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Dynamic skin behaviors in cephalopods

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Abstract

The coleoid cephalopods (cuttlefish, octopus, and squid) are a group of soft-bodied mollusks that exhibit a wealth of complex behaviors, including dynamic camouflage, object mimicry, skin-based visual communication, and dynamic body patterns during sleep. Many of these behaviors are visually driven and engage the animals' color changing skin, a pixelated display that is directly controlled by neurons projecting from the brain. Thus, cephalopod skin provides a direct readout of neural activity in the brain. During camouflage, cephalopods recreate on their skin an approximation of what they see, providing a window into perceptual processes in the brain. Additionally, cephalopods communicate their internal state during social encounters using innate skin patterns, and create waves of pigmentation on their skin during periods of arousal. Thus, by leveraging the visual displays of cephalopods, we can gain insight into how the external world is represented in the brain and how this representation is transformed into a recapitulation of the world on the skin. Here, we describe the rich skin behaviors of the coleoid cephalopods, what is known about cephalopod neuroanatomy, and how advancements in gene editing, machine learning, optical imaging, and electrophysiological tools may provide an opportunity to explore the neural bases of these fascinating behaviors.

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Cephalopod, Chromatophore, Camouflage, Social behavior, Sensorimotor transformation, Internal state, Arousal.

Introduction

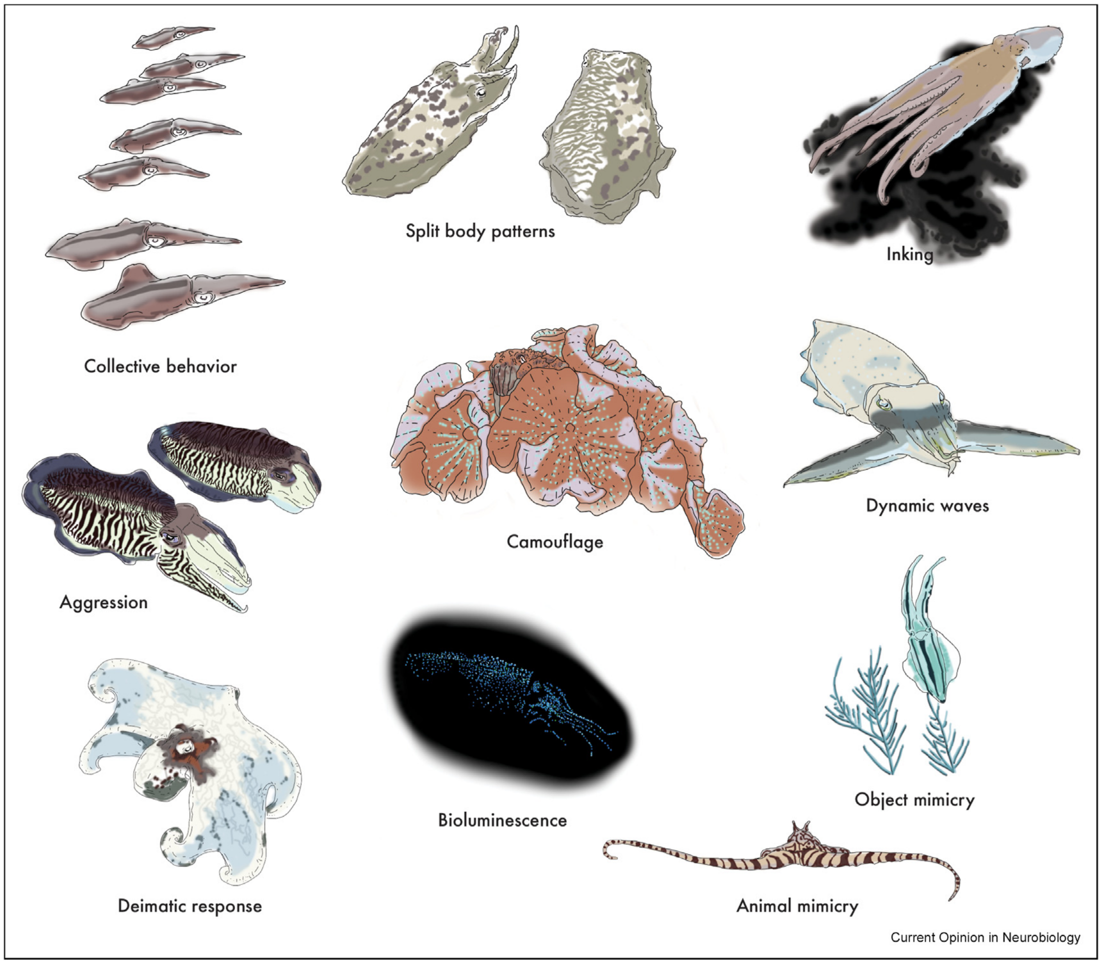
250 million years before the first dinosaurs, cephalopods were dominant predators of the sea. The ancient cephalopods had large shells, small brains, and likely static skin. Using their chambered shells, they evolved a mechanism to ascend into the water column, hunting their bottom-dwelling prey from above [1]. The Cambrian explosion brought rapid species radiation, physiological innovations, and the emergence of fish. Evolutionary competition developed between the cephalopods and vertebrates, leading to a radiation of cephalopods that shed the cumbersome shells of their ancestors and evolved soft malleable bodies that favored speed and maneuverability [2]. Devoid of physical protection, the coleoid cephalopods evolved large brains, complex behaviors, camera-type eyes, ink, bioluminescence, and the most elaborate and dynamic camouflage displays among animals (Figure 1).

Modern-day cephalopods are globally distributed and occupy diverse niches, from bright coral reefs to deep oceanic trenches. They comprise ∼800 species of coleoids (squid, cuttlefish, and octopus) and at least 6 species of nautilus, whose chambered shell, pinhole eyes, and small brain resemble the anatomy of their ancestors [3,4]. The coleoids use their dynamic, neurally controlled skin during social communication, collective behaviors, hunting, and defense (Figure 1). In this review, we describe the dynamic skin behaviors of the coleoid cephalopods and argue that by exploiting these visual displays, we can gain insight into both internal states and how the brain transforms sensory information into representations of the visual world. A recent drive to develop neurobiological tools for the coleoid cephalopods is providing an opportunity to explore their exciting neurobiology mechanistically.

Cephalopod skin

Cephalopods alter their skin color by engaging an array of hundreds of thousands to millions of pigment-filled

Figure 1



Cephalopods alter the color, pattern and texture of their skin during camouflage and social behaviors. Illustrations by Joe Echeverri.

chromatophores in their skin [5] (Figure 2a,b). Each chromatophore is a neuromuscular organ comprising a pigmented sac connected to a radial array of muscles, which is under the control of motor neurons projecting from the brain [6,7] (Figure 2a). Upon neuronal activation, the muscles contract, stretching the sac to create a colored spot that is visible on the skin. In the absence of neuronal activity, the muscles relax, shrinking the pigmented sac to an almost undetectable dot [5] (Figure 2a,b). The chromatophores of cephalopod skin typically come in three colors [8] and are akin to the pixels of a computer image. By combining points of various colors, the animal can create complex naturalistic patterns (Figures 2b, 3).

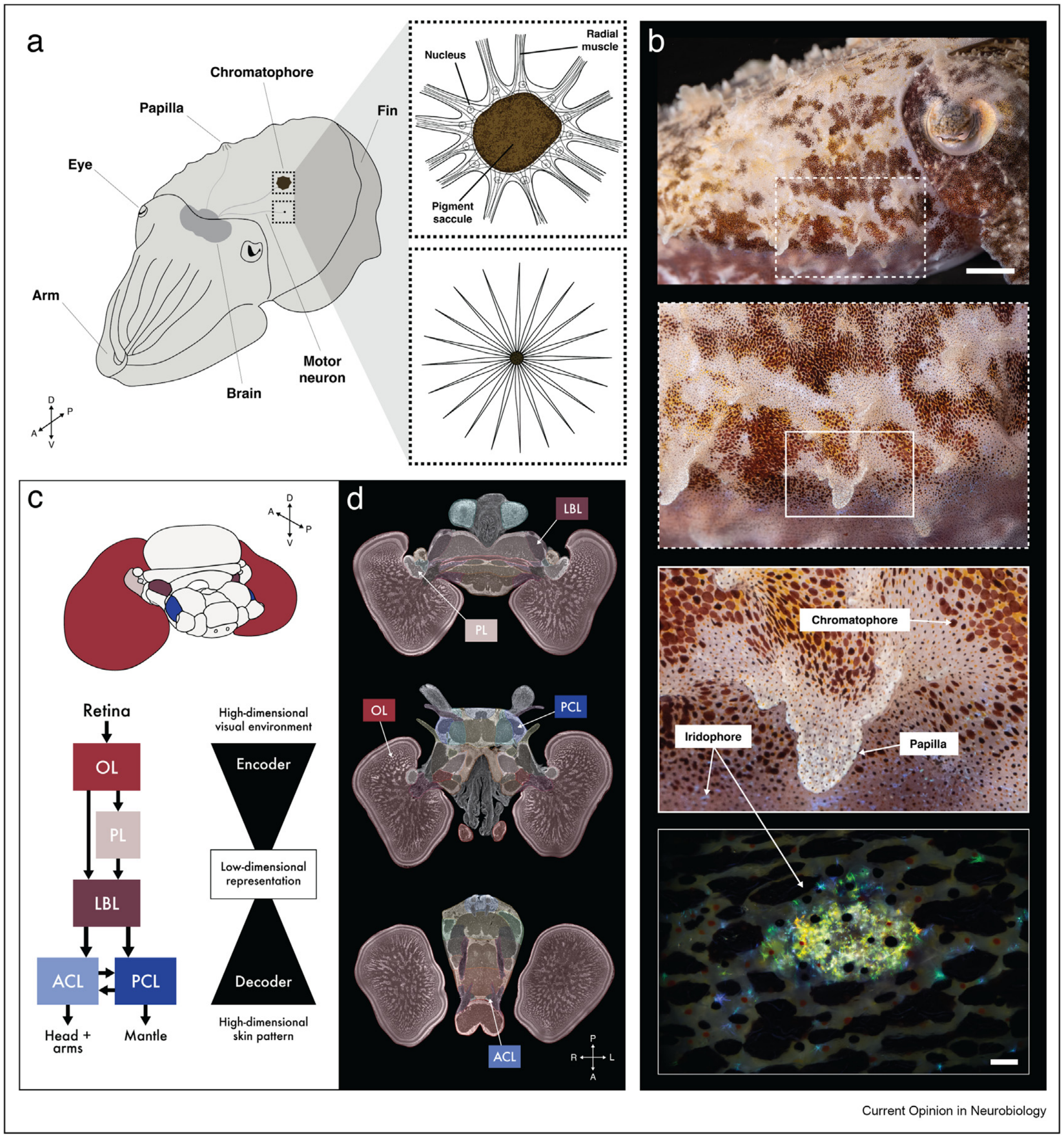
Two non-pigmentary cell types aid the animal's dynamic color generation. Iridophores use sub-cellular microstructures to generate iridescent colors by thin-film interference, a form of structural color [9,10] (Figure 2b). Leucophores lie beneath the iridophores and chromatophores in cuttlefish and octopus skin, and diffusely reflect all visible wavelengths, creating a white backdrop to the colorful patterns [11,12]. Finally, papillae—small muscles under the skin that contract and relax—allow cuttlefish and octopus to adjust their three-dimensional skin texture [13] (Figure 2b).

Camouflage

Cephalopods are masters of camouflage. They can dynamically alter the color, pattern and texture of their skin [14], mimic inanimate objects or other animal species [8], create counter-shading through bioluminescence [15], and expel clouds of ink to hide their escape [16] (Figures 1,3). Most remarkably, their skin patterns change in less than a second, creating the fastest known color change among animals [14,17,18] (Figure 3a).

Rather than match their surroundings on their skin pixel-for-pixel, cephalopods have evolved an interesting algorithm: they produce an imperfect approximation of their environment that is plausible enough to often avoid detection by predators and prey [19]

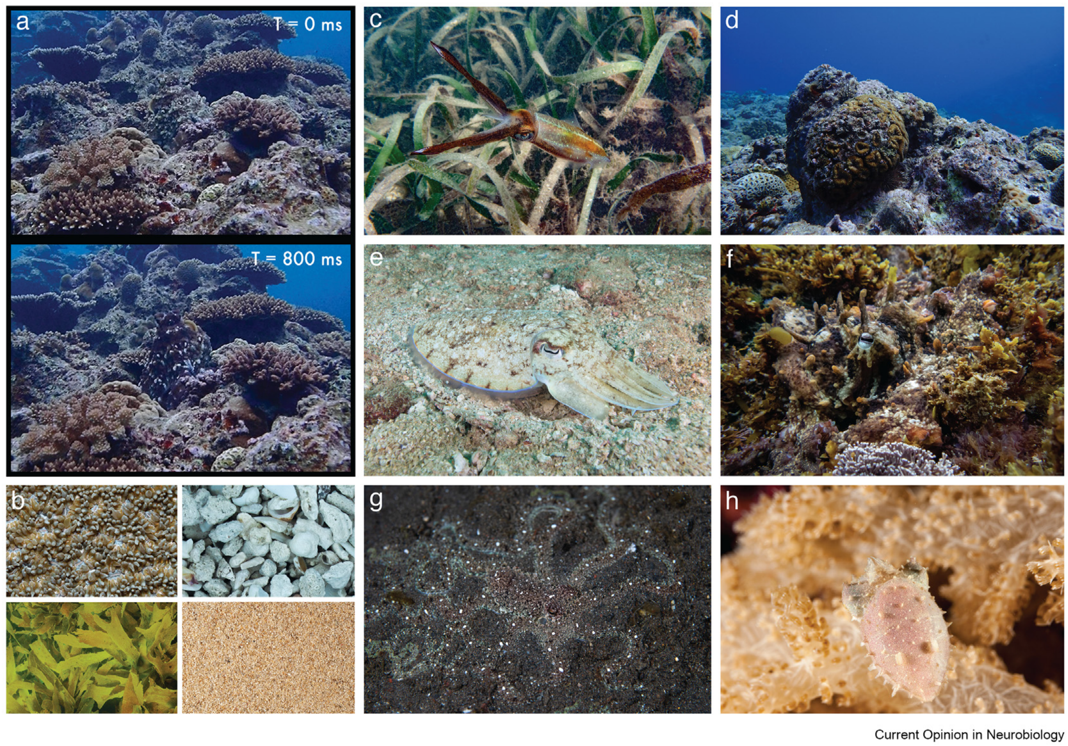
Figure 2



Cephalopod dynamic skin is controlled by the brain. a) Cephalopod skin is covered in thousands to millions of chromatophores—expandable neuromuscular organs that are controlled by motor neurons projecting from the brain. Each chromatophore is innervated by multiple motor neurons, and each motor neuron innervates multiple chromatophores [6,122,123]. Upper box: expanded chromatophore; lower box: relaxed chromatophore. Illustrations by Joe Echeverri. b) Cephalopods create complex skin patterns by expanding chromatophores of different colors. Three-dimensional texture is created using muscular papillae, and iridescent colors are created using iridophores. Top three images are from the same cuttlefish (*Sepia bandensis*, dwarf cuttlefish). Bottom image of an iridophore is from a different individual. Top scale bar, 500 um; bottom scale bar, 100 um. c) Diagram of a cuttlefish brain, based on the dwarf cuttlefish brain atlas [34]. The dwarf cuttlefish is a pygmy cephalopod species with a mantle length of ~60 mm. It has an almost identical brain volume to a laboratory mouse [34]. The cephalopod skin patterning circuit may function like an autoencoder during camouflage, in which a high-dimensional input is compressed into a low-dimensional representation, from which a high dimensional approximation of the input is generated. d) Horizontal histological sections of the dwarf cuttlefish brain stained with NeuroTrace, a Nissl stain that labels cell bodies (from Ref. [34]). A, anterior; D, dorsal; L, left; P, posterior; R, right; V, ventral; OL, optic lobe; PL, peduncle lobe; LBL, lateral basal lobe; ACL, anterior chromatophore lobe; PCL, posterior chromatophore lobe.

(Figure 3). This inexact yet effective strategy solves a computational problem that even machine learning algorithms have found challenging [20–22]. Cephalopods cannot create any pattern. Instead, each species has evolved a range of patterns that is likely adapted to both their physical environment and the visual systems of their predators and prey. Traditionally considered to be low dimensional, cuttlefish camouflage patterns have been divided into three discrete categories—uniform, mottled and disruptive—which have been further subdivided into around 30 pattern components [8,23,24]. However, recent

Figure 3



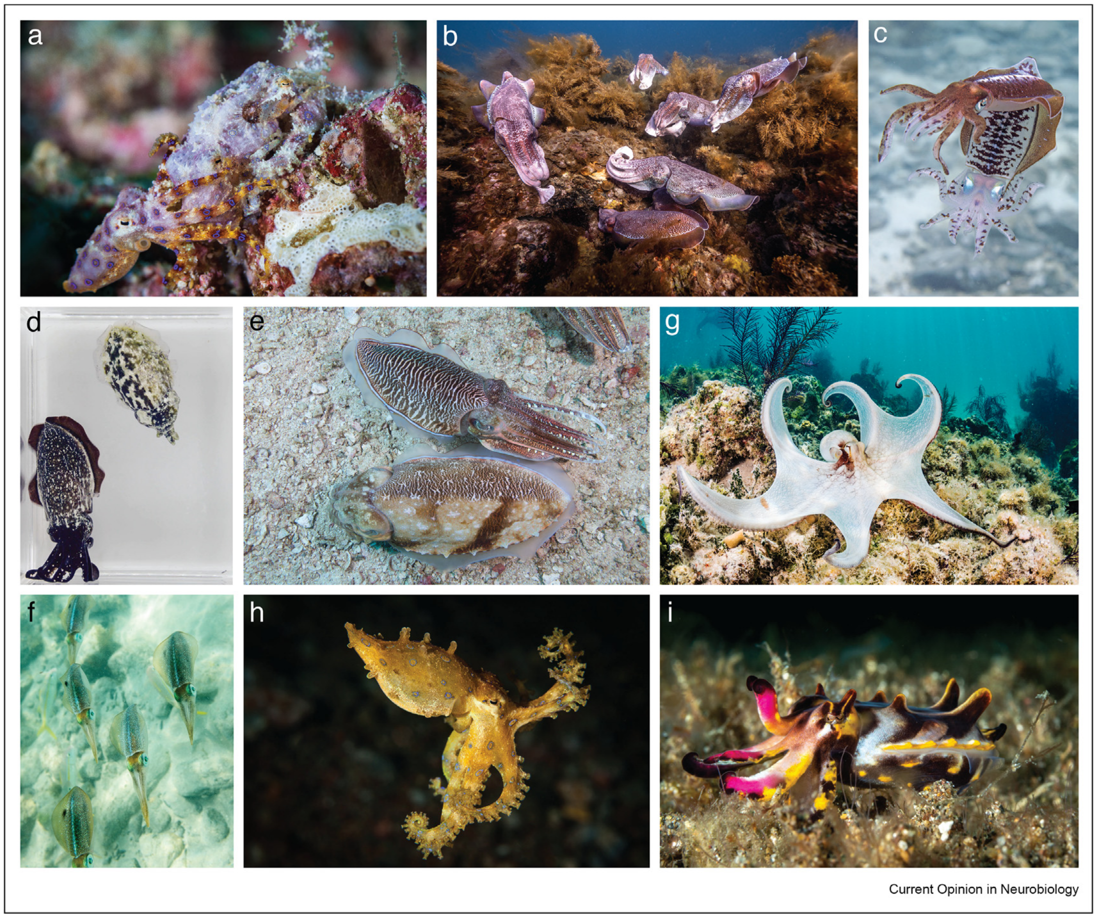
Cephalopod camouflage behavior. a) Two video frames of a day octopus, *Octopus cyanea,* changing color in less than a second (video: Keishu Asada). b) Examples of aquatic visual textures—defined as spatially homogenous images based on repeating structures and some random variation [27]. Coral (photo: Andrey Savin), gravel (photo: Axel lab), kelp (photo: Daniel Poloha), sand (photo: Nik Merkulov). c–h) Examples of cephalopod camouflage behavior. c) Caribbean reef squid, *Sepioteuthis sepioidea* (photo: Kasper, Adobe Stock). d) Day octopus, *Octopus cyanea* (photo: Keishu Asada). e) Pharaoh cuttlefish, *Sepia pharaonis* (photo: Magnus Larsson). f) Gloomy octopus, *Octopus tetricus* (photo: Elly Gearing). g) Indo-Pacific long arm octopus, *Abdopus sp* (tentative) (photo: Magnus Larsson). h) Dwarf cuttlefish, *Sepia bandensis* (tentative) (photo: Gerald Robert Fischer, Adobe Stock).

analyses using large-scale imaging and machine learning have suggested that skin patterns are far more high-dimensional and dynamic than previously thought [25,26]. The skin meanders between different patterns, accelerating and decelerating, and sometimes creates near-identical body patterns using different chromatophores [26]. These studies raise some questions: Are cephalopod camouflage patterns created through the summation of smaller features? Or is each pattern a more global representation rather than a summation of features? The dimensionality of camouflage patterning has important implications for its representation in the brain.

Cephalopod camouflage is visually driven [23] (Figure 2c). Observing the animal's skin pattern therefore provides a window into the animal's perception of the visual world. How do cephalopods create a neural representation of the visual world and then use this representation to generate an approximation of the world on their skin? One possibility is that the cephalopod brain represents the visual world using "visual textures," defined as spatially homogenous images based on repeating structures with some random variation (such as sand or seaweed) [27] (Figure 3b). Visual textures can be efficiently encoded using a small set of summary statistics from which a perceptually indistinguishable approximation of the original texture can be created [27,28]. The primate visual system is thought to encode visual textures in area V2 of the visual cortex, and it is possible that the cephalopod brain has evolved to exploit similar computations [29,30]. Moreover, the cephalopod brain could employ feature detectors to identify specific elements in the environment (such as pebbles of a specific size and color), which could trigger pattern components in the skin of similar size and shape [24,31]. These observations raise interesting questions: What does the animal actually see and how does it "choose" what to camouflage to?

Despite the fact that cephalopods did not evolve to fool the human visual system, we still struggle to detect them (Figure 3). Thus, analyzing cephalopod camouflage patterns may provide insight into general properties of visual perception. Uncovering the algorithms that transform the visual world into an approximation on the

Figure 4



Cephalopod social behavior. a) Greater blue-ringed octopus, *Hapalochlaena lunulata.* Two males compete to mate with a female (photo: Kimberly Tripp Randal). b) Mating aggregation of Australian giant cuttlefish, *Sepia apama* (photo: Terence Tong). c) Aggression display of Caribbean reef squid, *Sepioteuthis sepioidea* (photo: Andre Michael Goolishian Hernandez). d) Aggression display (bottom left) and half "leopard" display (top right) of dwarf cuttlefish, *Sepia bandensis* (photo: Axel lab). e) Split body pattern of a pharaoh cuttlefish, *Sepia pharaonis* (photo: Magnus Larsson). f) Coordinated skin patterns in a shoal of Caribbean reef squid, *Sepioteuthis sepioidea* (photo: Kirk, Adobe Stock). g) Deimatic display of *Octopus insularis* (photo: Shane Gross). h) Threat display of a greater blue-ringed octopus, *Hapalochlaena lunulata* (photo: Kimberly Tripp Randal). I) Dynamic waves pass across the skin of a flamboyant cuttlefish, *Metasepia pfefferi* (photo: Christian Horras).

skin will require methods for optical imaging or electrophysiological recording of neural activity alongside high-resolution imaging of the skin (see *Tools for studying the cephalopod brain*).

Neuroanatomy

The rich behaviors of cephalopods are controlled by a large and centralized nervous system that, despite ~600 million years of independent evolution [32,33], converged on strikingly similar neuroanatomy to that of fruit flies. The central brain is intersected by the esophagus and is flanked by two large optic lobes that receive direct input from the retina (Figure 2c,d). Based on anatomical and electrophysiological studies, the cephalopod brain has been divided into ~30 lobes with sensory, motor, and cognitive functions [34–55]. Most cephalopod brain lobes exhibit typical invertebrate structure, consisting primarily of monopolar neurons organized into a rind of cell bodies that surrounds a neuropil core [35,56]. The optic lobe is a notable exception. Two outer layers enclose a complex "tree" of cell bodies and neuropil that includes a diverse array of neuronal morphologies [35,57–59] (Figure 2d). The majority of synapses in the cephalopod brain appear to be chemical [60–63], and there is widespread use of the neurotransmitters dopamine, glutamate, GABA, serotonin, acetylcholine, and octopamine, as well as neuropeptides, including FMRFamide [5,64,65]. It is unclear what proportion of cephalopod neurons utilize action potentials. For instance, although some voltage-gated sodium channel-generated spikes have been measured (notably, in the squid giant axon [66]), the distribution and function of ion channels across the cephalopod brain, and their effects on neural physiology, are largely unknown and are likely complicated by an exceptionally high degree of mRNA editing [67].

Cephalopod dynamic skin patterning is thought to be controlled by a relatively shallow circuit [5,35,36] (Figure 2c). Neurons in the retina project to the optic lobe, the largest sensory area of the brain [34,68]. Similar to many other organisms, the octopus optic lobe exhibits retinotopy and ON and OFF receptive fields [69]. Neurons in the optic lobe project to many brain areas, including the peduncle lobe and the lateral basal lobe, a region involved in skin patterning whose precise function is unknown [35,36]. Finally, lateral basal lobe neurons project to the anterior and posterior chromatophore lobes, two sensorimotor areas that project motor neurons that directly innervate the chromatophores of the head and mantle, respectively [5,35] (Figure 2c,d).

During camouflage, it is plausible that high-dimensional visual input is compressed into a low-dimensional representation in the brain before the generation of motor output. This model is reminiscent of a computational model called an autoencoder, in which a high-dimensional input is compressed into a low-dimensional representation, from which a high dimensional approximation of the input is generated [70] (Figure 2c). The low-dimensional representation could encode visual texture, which can be efficiently encoded using a small set of statistics [27,28]. Alternatively, it might encode visual features detected by feature detectors upstream in the pathway. Determining whether there is a low-dimensional representation, what is contained within it, and how it is transformed into a skin pattern, could yield insights into the neural algorithm underlying camouflage.

Remarkably, despite their color-changing behaviors, cephalopods appear to be colorblind, possessing only a single photoreceptor gene [71,72], yet they can detect the polarization of light [73]. How, then, do cephalopods match the color of their environment? Furthermore, there is currently no evidence of feedback from the skin to the brain [5]. It is possible that cephalopods can see their own skin and make visually driven adjustments, or perhaps feedback exists within the brain. However, no evidence has been found yet to support either scenario.

Social communication

Like the blush of a human, or the color shift of a chameleon, cephalopods can communicate their social state on their skin, using distinct skin patterns for courtship, antagonism, hunting and collective behaviors [8] (Figure 4). Cephalopod skin patterns may therefore reflect internal states such as fear, arousal, aggression and hunger, which affect the processing of sensory input and generation of appropriate behavioral output [74]. The skin patterns engaged during social behaviors are innate and stereotyped, and emerge during sexual maturation [75]. We have limited knowledge of the cephalopod visual vocabulary used during signaling or whether the same neural circuits control camouflage and social displays.

Intraspecific behaviors: courtship, conflict, deception, and collective behaviors

Most cephalopod species lead solitary lives punctuated by social interactions that revolve around courtship [8] (Figure 4a). In an extreme example, every winter, thousands of Australian giant cuttlefish aggregate off the coast of Australia in a copulation frenzy [76] (Figure 4b). During cephalopod courtship and conflict, males of many cephalopod species use a high contrast zebra pattern of black and white stripes, which is often coupled with dilated pupils, erect arms, and fluttering fins [8,77,78] (Figure 4b,c,e). Male-to-male displays are not static patterns but rather dynamic sequences that often escalate into physical conflict. *Sepia bandensis*, the dwarf cuttlefish, has an unusual aggression pattern among cuttlefish species, featuring a dark body with small white flecks [79] (Figure 4d). Pattern variations often emerge during dwarf cuttlefish conflict, including a blanched aggression pattern, the superimposition of dynamic waves, and a distinct "leopard" pattern (Figure 4d). The dynamics of these patterns are reminiscent of internal states, which are characterized by persistence and scalability [80]. This raises a number of questions: Are the dynamic skin patterns we observe on the skin a direct readout of changes in internal state? Is there a predictable sequence of patterns in the escalation or de-escalation of conflict? Can we build a model that can decipher these sequences and predict behavioral outcome? Is the neural pathway the same as adaptive camouflage? Is there a social hierarchy, and if so, does it manifest on the skin?

Cephalopod courtship ranges from a seemingly simple chase to an elaborate dance of pursuit, intimidation, rejection, and deception. Intriguingly, small male Australian giant cuttlefish have been observed impersonating females in the wild—sneaking up to them in the presence of larger males and copulating using a "female" pattern [81]. Furthermore, small male mourning cuttlefish, *Sepia plangon*, have been observed presenting two patterns at once: a courtship pattern to a receptive female on one side of their body, and the "female" pattern on the other side that faces a rival male [82,83] (Figure 4e). Such split body patterns are reminiscent of divided attention—the monitoring and integration of parallel information streams [84].

Squids are arguably the most social cephalopods, traveling in shoals of tens to thousands of individuals [85]. *Sepioteuthis* species possess fewer and more discrete skin patterns than cuttlefish or octopus [86]. These patterns have been observed spreading throughout groups of schooling squid, creating the appearance of coordinated skin patterns (Figure 4f). This raises the possibility that squid may exhibit collective behavior on their skin [87]. Octopuses, by contrast, have traditionally been considered asocial and cannibalistic. However, recent observations in the wild indicate that some octopuses use intraspecific visual signals [88] and even engage in communal living [89].

Interspecific behaviors: deimatic and threat behaviors

When discovered by predators, cephalopods often swiftly transition from camouflage into a different mode of skin patterning—that of a deimatic or threat pattern [8,90], which may be a physical manifestation of an internal state of fear. Deimatic displays often include dramatic paling, stretching of the body and arms (that may give the impression of a larger body size), darkening of the eyes, and the creation of false eye spots on the mantle [8,18] (Figure 4g). Some octopus species reveal rings of bright blue iridophores on their skin in response to threats, disclosing their venomous nature [91] (Figure 4h). Quantification of the change from camouflage to paling at chromatophore-level resolution in *Sepia officinalis* has identified a fast and direct transition, followed by a precise return to the original skin pattern [26]. Paling results from the relaxation of all chromatophore muscles, thus, deimatic displays might result from uniform inhibition of the skin patterning circuit. Neural recordings in the chromatophore lobe could test this hypothesis, but which region of the brain controls deimatic behaviors is currently unknown.

Waves, flashes, and pulses

Some of the most bizarre skin behaviors of the coleoid cephalopods involve dramatic flashes, chromatic pulses, and rhythmic waves that undulate across the skin [92]. Generated by the action of chromatophores, the waves (or "passing clouds") have been observed in multiple contexts (Figure 4i), including hunting, swimming, walking, mating, and in response to threats [93,94], suggesting they may reflect a state of arousal. Although the functions of most dynamic patterns are unclear, the broadclub cuttlefish *Sepia latimanus* has been witnessed producing dramatic waves from the head to arm tips before striking prey, suggesting that the waves may be produced to stun animals before an attack [92]. Similarly, the deep-sea bioluminescent squid *Taningia danae* has been observed producing flashes of bioluminescence before an attack, using the largest known photophores of any living organism [95]. Analysis of the multidirectional waves of the paintpot cuttlefish *Metasepia tullbergi* has revealed that the rhythmic waves can be superimposed upon different body patterns, and may result from a central pattern generator in the brain [94]. If the chromatophore lobe of the brain is topographically structured, the skin waves might reflect corresponding waves of neural activity in the brain. The persistent nature of these waves and their ability to be superimposed on other patterns is consistent with their reflection of an internal state [74].

Tools for studying the cephalopod brain

Coleoid cephalopods perform a wealth of complex skin behaviors that may reflect internal states and the animal's internal perception of the visual world. Uncovering the neural bases of these behaviors and answering many of the questions posed above requires neurobiological tools. The development of methods to track the expansion state of thousands of individual chromatophores across the skin of a cuttlefish has already provided insights into chromatophore development, control, dynamics, and pattern-matching [25,26]. Precise tracking of multiple animals, quantification of camouflage patterns, and automatic classification of social patterns should allow us to relate camouflage patterns on the skin to visual features in the environment, as well as decode the visual vocabulary of cephalopod communication. Thanks to recent advances in machine learning, these analyses are now feasible.

There are currently no viral tools for cephalopods and only limited electrophysiological recordings have been performed. However, recordings in freely moving animals using both classical electrodes [51,96] and Neuropixel silicon probes [55] have shown some success. Furthermore, transgenic cephalopods that express genetically encoded calcium indicators (e.g. GCaMP) and light-activated channels are currently being developed. Transgenic technology is feasible thanks to cephalopod genome and transcriptome sequences [64,97–109], descriptions of embryonic development [79,110–116], cephalopod gene editing methods [117,118] and protocols for culturing cephalopods through multiple generations in the lab [118,119]. Despite the challenges of performing neural imaging in large animals with no skull, the miniaturization of microscopes and development of cephalopod head fixation methods is permitting the adaptation of neural imaging to life underwater. Finally, cephalopod connectomes [63] and brain atlases [34,37,120,121] have expanded our knowledge of cephalopod circuit architecture and are aiding the localization of electrodes and lenses to appropriate areas of the brain. Soon, the ability to couple neural imaging or recordings with behavior will allow us to explore the neural basis of many fascinating cephalopod behaviors.

Thus, with a growing toolkit, community, and plethora of open questions, cephalopods provide an exciting system for scientific exploration. The intersection of neuroscience, behavior, genetics, computation, and theory will be required to uncover the neural basis of cephalopod skin behaviors.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

Data availability

No data were used for the research described in the article.

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