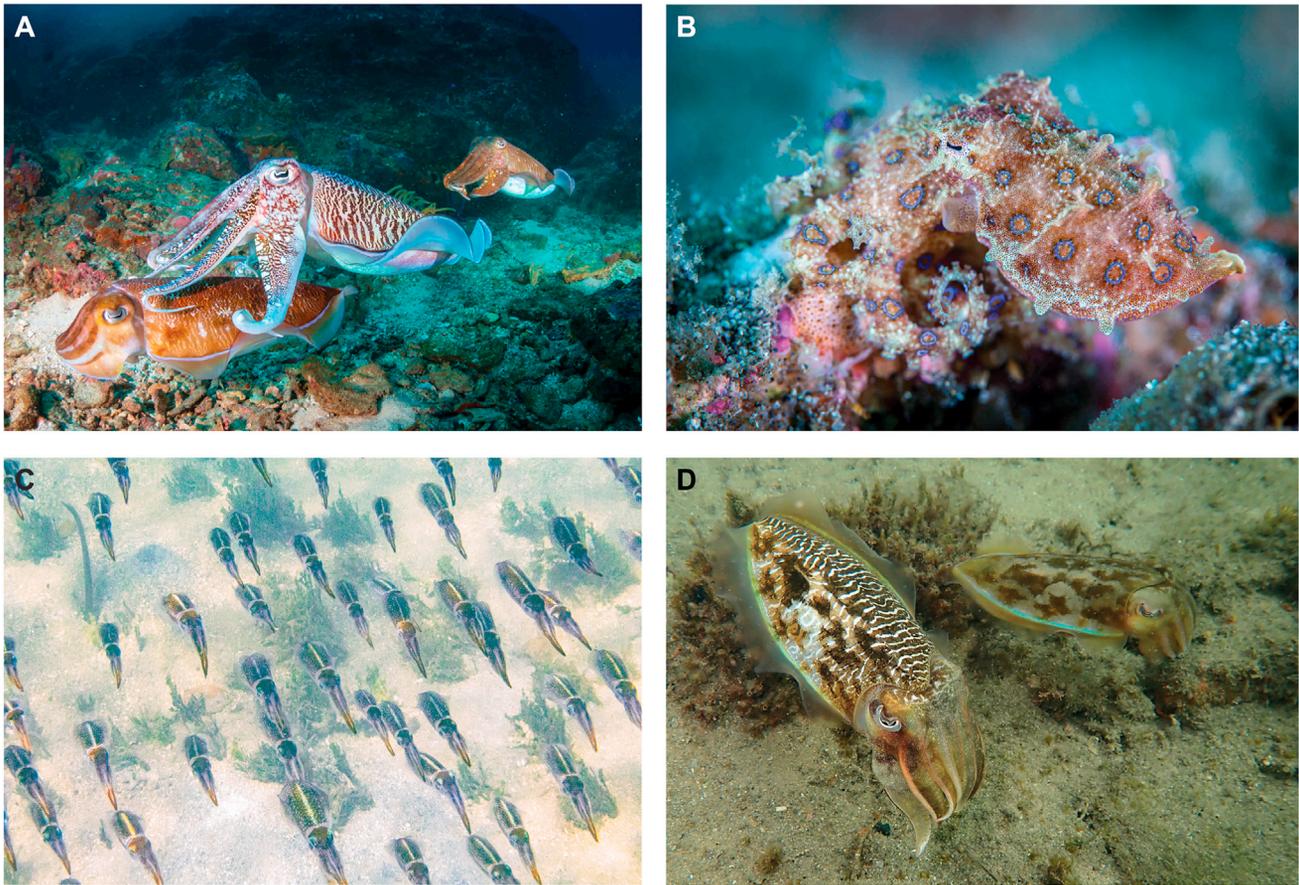
Figure 3. Cephalopod dynamic skin social behaviors.
(A) Pharaoh cuttlefish (*Sepia pharaonis*) use stereotyped striped patterns during aggressive interactions and mating (photo: Richard Whitcombe). (B) Greater blue-ringed octopuses (*Hapalochlaena lunulata*) reveal their iridophore-based blue rings when threatened (photo: Kimberly Tripp Randal). (C) Caribbean reef squid (*Sepioteuthis sepioidea*) can coordinate skin patterns during collective behaviors (photo: Eduardo Estrada). (D) Mourning cuttlefish (*Sepia plangon*) can split their body patterns to signal to another animal on only one side of their body (photo: John Sear).

chromatophore lobes. Motor neurons in the chromatophore lobes directly innervate the radial muscles of the chromatophores in the skin (Figure 2A).

To determine how the world is represented and transformed in the cephalopod brain during dynamic camouflage, we will need optical or electrophysiological recordings of neurons in each of those lobes. Until those experiments are possible, our knowledge of cephalopod neuroanatomy and some computational models could provide initial insight. The first station in the camouflage pathway, the optic lobe, is a massive bean-shaped structure with a layered outer rind that has been hypothesized to function like the vertebrate retina, carrying out the initial stages of visual processing. After the outer layers, the optic lobe gets weird. The neuronal somata cluster together in 'cell islands' within a sea of neuropils (Figure 2A). Despite their name, the islands are actually connected like branches in an elaborate tree. At the optic lobe periphery, the islands form the smallest branches, and as they project further into the lobe, the branches merge into larger ones until they form a trunk of fibers that exits the optic lobe and disperses to other parts of the brain. The optic lobe's branching structure suggests that it might be structured hierarchically, with each level of the optic tree carrying out a filtering step of the visual scene. The lateral basal lobe and chromatophore lobes are much smaller than the optic lobe and comprise an outer layer of cell bodies and an inner core of neuropils. We currently have little insight into their functional organization.

What type of visual information is encoded by the cephalopod brain? Most natural scenes consist of objects and visual textures, defined as spatially homogenous areas consisting of repeated elements, such as grass. The cephalopod visual system might be tuned to visual textures that are widespread in aquatic environments, such as sand, corals and seaweed. Visual textures are special because, unlike objects, they can be mathematically encoded in a relatively low-dimensional form via a small set of summary statistics. This representation is efficient, capturing the essence of the texture, and sufficient to create a new approximation of the texture. It is possible that the cephalopod visual system encodes visual texture (as does area V2 of the primate visual cortex), and then recreates an approximation of the visual texture on the skin (Figure 2B). In this scenario, the brain extracts visual statistics from a scene to yield a low-dimensional representation of the environment and then generates a high-dimensional skin

pattern that matches the extracted summary statistics. This process of encoding high-dimensional information into a compressed representation and then generating a high-dimensional output that approximates the input is reminiscent of a computational model known as a 'variational autoencoder' (Figure 2B). The approximation of visual texture in the brain may be precisely what allows inexact camouflage patterns to fool the visual systems of predators, prey and even humans.

An alternative model to visual texture encoding posits that cephalopods use feature detectors to encode specific elements of the environment. In this scenario, the encoder decomposes a visual scene into a representation of specific features, such as white spots of a certain size. The decoder then maps those representations onto skin components and sums them to create an appropriate skin pattern (Figure 2B). It is plausible that any of these representations could trigger entire, predetermined skin patterns, but behavioral data suggest that such predetermined patterns are used for social interactions and deimatic (threat) behaviors, not for camouflage. Finally, more complex models that unify or extend these frameworks are also possible.

The initial computations that encode the visual scene may occur in the optic lobe, due to its complex and hierarchical structure. The hypothetical low-dimensional representation of the environment could be found in the lateral basal lobe, and the subsequent expansion of the low-dimensional representation could occur in the chromatophore lobes to instruct the pattern on the skin. Identifying the representations, transformations, and network architecture in the camouflage circuit will require instantiation of these hypotheses in computational models, and delineation of these models using large-scale neural recordings.

Studying cephalopod camouflage

Thanks to the work of scientists over the last century, we already have a good understanding of the cells, organs and brain regions involved in camouflage. However, we know almost nothing about how the activity of neurons encodes the visual world and transforms it into a reproduction on the skin. To answer those questions, as well as many others, we

need to perform large-scale recordings in the cephalopod brain. Extracellular electrophysiological recordings have been notoriously difficult in cephalopods, but calcium imaging is a promising alternative. Calcium dyes are showing some success in cephalopods, and the generation of transgenic cephalopods that express genetically-encoded calcium indicators and light-activated channels are becoming a real possibility. To generate such animals, a transgene encoding a calcium indicator, such as GCaMP, must be introduced into recently fertilized cephalopod eggs along with gene editing reagents that will integrate the gene into the genome under the control of a neuronal promoter. Such approaches are feasible thanks to advances in cephalopod culturing techniques, gene-editing methods and sequencing projects.

Beyond the development of genetic tools, we will require intimate knowledge of cephalopod brain anatomy to enable the appropriate placement of microscope lenses and electrodes in the brain. The generation of a 3D and histological brain atlas for the dwarf cuttlefish (cuttlebase.org) has allowed us to develop methods to anchor lenses in the brain, and to head-fix animals, which can permit two-photon imaging of the brain. Additionally, because cephalopod skin patterns are a manifestation of perceptual processes in the brain, we can learn about the encoding of the visual world through computational analysis of the skin alone. New behavioral tools are being developed for cephalopods, including virtual environments to present digital stimuli to cuttlefish, and imaging methods to track almost every chromatophore on the skin of a cephalopod during behavior. In combination, these or similar methods can be used to create closed-loop experiments: presenting a digital stimulus, analyzing the animal's resulting skin pattern, and then choosing a new stimulus in real-time based on the animal's response. This could uncover the landscape of visual stimuli that animals respond to and permit real-time perturbations of their behavior. Ultimately, imaging neural activity at each station of the camouflage pathway while the animal camouflages in a virtual environment, and then perturbing that activity through optogenetics, could reveal how visual information is encoded in the brain and ultimately transformed into a perception of the world.

Cephalopod skin is a manifestation of the brain, and the patterns the animal can generate are not restricted to camouflage. During social encounters, cephalopods communicate with their skin using a series of innate skin patterns. Cuttlefish create aggression patterns when they are ready to fight or are attempting to mate (Figure 3A), cuttlefish, squid and octopus create threat patterns at the appearance of predators (Figure 3B), schooling squid create coordinated skin patterns during collective behavior (Figure 3C) and some octopus, cuttlefish and squid create strobing skin waves of unknown function. Squid and cuttlefish can even create different patterns on each half of their body, simultaneously signaling to a female on one side and signaling to a rival male on the other (Figure 3D). Thus, cephalopods can both show us what they perceive, through camouflage, and how they feel, through innate patterning. Do the same circuits encode innate patterns and camouflage patterns? What is the interplay between these states?

Beyond communication, the skin may reveal other brain states that are otherwise hidden. During a particular stage of sleep, cephalopods display dramatic and dynamic skin patterns that appear to be maladaptive from the standpoint of camouflage. Such patterns may represent dreams, or perhaps are a physical manifestation of replay on the skin, akin to the hippocampal replay of vertebrate place cells. Neural imaging during sleep and comparison with prior awake experiences could uncover the neural mechanisms involved in these phenomena. In conclusion, dynamic camouflage is a rare behavior restricted to just a handful of organisms, yet uncovering its neural basis may teach us how information is represented in all brains. What other animal can show you its perception of the world?

DECLARATION OF INTERESTS

The author declares no competing interests.

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Primer

Cephalopod versus vertebrate eyes

Dan-E. Nilsson[1,*], Sönke Johnsen[2], and Eric Warrant[1]

Vertebrates and cephalopods are the two major animal groups that view the world through sophisticated camera-type eyes. There are of course exceptions: nautiloid cephalopods have more simply built pinhole eyes. Excellent camera type eyes are also found in other animals, such as some spider groups, a few snails, and certain marine worms, but the vast majority of large camera-type eyes belong to cephalopods and vertebrates. Vertebrates and cephalopods also devote major parts of their brains to the processing of visual information. Obviously, there are differences in eye performance among cephalopods and vertebrates, but there are no major subgroups where vision seems to have low priority. The similarity in eye geometry is striking, especially between fish and coleoid cephalopods, with a hemispherical retina centred around a spherical lens. Do these similarities mean that vertebrate and cephalopod eyes are equally good? Comparing the eyes of vertebrates and cephalopods reveals many fundamental differences with surprisingly small consequences for vision, but also one difference that means that cephalopods and vertebrates do not share the same visual world.

The eyes of fish, amphibians, reptiles, birds, and mammals are remarkably similar to one another, all following the same developmental plan. The same is true for the different major cephalopod groups — colloquially known as octopus, cuttlefish, and squid — but the developmental plan and the origin of its components are fundamentally different to those uniting the vertebrate eyes (Katz and Lyons, 2023). So, despite the superficial similarities of vertebrate and cephalopod eyes, virtually every detail in their eyes has a different origin in the two groups: the retina has opposite orientation; the photoreceptor cells use different membrane structures to build their light-sensitive segments; the visual pigments belong to different families; and light is turned into neural signals by different molecular machineries.

In this primer, we will focus on the major differences and see what consequences they have for vision and visual performance. We will also look at general differences in eye allometry, and some low-light specialisations specific to vertebrate eyes, and ask if they too are consequences of the very different ways eyes are built in the two animal groups.

Different development reveals different origins

Before we compare the vertebrate and cephalopod approaches to camera type eyes, we should say a few words about the developmental origin of their eye cups. The reason why the vertebrate retina has photoreceptors facing away from the light is that the nervous system forms from part of the neural tube, which invaginates from the dorsal ectoderm. In this process, the original outside becomes the inside of the neural tube. During development, the front of the neural tube becomes the brain, and lateral bulges invaginate into eye cups — still with the original outside facing inwards. When the photoreceptor cells differentiate from the epithelium, they follow ancestral rules and form their sensory segments on the original outside and send their axons to the original inside, resulting in an inverted retina with receptors pointing away from the light (Figure 1). The lens is then formed by an invagination of the skin directly outside the eye cup.

In cephalopods, the eye-cup develops in a different manner, by epithelial invagination of the skin. Because the epithelium then retains its original orientation, photoreceptors will send their axons out from the back of the eye cup (Figure 1). The lens develops on both sides of the epithelial fold that closes the eye cup (Arnold, 1967; Brahma, 1978). This means that the epithelium that generates the lens runs straight through it. The vertebrate solution for lens development is rather different, because here an invagination of the ectoderm (skin) forms a vesicle where the lens fills the inside, surrounded by the epithelium that generated it. Special proteins, known as crystallins, are responsible for the optical properties