Body patterning and cognition in cephalopods - a literature review

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Kroppsmönster och kognition hos cephalopoda - en litteraturöversikt

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Abstract

Cephalopods are a valuable model for studying the evolution of cognition due to their distinctive brain structure, organisation, and connectivity patterns compared to vertebrates. The development of large brains and behavioural complexities are believed to be triggered by evolutionary pressures stemming from factors like heightened predation, more demanding foraging conditions, and intense mating competition. While the differences between corvid and mammals are less pronounced, the cephalopod brain is closer to the vertebrate brain in terms of encephalisation of ganglionic masses observed by nerve cell clusters. The cerebral ganglion in cephalopods is similar to the vertebrate forebrain and midbrain, while the vertical lobe is similar to the vertebrate cerebral cortex and hippocampus formation, which are involved in learning and memory. These brain regions function in a hierarchical system and are intimately connected with their eyes and optic lobes where visual inputs are processed, motor commands are transmitted to the lower motor centre. Chromatophores are skin elements and the physiological control of body patterning and are visually driven and light sensitive. This sets cephalopods apart from their molluscan families such as gastropods and bivalves. Recent studies have revealed that the opsins present in the skin are like those occurring in the retina. This infers that the connection between visual processing and body patterns is not exclusively innate. Expanding on Macphail's Null Hypothesis which posits no significant qualitative or quantitative differences in intelligence across vertebrates, this study seeks to explore the link between body patterning and cognitive abilities across cephalopod species. By comparing patterns of similarities and differences in cognitive abilities, this study aims to investigate whether body patterning can serve as an indicator of cognitive capacity. In conclusion, the study finds the presence of interindividual variations within species and disparities across different species in both body patterning and cognitive abilities. There are associations between cognitive capacity and body patterns. However, establishing a direct and conclusive connection between high-level cognitive abilities and the expression of body patterns remains elusive, as concrete evidence supporting such a relationship is lacking.

Sammanfattning

Cephalopoda utgör en värdefull modell för att studera den kognitiva evolutionen på grund av deras distinkta hjärnstruktur, organisation och nervernas kontaktmönster jämfört med ryggradsdjur. Utvecklingen av stora hjärnor och komplexa beteenden tros vara resultatet av evolutionär press från faktorer som ökad predation, mer krävande födosökningsförhållanden och intensiv parningskonkurrens. Medan skillnaderna mellan kråkfåglar och däggdjur är mindre uttalade, är bläckfiskhjärnan närmare ryggradsdjurshjärnan när det gäller encefalisering av nervcellkluster. Det cerebrala ganglie hos bläckfiskar liknar ryggradsdjurens främre hjärna och mellanhjärna, medan den vertikala loben liknar ryggradsdjurens hjärnbark och hippocampusformation, som är involverade i inlärning och minne. Dessa hjärnregioner fungerar inom ett hierarkiskt system och är intimt kopplade till deras ögon och optiska lober där visuell information bearbetas och motoriska kommandon överförs till de nedre motoriska centrarna. Kromatoforer är hudstrukturer som fysiologiskt kontrollerar kroppsmönster och är visuellt styrda och ljuskänsliga. Detta skiljer cephalopoder från andra molluskfamiljer som gastropoder och musslor. Studier har nyligenavslöjat att de opsin som finns i huden liknar de som förekommer i näthinnan. Detta antyder att sambandet mellan visuell bearbetning och kroppsmönster inte är uteslutande medföd. Utöver Macphails nollhypotes, som hävdar att det inte finns några signifikanta kvalitativa eller kvantitativa skillnader i intelligens mellan ryggradsdjur, ämnar denna studie utforska kopplingen mellan kroppsmönster och kognitiva förmågor hos cephalopoda. Genom att jämföra likheter och skillnader i kognitiva förmågor syftar denna studie till att undersöka om kroppsmönster kan fungera som en indikator på kognitiv kapacitet. Resultaten visar på förekomst av variationer mellan individer inom arter och skillnader mellan olika arter både vad gäller kroppsmönster och kognitiva förmågor. Det finns samband mellan kognitiv kapacitet och funktioner samt kroppsmönster. Dock är det fortfarande svårt att fastställa en direkt och definitiv koppling mellan hög kognitiva förmågor och uttrycket av kroppsmönster, eftersom konkret bevis som stöder ett sådant samband saknas.

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Terminologies and abbreviations

Terms	Definitions
5-HT	Serotonin
ACh	Acetylcholine
AM	Amacrine interneuron is a type of specialized cell found in the retina of the eye.
Behaviour	It encompasses various actions that an organism can perform, which include movements of body parts, emission of sounds or chemicals, and dynamic changes in colour or body patterns (Drinkwater et al. 2022).
Benthic	Occurring at the base of oceans, water, lakes, and seas i.e. life attached to the bottom or moving the bottom mud (Oxford Reference 2023).
C2H2	Zinc-finger transcription factors superfamily are proteins that control the expression of genes by influencing the transcription of DNA to RNA (Albertin et al. 2015)
CNS	Central Nervous System.
CPD	Cycles per degree.
Camouflage	Involves blending in with the environment to avoid detection by predators or prey – achieved through rapid changes in skin colour and texture enabling to match the surrounding and become nearly invisible.
Chromatic aberration	The mechanism involves the use of an off-axis pupil, and the principle of chromatic aberration in the context refers to where the light of different wavelengths is focused differently i.e. where different wavelengths come to focus at different distances behind a lens (Hanke & Kelber 2020; Stubbs & Stubbs 2016).
Convergent evolutionary process	Natural selection of analogous systems in phylogenetically remote animals (Hochner et al. 2006).
Courtship	Activities that coordinate with sexual partner in time, space, and motivation (Hanlon & Messenger 2018).
Countershading	The animal is difficult to identify or recognise from its background when the chromatophores on the dorsal surface expand to produce dark colour while the interaction of chromatophores and iridophores on the ventral surface enhances reflection (Ikeda 2021).
Crypsis	Primary function is to minimise the chances of being detected or eaten – through a combined techniques or strategies (camouflage, masquerade other adaptation) and involves both visual and behavioural adaptations.
Crystallin	Water-soluble structural proteins tightly pack to effectively increase the refractive index of tissue to enable transparency (Koenig & Gross 2020).

Deimatic Display	An antipredator defence namely, a display used against predators or rivals when startled or faced with a threat, e.g., eyespot (Hanlon & Messenger 2018; Drinkwater et al. 2022).
Epipelagic	Life in relatively shallow water i.e. 200 m. Pelagic refers to organisms that swim or drift in a sea or a lake (e.g., plankton and nekton) contrary to those that live on the bottom or seafloor. (Oxford Reference 2023).
FLX	Fluoxetine is a selective serotonin reuptake inhibitor (SSRI), in this context referring to subchronic waterborne fluoxetine, an organic contaminant, and its effect on body patterning (Bidel et al. 2016).
Flamboyant Display	A visual appearance characterised by a dark mantle with prominent white markings, yellow lateral stripe, white head, and arms, and red arm-tips which often includes Passing Cloud-like patterns on both the front and back of the mantle; It encompasses communicating an individual's fitness, competitiveness, territorial defence, warning signals (Hanlon & McManus 2020).
Gqα	A specific subtype of the G protein alpha subunit has a crucial role in cellular signalling pathways (Kingston et al. 2015).
GPCRs	G protein-coupled receptors, a large family of cell surface receptors involved in transmitting signals from the extracellular environment to the inside of the cells. GPCRs involve physiological processes such as sensory perception, neurotransmission, and hormone response.
Horizontal Gene Transfer (HGT)	It is a mechanism by which genes are transferred between different species, often unrelated ones. For e.g., the reflectin gene might not have originated within the Octopus bimaculoides lineage itself as suggested by Albertin et al. (2015), but could have been acquired from another organism through HGT.
Intra-phyletic	In this context refers to something that happens within the same taxonomic group or phylum and in terms of convergence evolution it means plasticity changes that occur within a single phylum evolutionarily.
Invertebrate ganglia	clusters of nerve cell bodies that make up the central nervous system, dispersed throughout the body and interconnected by nerves that control sensory and motor functions via processing information (Shigeno et al. 2018).
John Zachary Young (1907-1997)	An English zoologist, neuroanatomist, and physiologist began a systematic analysis of the neural correlates of predatory behaviour or cephalopods (Hochner et al. 2006; Messenger 2001).
L-glu	L-glutamate
LACE	Refers to light-activated chromatophore expansion, a behaviour observed in the skin of octopus when exposed to light; LACE is most quickly induced by blue light, with an estimated maximum sensitivity (λmax) at 480 nm aligns with the known spectral sensitivity of opsin in octopuses' eyes (Ramirez & Oakley 2015).
LPSO	Larger Pacific Striped Octopus (Official name not yet given).
LTD	Long-term depression.

LTM	Long-term memory.
LTP	long-term potentiation
mRNA	Messenger RNA is a type of ribonucleic acid molecule that plays a crucial role in protein synthesis (Kingston et al. 2015).
MDMA	Methylenedioxymethamphetamine.
Masquerade	A form of camouflage where an animal takes the appearance of an inedible object to deceive predators – cephalopods could mimic rocks, coral, or toxic animals to avoid being preyed on. This relies on the ability of the predator to recognise the masquerading species as potential prey.
Mimicry	considered a form of adaption and can be a part of masquerade; a phenomenon where both defended and undefended species exhibit visual signals resembling those of a coexisting defended species (Skelhorn & Rowe 2016).
NMDAR	N-methyl-D-aspartate-like receptors.
OL	Optic lobe.
Organogenesis	refers to stages 18-30 of the developmental stages of embryonic tissue (O'Brien et al. 2017) – a critical phase in development that contributes to the overall formation of fully developed organisms.
Opsin	Light-sensitive proteins located in the photoreceptor cells, a subfamily of G-protein-coupled receptor proteins with 3 major groups of opsins: the r-opsins, c-opsins, and Go/RGR (retinal G-protein-coupled receptor) opsins (Ramirez & Oakley 2015; Koenig & Gross 2020).
PL	Peduncle lobe.
Pallial nerve	Primary pathway from the lower motor centres to the stellate ganglia in the mantle (mixed nerves) (Dubas et al. 1986).
Passing Cloud	A form of body patterning commonly known as unique interspecific visual signalling or communication with prey or predators, characterised by synchronised wave-like movement generated by chromatophores flowing throughout the cephalopod body which has also been referred to as chromatic pulse or wandering cloud by different authors (Mather & Mather 2004; Caldwell et al 2015; How et al. 2017; Hanlon & Messenger 2018).
PO-like activity	Enzymatic activity is similar to phenoloxidases (POs), a group of enzymes found in many insects and mollusks. These enzymes play a crucial role in the immune response and wound-healing processes of these animals.
Polarisation horizontal or vertical orientation	The terms refer to the orientation of polarisation filters, in this context, polarisation vision is the ability cephalopods (and some animals) have in detecting and using polarised light for visual communication, navigation, and object detection (See 3.6).
Protocadherins	Family of cell adhesion molecules that are particularly important during the development of the nervous system. These proteins are involved in

	maintaining the connections between neurons essential for proper brain functions.
RT-PCR	Reverse Transcription Polymerase Chain Reaction, is a laboratory technique to identify specific RNA molecules (Kingston et al. 2015).
Reflectin gene	It is a gene responsible for producing a protein called reflectin known for its unique properties that allow it to control how light interacts with it, leading to effects like iridescence and structural colour changes (Albertin et al. 2015)
STM	Short-term memory.
Sinusoidal grating	A grating in which the luminance of the image undulates at a regular spatial frequency along an axis, increasing and decreasing according to the sine curve $y = \sin x$; To investigate visual perception, acuity, contrast sensitivity, spatial frequency tuning of the visual system (See 3.6; Nahmad-Rohen & Vorobyev 2020).
SFL	Superior frontal lobe.
VL	Vertical lobe.
WWW	What-where-when episodic-like components.
Wavelength	The physical property of light typically refers to the distance between two consecutive peaks or troughs of a wave; typically measured in nanometres and meters and used in describing the colour of the light (Guidetti et al. 2021). E.g., blue light has a shorter wavelength than red light – the wavelength of light affects how the material appears to the human eye (Ikeda 2021).

Background

1.1   Introduction

Recent advancements in neurophysiological methods such as Magnetic Resonance Imaging (MRI), intracranial recordings, immunohistochemistry labelling, genomic sequencing, high-speed video microscopy, and field video recordings have enabled researchers to build upon the pioneering work of JZ Young in studying the cephalopod brain and nervous system (Hochner et al. 2006; Shomrat et al. 2015; Shigeno et al. 2018). Octopuses are not feasible to keep in the laboratory or study in the wild, making these new techniques crucial. The modern Coleoidea consists of octopus, squid, and cuttlefish which belong to a group of the molluscan class Cephalopoda (collectively referred to as 'cephalopod(s)'; See Figure 1).
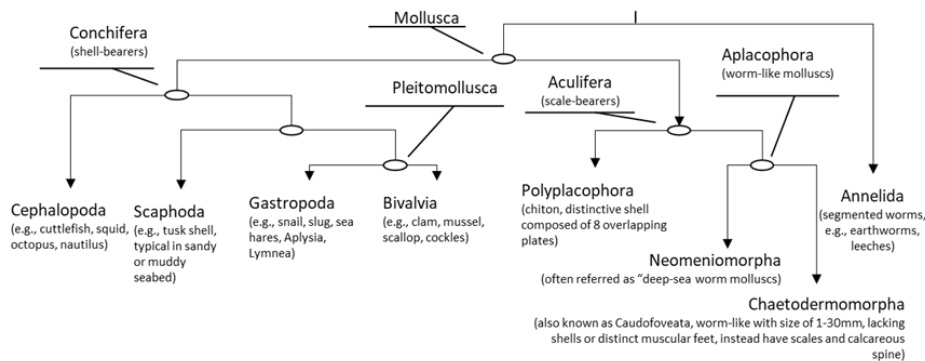
Figure 1 Molluscan phylogeny adapted from Shomrat et al. (2015) findings, showing cephalopods belong to the Mollusca phylum. Notably, cephalopods and gastropods are not sister groups, but both have most developed central nervous systems.

Hochner et al. (2006) suggest that they are invertebrates that have changed radically over evolution with distinct brain structures that differ from the rest of their nervous system, soft-bodied with long appendages and dissimilar life stories than their old cephalopod relative, the shell-bearing Nautilus (Nautiloidea). Although our understanding of phylogenetic origins of cephalopod neural centres are impoverished, the longitudinal work of JZ Young and Brian Boycott which began in 1947 aimed at building a brain model that combined behavioural observations (positive and negative reinforcement) and methods used in a range of biochemistry

and physiology methods e.g., removing certain lobes and tissues of the brain (Marini et al. 2017; Shigeno et al. 2018). In particular, experimentation of cephalopods with lesions in the neural centres uncovered the functional organisation of the cephalopod brain, as well as their learning capabilities and behaviours. Researchers have compared cephalopod brain functioning to that of mammals and other vertebrates (Shigeno et al. 2018). One theory proposes that selective pressures particularly, in competition with teleosts and reptiles, have played a significant role in driving evolutionary changes within molluscan phyla (Packard 1972 in Hochner et al. 2006). These adaptations have enabled modern cephalopods to survive and thrive with exceptional vision, flexible arms, learning abilities, and a unique chromatophore system (Amodio & Fiorito 2013).

The thesis is grounded in the notion that despite the phylogenetic distance between cephalopods and vertebrates, they share certain properties crucial for learning and memory (Messenger 2001; Hochner et al. 2006; Katz 2016; Shomrat et al. 2015; Marini et al. 2017; Shigeno et al. 2018; See Figure 2).
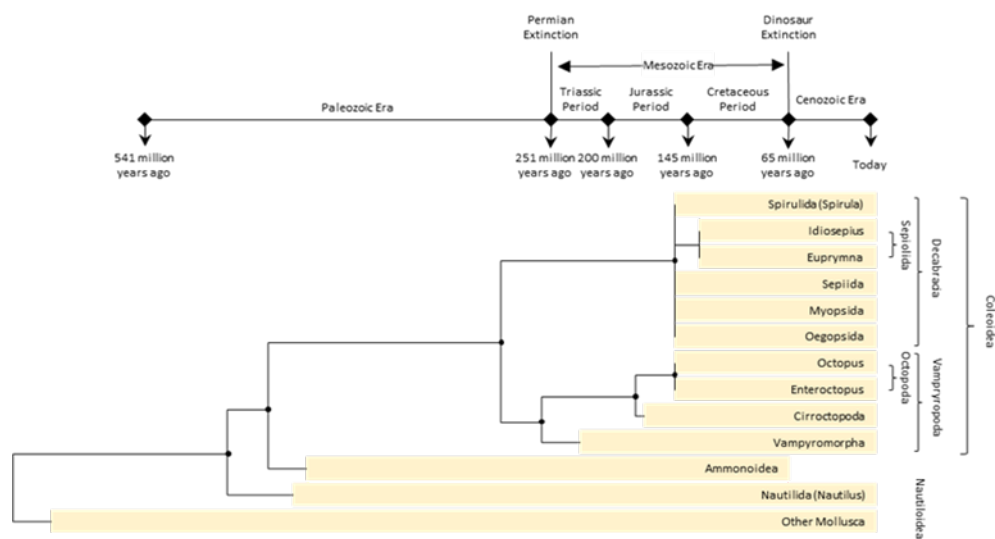
Figure 2. Cladogram of relationships based on (Kröger) 2011 in Shomrat et al. (2015).

Figure 2 depicts the evolutionary divergence between cephalopods and other molluscs—approximately 416 million years ago, a significant separation occurred between nautilids and coleoids, marking a crucial evolutionary milestone in the lineage of cephalopods. Shomrat et al. (2015) suggest that convergent evolution is evident in cephalopods, as they possess neural organisation and activity-dependent long-term synaptic plasticity similar to vertebrates, including structures involved in sensory processing and memory formation. Morphological similarities exist between the cephalopod vertical lobe and the mammalian hippocampus, cerebellum, and insect mushroom bodies, characterised by many small intrinsic interneurons and a stratified anatomical organisation resembling vertebrates (Shomrat et al. 2015; Shigeno et al. 2018; See Table 1).

Table 1 Comparisons between the cephalopod and vertebrate brains

	Cephalopod brain	Vertebrate brain
Structure	The vertical lobe is analogous to vertebrates' hippocampus in terms of cognitive function, connectivity, and neurochemistry (Shomrat et al. 2015).	Formation of the hippocampal is a major component and is implicated in memory, learning, and spatial navigation (Doeller et al. 2008).
Organisation	Composed of ganglia that formed 30 to 40 lobes – has no apparent right or left hemispheres. Some theorised embodied organisation whereby the overlapping circuits from individual motors controlled the movements (Zullo & Hochner 2011; Levy & Hochner 2017).	There is a division of the right and left hemispheres which consist of five lobes and are organised according to body moments and the central nervous system (Sanes & Schiebert 2001).
Connectivity patterns	A high degree of crosstalk between lobes because of interconnected tracts and commissures in the lobes (Williamson & Chrachri 2004).	Five lobes and two hemispheres are interconnected by commissures (Suárez et al. 2014).

This vertebrate-like organisation has inspired investigations of the structure and function of neural networks that mediate memory acquisition and other cognitive functions (Hochner et al. 2006; Hochner et al. 2012; Katz 2016; Levy & Hochner 2017). For instance, their vertical lobes are valuable models for understanding the connectivity, neural plasticity, and functional involvement of the brain structure concerning learning and memory. Octopuses, with around half a billion neurons, have a highly evolved nervous system that controls complex and advanced behaviour (Shomrat et al. 2015). Their cognitive abilities involve various systems such as decision-making, manipulation of arms, chromatophores, and potential consciousness (Mather & Dickel 2017; Amodio et al. 2019). This makes octopuses ideal subjects for studying cognitive functions due to their problem-solving abilities, non-stereotypical motor actions, adaptability to different task demands (Richter et al. 2016), and capacity for conditional discrimination (Hvorecny et al. 2007).

Broadly, cognition pertains to the processes through which cephalopods perceive, gather, process, learn, retain, and respond to environmental information encompassing decision-making based on perception, evaluation, and expression drawing upon prior knowledge or experiences (Schnell et al. 2020; Mather & Dickel 2017; Skelhorn & Rowe 2016). Skelhorn and Rowe (2016) posit that cognition may emerge as a significant selective force driving camouflage evolution, further suggesting that the study of cognitive processes in animals is informative in comprehending the trajectories of camouflage and vice versa. Nevertheless, several challenges are evident in studying body patterning and cognition in non-verbal cephalopods. First, the concept of cognition remains contentious. In particular,

differentiating between simple and complex cognition is challenging, with complex cognition involving the application of learned rules to solve problems effectively (Pepperberg 2020). This entails establishing criteria in linking abilities to socio-ecological challenges, establishing behavioural indicators, and ruling out alternative explanations (Schnell et al. 2020). While Schnell et al. (2020) provide a comprehensive validation of methods for assessing foraging and caching in cephalopods, they lack clarification concerning anti-predatory and mating behaviours associated with environmental factors such as handling, noise levels, and season. This thesis raises questions concerning anti-predatory and mating behaviours, which are intimately linked to camouflage and inter- and intraspecific signalling. These aspects have not been adequately and systematically addressed. Furthermore, the lack of comprehensive understanding regarding the influence of cognition on animal camouflage within an ecological context is also highlighted in Skelhorn and Rowe (2016). It is unclear whether masquerading species evolved from cryptic ancestors through gradual resemblance enhancement or larger mutations leading to an imperfect masquerade—few experiments studied predator discrimination of masquerading species versus inedible models, often with the former as the sole food. Although the assumption is predators make adaptive decisions for optimal investment, the lack of experimental evidence hinders identifying selection pressures that drive the masquerading prey's appearance. Meanwhile, the existing research primarily concentrates on how various crypsis strategies capitalise on predators' sensory mechanisms disregarding the potential impact on attentional and cognitive processes. As such, these present a critical consideration in the pursuit of ensuring the replicability of behavioural data through appropriate methodologies, which in turn can contribute to the resolution of existing disputes.

Second, octopuses have been suggested to possess a complex nervous system with the potential for capacity for long-term and intricate forms of memory comparable to certain mammals. However, limited evidence and inconsistent results stemming from data collection limitations, hinder our understanding (Marini et al. 2017). The notion is that human brains have an organised system of rhythms that are perfectly tuned to observe the regularities in the environment (Buzsáki 2006), e.g., the timing to catch a ball and play the string quartet. Characterising brain dynamics in humans is made possible by testing the moment at which a specific mental process becomes decodable with electroencephalography and magnetoencephalography. By pinpointing the specific time, researchers acquire valuable insights into the temporal arrangement of information processing within the human brain (King & Dehaene 2014). This understanding contributes to our knowledge of how the brain organises and processes information over time. Studying cephalopods' cognition in similar manners poses ethical and practical challenges. Nonetheless, their remarkable behaviour including rapid and intricate

body patterns and colour changes demonstrates their unique abilities within the animal kingdom.

Third, most laboratory studies are conducted on cuttlefish and squid, less on octopuses due to their bigger sizes and ability to escape their captivity or tank. It is noted that benthic octopuses use their arms extensively for various actions, possibly exhibiting decentralised control with a central brain for decision-making and arm ganglia for spatial information integration (Mather & Dickel 2017). For instance, octopuses use different propulsion actions and arm movements in locomotion and exploration. They often rely on tactile, visual, and chemotactile cues for tasks like prey capture and manipulation. Whereas cuttlefish and squid behaviour are mainly visually guided, with tactile exploration observed less frequently in the laboratory conditions. Optic and frontal lobes play roles in visual and tactile information processing for learning and actions in cephalopods (See Results), studies rarely differentiate and contrast how such information is processed by each species.

Despite differences in brain structure, organisation, and connectivity patterns from vertebrates and invertebrates, the cephalopod brain is closer to the vertebrate brain due to the encephalisation of the ganglionic masses observed by the nerve cell clusters, than the ganglionic clusters of its molluscan families such as gastropods and bivalves (Hochner et al. 2006; Schnell et al. 2020). Essentially, the cerebral ganglion in cephalopods is analogous to the vertebrate forebrain and midbrain while its vertical lobe is analogous to the vertebrate cerebral cortex and hippocampal formation. Parallels can be observed in the arrangements of folia within the vertebrate cerebellum and the neural architecture of the peduncle lobe within the octopus's brain. Furthermore, affinities exist between the cephalopod optic lobe and the deep retina of fish as well as between the cephalopod vertical lobe and vertebrate cerebral cortex and thalamus (Shigeno et al. 2018; Shomrat et al. 2015). These regions are intimately involved in the production of skin and body patterning. As such, cephalopods are believed to be "an important biological comparative model in search of location and function of higher-order cognition and its relationship to the environment" (Marini et al. 2017, p. 457).

The concept of body patterning involves the synthesis of chromatic, textural, postural, and locomotor elements, forming distinct patterns in cephalopods (Hanlon & Messenger 2018; Messenger 2001). This is achieved through the interplay of reflecting cells, skin muscles, and chromatophores. Broadly, three primary body patterns exist: Disruptive, Mottle, and Uniform. Cephalopod's defence mechanisms encompass primary and secondary strategies, with rapid transitions between them referred to as 'rapid neural polyphenism' (Hanlon & Messenger 2018). The optic lobes process crucial cues related to light objects, edges, spatial size of backgrounds, and the vertical visual field, influencing cephalopod body expressions (Messenger 2001). Body patterns are characterised by transitions encompassing 20 to 30 patterns with around 36 chromatic elements (Messenger 2001) and the transitions can be either chronic for camouflage or acute for signalling, lasting from

minutes to days and seconds to minutes respectively. Cephalopods express themselves by camouflage, masquerade, and crypsis strategies. Camouflage means blending with the environment, while masquerade entails assuming the appearance of inedible objects. Crypsis combines both strategies, involving physical adaptations for blending. These strategies rely on eyes, the central nervous system, and skin chromatophores and occur within milliseconds (Messenger 2001), which in turn contributes to vanishing effects, preventing detection by other animals. Recent studies in genomic sequencing (Albertin et al. 2015) revealed that *Octopus bimaculoides* exhibit a basic neuronal gene repertoire akin to that of fellow invertebrates. However, a distinctive feature of the octopus genome lies in the marked proliferation of transposons and various gene families. Such proliferation was observed in the protocadherins and C2H2, an occurrence uncommon amongst invertebrates. The origin of the reflectin gene might be through HGT, which in turn facilitated the cephalopod's dynamic iridescence and the ability to undergo structural colour change (Albertin et al. 2015; Guan et al. 2017). This essay provides an overview of the reported and published species to enhance our understanding of their diversity. As of 2005, information was available on 374 nominal species of octopus, with around 186 representing valid names. However, this is likely an underestimate of the total number of extant species because there existed over 150 undescribed species in the museum collections in the past 17 years (Norman & Hochberg 2005). This entails a greater diversity of octopuses that remains unknown to us, emphasising the need to explore and understand the various species sharing our planet.

This essay will explore the multifaceted roles that body patterns serve, encompassing functions such as camouflage, intimidation or manipulation of prey, predator evasion, and inter-individual communication. Specifically, highlight that skin display is not only a basic stimulus-response process as demonstrated by the opsins in the skin automatically control darkening (Ramirez & Oakley 2015; Kinston et al. 2015; Williams et al. 2019) often regarded as innate, rapid neural polyphenism to allow rapid concealment (Hanlon 2007; Hanlon & Messenger 2018), or unique pupil shape that generated chromatic blurring on the retina to enable perceiving spectral information (Stubbs & Stubbs 2016). Body pattern also provides an insight into cognitive processing particularly in the animals' interaction with predators (Skelhorn & Rowe 2016), in which their versatile skin appearance plays critical roles in camouflage, predation, and communication (Mather & Dickel 2017). Recent evidence has revealed that cuttlefish exhibited the ability to perceive and learn from their environment, all while undergoing development without direct parental care during the embryonic stage (Obrien et al. 2017). Their visual acuity, lateralisation, and polarisation sensitivity improve as the juveniles grow during the first months after hatching (Obrien et al. 2017; Darmaillacq et al. 2017). This developmental progression coincides with the enlargement and maturation of the vertical lobe, akin to the mammalian hippocampus in cephalopods.

The essay further finds the challenges lie in objectively linking their learning capabilities and their capacity to manipulate their arms and change their body features to adapt to their environments. It is important to clarify that no assumptions are made about cephalopods having higher-order cognition or assessing their personalities or emotions. The main point is that understanding cognitive abilities in a species requires studying how they solve problems, whether it's the species or their extant species or closely related families in the absence of fossil evidence.

1.2   Aim and research questions

The study proposes extending Macphail's Null Hypothesis (1987) to include invertebrates in particular cephalopods, considering the recent surge of interest in their neural correlates and mental abilities. Macphail's (1987) Null Hypothesis suggests that there are no significant qualitative or quantitative differences in intelligence across vertebrates. Macphail (1985), p. 38 asserts that qualitative difference between species means "*the possession by one species of a mechanism that is absent in another; prima facie evidence of a qualitative difference might be the observation that there was some task or set of tasks that could be solved by one species, but not by another. A quantitative difference between two species would mean that one species used a mechanism or mechanisms common to both species more efficiently than the other, and this might be reflected in a faster rate of solution or better asymptotic performance level by one species in some task solved by both*".

This literature review aims to investigate whether body patterning can indicate cognitive capacity in cephalopods. The study explores the influence of cognitive processing on camouflage strategies. A review is deemed appropriate to gather relevant data to find out the time course(s) (intervals) during or between which octopuses react or move in response to learning and environmental cues. The references can then form the basis for future investigations of these behaviours and their related faculties namely, chromatophores and visual systems. The research questions asked are:

1. Which cognitive processes are associated with changes in body patterns in cephalopods?
2. How fast can cephalopods change their body patterning in response to stimuli in their environment?
3. Which cognitive mechanisms affect how cephalopods solve a given task?
4. What are the neurophysiological properties in cephalopods that drive learning and memory?
5. Which physiological properties in cephalopods drive body patterning?

Methods

2.1 Literature review

Table 1 depicts searches done in two sessions. From January 1st, 2015 up to December 1st, 2022, Google Scholar database yielded 147 results whereas the PubMed database yielded 28 results with the following key term combinations 'octopus rapid neural polyphenism', 'octopus memory learning by camouflage behaviour skin change information processing', 'octopus memory learning by camouflage behaviour skin change'. From January 1st, 2015 up to April 1st, 2023, Google Scholar database yielded 354 results, the PubMed database yielded 360 results, and the Web of Science database yielded 160 results with the following key term combinations 'octopus skin pattern colour research method', 'Cephalopod OR octopus OR octopi AND camouflage AND body pattern AND colour change OR color change', 'Octopus OR cephalopod AND chromatophores OR pigments AND body patterning AND motor system AND camouflage AND signalling OR signalling AND vision', 'cephalopods OR octopus AND body patterning OR skin patterning OR neural polymorphism AND colour OR color'. The studies included peer-reviewed journals in the English language.

Table 1 Database search results

	December 2022	April 2023
Google Scholar	147	354
PubMed	28	360
Web of Science	NA	160

The following exclusion criteria were applied and screened through (1) non-evidence based including commentaries and letters; (2) studies focusing on other fields such as bio-inspired technologies, humans, fisheries, medicine, and fields outside the focus of biology, neuroscience, zoology, psychology, behavioural- and marine-related science; (3) studies focusing on other animals than cephalopods or without comparative approaches with cephalopods; (4) Abstracts that did not contain any of the key terms were excluded. There may be bias in using the terms

'body pattern', 'skin pattern' 'colour change' 'chromatophores', or 'camouflage' as not all researchers in the fields use the same terms in their references.

A total of 86 studies met the study criteria and due to space limitations, Table 3 of the selected summary of cephalopod literature is presented in the Appendix.

2.2 Limitations

Efficiency in the literature searches is impeded because the use of terminologies and consistency in pattern evaluation and naming are different among researchers due to the cephalopods' dynamic and complex nature and behaviours (Mather & Mather 2004; How et al. 2017; Hanlon & Messenger 2018). For instance, the patterns referred to as 'Mottle' and 'Disruptive', strategies involving 'masquerade', 'crypsis' 'camouflage' or 'mimicry', are some of the contentious areas with researchers having their own beliefs. Additionally, the words 'dynamic patterns' are differently used relative to 'dynamic camouflage' as well as it conveys different meanings relative to 'dynamic mimicry' as well as 'passing cloud' or 'wandering cloud' that is also referred to as 'chromatic pulse' by How et al. (2017), Caldwell et al. (2015) contrary to Hanlon & Messenger (2018).

In this thesis, *perception* refers to the gathering of information from the environment through acute vision and sensory organs – where the eyes with complex retinas detect and analyse light and contrast, whilst other organs like chromatophores and statocysts at the skin level sense orientation changes. In short, this thesis limits the discussion of body patterns in the visual domain. While *processing* occurs in the optic and vertical lobes, where visual information is processed and stored, and the nervous system integrates and interprets the input, the octopus *expresses* itself by displaying body patterns in response to stimuli. Furthermore, the thesis limits its content to the physiological properties of body patterning concerning the brain, visual, chromatophore, and skin systems. It does not cover the papillae and statocyst systems, which are complex sensory organs involved in dermal senses, body, and arm orientation. The study focusses on common body pattern attributes relevant to the context and does not evaluate sense organs or effectors. It is also unrealistic to draw parallels between more than 30 differentiated lobes to its central nervous system. As stated in the introduction, this essay provides an overview of the reported species to augment our comprehension of their shared characteristics and distinctive attributes.

Results & Analyses

In order to provide an overview of the existing body of literature pertaining to cephalopod body patterning and cognition, Table 3 in Appendix 1 is curated to summarise key findings from a selection of pertinent studies. This compilation aims to offer readers a succinct synthesis of the diverse insights obtained from various investigations into cephalopod capabilities. Table 3 organises the summaries based on thematic categories. Each entry within the table encapsulates significant findings, methodologies, and outcomes, thus facilitating a holistic understanding of the current state of cephalopod research. The table is presented as a valuable resource to contextualise the posed research enquiries and to structure the subsequent discussion within the broader landscape of cephalopod cognition and behavioural studies.

3.1 Which cognitive processes are associated with body patterns in cephalopods?

Cephalopods' body pattern elements including chromatophores serve many purposes (See 3.5) – they are informative to study cognitive processing at predator and prey levels (Mather & Dickel 2017; Skelhorn & Rowe 2016). Hanlon and Messenger (2018) suggest that they are primarily related to communication, predator avoidance, feeding, and mating, and these functions are structured and organised within a hierarchical system. The authors further suggest that octopuses, along with squid and cuttlefish, possess the ability to rapidly alter their body patterns within milliseconds namely, 'rapid neural polyphenism'. This way, their rapid adaptation aids effective camouflage by aligning appearance with their surroundings—crucial for their survival in diverse environments.

During their developmental phases, cuttlefish have demonstrated cognitive capabilities. O'Brien et al. (2017) suggest that hatchlings of cuttlefish *Sepia officinalis* already possessed abilities of chemoreceptor and mechanoreceptor functions with the receptor cells found in the arms' suckers, tentacles, and areas around the mouth at hatching—although the duration it takes for maturation of chemoreceptor function is unclear. Embryonic studies from Romagny et al. (2012), Andouche et al. (2013), and Dickel et al. (1997) cited in O'Brien et al. (2017)

suggest that at stage 23, cuttlefish embryos could perceive waterborne chemical cues diffused through the egg membrane and tactile stimuli from the environment; by stage 25 their responses to visual stimulation from the external environment are observable; at stage 25 chromatophores begin to show; at hatching, body patterning controlled by the optic lobes, lateral basal lobes, and chromatophores lobes are well-developed (not mature). O'Brien et al. (2017) suggest that their ability to detect vibrations from the surroundings which in turn induce their defensive behaviours such as alteration in body pattern and movement. These have important implications for the way cuttlefish perceive, process, learn, and respond to their surroundings as early as pre- and post-hatching. On the other hand, Hough et al.'s (2016) experiments with *Sepia Officinalis* found that the species could be conditioned to exhibit rapid body pattern changes namely, break camouflage when rewarded after the insertion of a probe. Cuttlefish in the experimental group, rewarded for changing their body patterning within 15 s of the probe insertion, responded faster and more consistently compared to the control group. The authors suggest that body patterning in cuttlefish may not be innate but shaped by individual experience and is more flexible than previously thought. Interestingly, the cuttlefish in the white tank do not respond to the probe as often, which led the authors to postulate as habituation. This indicates an association between body patterns and cognitive capacities in cephalopods.

Body patterning is evident in the context of sexual signalling during mating. This is particularly pronounced towards the end of an individual's lifespan (Mather & Dickel 2017). How et al. (2017) observed that in encounters between male reef-dwelling cuttlefish *Sepia latimanus* the smaller male exhibited a Mottle Display and white head with closely tucked arms, then dark blush on its head before expelling dark ink concurrently dark blush shifting or expanding downward. How et al. (2017) suggest that this behaviour indicates combative or aggressive signalling towards the larger mate-guarding male, suggesting territorial rivalry. These behaviours were similar in reef squid *Sepioteuthis lessoniana* except without the production of ink cloud. Both squid and cuttlefish exhibit a diverse range of sexual and agonistic patterns. The range is so extensive that they may constitute a visual language, a form of communication at different cognitive levels encompassing sensory discrimination, learning, and memory (Mather & Dickel 2017).

Hanlon and McManus (2020) examined the behaviours of cuttlefish *Metasepia pfefferi*, which exhibited a mating system involving the male species that are much smaller in size than the female species, and unique courtship behaviours. Notably, these behaviours are observed in both wild and captive environments for an extensive duration, with male species performing 'Flamboyant Display' around the female occasionally extending its arm to 'touch' while simultaneously exhibiting elaborate behaviour such as passing waves. When in competition with another male, it shows unilateral signalling with white paler colour facing the male performing the courtship. The competition can get aggressive and cannibalistic if the rival is of

similar size. The female is however not responsive but appears to continue foraging. Hanlon & McManus (2020) suggest that this behaviour implies intricate communication and signalling mechanisms. While the secondary defence in this study refers to the 'Deimatic Display', the primary defence in this animal is camouflage by blending in with the 3-dimensional objects in the surroundings (uniform and mottle, disruptive are less common) such as small rocks or algae, or masquerade as an object when out in the open (Hanlon & McManus 2020). The authors suggest that a scene of a female species foraging in camouflage, while it was detected by other fishes in close range, changed from camouflage to flamboyant in 700 ms and back to camouflage upon their leaving. Further suggests that this species was always in the form of camouflage contradicts the findings in the aquarium-raised *Metasepia pfefferi* by Thomas and MacDonald (2016). Thomas and MacDonald (2016) documented an extensive list of 11 distinct body patterns representing a combination of 7 textural, 14 postural, 7 locomotors and between 42 and 75 chromatic components in the dorsal areas the animals, in particular, suggest that the animals are always in the Flamboyant Display. Hanlon and McManus (2020) underscore these significant discrepancies between body patterns and displays in the wild and captivity, given that the aquarium-raised cuttlefish originated from a fifth-generation inbreeding cultured lineage. The substantial impact of the artificial environment has played an influential role. Nonetheless, considering their observations, the exhibited body patterns, postures, and behaviours suggest potential connections with communication strategies, revealing the possibility of chronic signalling during courtship and mating, as well as acute signalling during secondary defence. This indicates that sexual and foraging signalling is a form of communication that involves cognitive processes.

Body patterning is evident in the context of foraging. During foraging and in the burrow, octopus *Wunderpus photogenicus* displayed a rhythmic unidirectional passing wave pattern with the head protruding (How et al. 2017). How et al. (2017) suggest that the expression was akin to a reef squid *Sepia lessoniana* filmed in the United Arab Emirates, except without ink expulsion. Contrary to *Octopus laqueus*, the squid pulses appeared to work in the opposite direction, from the arm tips to the head, and from the anterior edge of the mantle to the centre. This aligns with Mather and Mather (2004) description of Passing Clouds, waves, or pulse or patch movement of *Octopus cyanea* during foraging. Mather and Mather's (2004) analyses revealed that the passage or placement of patches is not fixed and bilaterally symmetrical patches rather than single patches on each side have been observed to shift across the body. These displays were associated with foraging or attempted prey capture linked to specific movement patterns and were interpreted as complex signals with potential cross-phyla communication. This indicates that body patterns during foraging are a form of communication signalling.

Body patterning is evident in behavioural strategies. How et al. (2017) suggest that the tropical octopus, *Octopus laqueus* which forages nocturnally, exhibits a

behaviour called chromatic pulse. This display involves a dark patch moving from the posterior part of the mantle, diverging bilaterally to the sides of the mantle, converging into a single patch at the head, and continuing to the tips of dorsal arm pairs. The pulse display synchronises with the stopping part of the locomotory pattern while the animal swims or crawls between places and probes under rubble and crevices. One potential function is that the display acts as a noticeable and attention-grabbing warning signal namely, 'conspicuous warning signal' (aposematism) which deters predators from approaching the cephalopods as the display might signal that the cephalopod is dangerous or unpalatable. Another function suggested refers to a form of motion camouflage. In low-light conditions, the display might create false motion cues for observers, making it difficult for them to accurately track the cephalopod's movements or predict the cephalopod's trajectory. Another function suggested refers to prey flushing – by creating sudden and surprising movements, the cephalopod might startle nearby prey, causing them to move and reveal their positions. This could potentially suggest cephalopod's deliberate intent to capture prey or its adeptness in proficiently employing such behaviours. In the context of deception, it encompasses deliberate efforts to mislead for specific gains. For instance, a male mourning cuttlefish *Sepia plangon,* was observed strategically employing its shape and colour-changing abilities to deceive conspecifics during courtship. This behaviour was observed only in specific contexts where cheating was possible, such as deceiving rival males with female patterns on one side of its body while continuing with courtship patterns with a receptive female (Brown et al. 2012), indicating an understanding of the context. This deception theory finds resonance in the behaviour of the Japanese pygmy squid, *Idiospeius paradoxus*, which employs a strategy involving the release of ink clouds followed by an attack from a startling angle (Sato et al. 2016)—indicating strategies employed are cognitive processing of a learned experience encompassing purposeful actions, reactions employed to achieve specific goals or navigate their environment.

Body patterning is evident in social interactions. Social behaviour plays a role in shaping an organism's cognitive ability as it often involves interactions and cognitive processes such as communication, cooperation, and social learning (Mather & Dickel 2017). Amodio and Fiorito's (2022) findings indicated that the octopuses in the Panel group showed stronger exploratory responses to the mirror and mirror-induced agonistic behaviours (See Appendix 1). The Social group displayed similar exploratory and agonistic behaviours towards both the mirror and a conspecific. In the Mark test, octopuses interacted with the mark, but similar responses were observed without the mirror and in sham-marked individuals, suggesting proprioceptive influence. The authors observed consistent behavioural patterns exhibited by certain individuals which led them to suggest the establishment of a dominant-subordinate relationship within each pair. Recent studies have revealed the social nature of octopuses *Octopus cyanea* and *Octopus*

tetricus including their sharing of dens and food, distinguishing them from *Octopus vulgaris* (Caldwell et al. 2015; Scheel et al. 2016; Chung et al. 2022). In particular, intriguing signalling behaviours are observed amongst *Octopus tetricus* with the utilisation of body patterns in antipredatory strategies and camouflage in activities, such as using specific arms or water jets to gather materials for expulsion during interactions and adopting a heightened 'standing tall' posture and darker colouration when engaged with conspecifics (Scheel et al. 2016; Scheel et al. 2017; Hanlon & Messenger 2018). In the case of *Sepia apama,* close interactions, and threat displays with conspecifics imply a communicative function, How et al. (2017) suggest that it is particularly prominent amongst males, possibly enhancing signal efficacy and simulating rival movements.

Additionally, the observed non-random associations between the highfin grouper fish, *Epinephelus maculatus,* and the reef octopus, *Octopus cyanea*, where they were found co-operating with each other during their hunting expedition (Bayley & Rose, 2020; Forsythe & Hanlon 1997) while *Octopus tetricus* exhibits distinct interactive behaviour with conspecifics (Scheel 2018; Scheel et al. 2016; Godfrey-Smith et al. 2022). This hints at interactions beyond chance occurrence and suggests potential cooperative hunting endeavours (Unsworth & Cullen-Unsworth 2012; Bayley & Rose 2020). At the interspecies level, *Octopus bimaculoides* can tolerate crowding whereas *Octopus briareus* cannot tolerate other conspecifics and is likely cannibalistic as some species are found to reside in high-density sites, colonies of 30-40 individuals and clumped dens, indicating they are not strictly solitary or asocial (Forsythe & Hanlon 1988; Huffard et al. 2008; Godfrey-Smith & Lawrence 2012; Caldwell et al. 2015; Hanlon & Messenger 2018; Chung et al. 2022). As such, social interactions may have implications on their learning and memory abilities. This implies that body patterning is indicative of communication signalling—inter- and intraspecies signalling.

Diverse behavioural strategies including camouflage, motion cues from a body posture or position as acts of intimidation, or rivalry simulation are used in decision-making processes. Panetta et al.'s (2017) findings revealed that cuttlefish's ability to adapt and change their skin colour and texture in 3-dimensional is likely a form of dynamic masquerade that enable them to mimic a wide range of objects (e.g., seaweed, rocks) to blend in the backgrounds to avoid detection by both prey and predators. They suggest that the process of decision-making is influenced by visual guidance rather than tactile contact. For instance, unlike octopus, it did not need to touch objects with suckers to guide papillae expression, suggesting vision guidance and while some touched rocks briefly, the vision seemed to guide expression in subsequent trials. In the study of squid *Sepioteuthis lessoniana*, Nakajima et al. (2022) findings revealed a strong positive correlation between colouration in the head and mantle similar to observations in cuttlefish, indicating a potential shared mechanism. The study noted that swimming orientation could influence colour change duration and the decision to change colour is made upon crossing a

boundary, suggesting an ability to adapt to diverse environments with varying light conditions such as coral lagoons and seagrass meadows. Their studies suggest that different camouflage strategies might be employed throughout their lifespan in response to different types of predators, potentially indicating a high level of sensory perception and cognitive processing. Further implies flexibility in learning and response mechanisms, that the animals' adjustment of their behaviours based on specific environment cues and contextual factors, indicating a level of cognitive adaptability and learning.

Additionally, Josef et al. (2015) showed that when cuttlefish *Sepia officinalis* is placed on a black and grey background tank, their reflectance appears to gradually alter ahead of the 'destination' as it approaches the background in a sigmoidal manner. Josef et al.'s (2015) experiment quantifies motion camouflage by systematically measuring the mantle reflectance changes by comparing the time the cuttlefish begins its change before crossing and post-crossing into the new background. Josef et al. (2015) suggest that to achieve motion camouflage, the cuttlefish is predicted to estimate in advance the time to reach the new background as well as anticipate the reflectance changes in approaching the new background, suggesting optic flow mimicry to deceive potential observers even though their motion is detected. Like cuttlefish, there was an anticipation to match the upcoming background to match accordingly, the colour change in squid is determined once they cross the boundary (Nakajima et al. 2022). Nakajima et al. (2022) suggest that the animals inhabit optically heterogeneous habitats like coral lagoons and seagrass meadows, camouflage to substrate adaptation (e.g., pelagic and reef environment) would be more effective than countershading, and that the camouflage strategies differ throughout lifespan likely in response to different predators. This indicates that body patterns are used in cognitive processes.

3.2 How fast can cephalopods change body patterning?

Rapid neural polyphenism encompasses the transition between primary and secondary defence mechanisms (Hanlon & Messenger 2018). It is dynamic within the range of seconds to show threat, as evidenced by the fully cryptic mottled pattern in *Octopus vulgaris* that changed to Deimatic Display to give a 3-dimensional texture in approximately 2 s (Hanlon 2007; Hanlon & Messenger 2018). Hanlon (2007) shows that this involves ca. 30 million chromatophores and thousands of skin papillae. Mäthger et al. (2012) suggest that the blue rings of the blue-ringed octopus *Hapalochlaena lunulata* can change within 0.3 s to 0.5 s for a range of patterns for communication and camouflage. The colour system is mediated by pigmented chromatophores and structural reflecting cells in which the multiple types of cells in the different layers of the skin structure enable the structural colour change in cephalopod multilayer reflectors or structural light

reflectors (iridophores and leucophores), affect the duration of peak wavelengths. The patterns change markedly with movement and direction, in squid, the movement is coordinated to fit a school of squid (Hanlon & Messenger 2018).

How et al.'s (2017) analyses encompass a comprehensive investigation into various aspects of body patterning within multiple species. Their research further elucidates the nuanced spatiotemporality aspects of these species. For instance, in a tropical habitat, the nocturnal *Octopus laqueus* exhibited the Passing Cloud or chromatic pulse pattern, totalling 33 'pulses' within 140 s with each lasting 0.55 (±SD 0.11 s) at a frequency of 0.25 Hz. When the animal forages by swimming or crawling from one place to another, and stops to probe under rubble and crevices, the pulse display is synchronised with this stopping locomotory pattern. Each time it pauses to probe with the arm tips, it moves 3.5 times faster before initiating a pulse display. An undescribed octopus took 1.2 (±SD 0.07 s) to complete a single pulse. In the context of an aggressive interaction with a larger mate-guarding male, *Sepia latimanus* exhibited a variant pulse pattern over 1 s followed by simultaneous expulsion of ink with arms tightly tucked together. *Octopus Wunderpus photogenicus* displays a rhythmic unidirectional passing wave pattern during foraging or burrowing originating from the eye stalks moving downwards over the head and to the junction of the mantle and arm crown at 1-2 Hz.

Studies revealed another light pathway that exists in the skin of cephalopods. It appears that chromatophore expansion can be induced by way of directing light onto the skin, which is sensitive to r-opsin i.e., the visual pigment, and this behaviour is coined as 'light-activated chromatophore expansion' (Ramirez & Oakley 2015). At the molecular level, there are at least three groups of opsins, a family of G-protein-coupled receptor proteins namely the r-opsins, c-opsins, and Go/retinal G-protein-coupled receptor opsins which are involved in the function as light receptors (Ramirez & Oakley 2015). The authors compared the chromatophores in both *Octopus bimaculoides* against Packard and Brancato's (1993) cited in Ramirez & Oakley (2015) preliminary observation of *Octopus vulgaris*. Their findings revealed that *Octopus bimaculoides* skin expands at an average of 6 s for adults and 15 s for hatchlings, whereas *Octopus vulgaris* skin expands at 1 s. The variations in species and methodology during the preparation stage could account for the discrepancies observed. The authors suggest that it is possible that exposing the skin to bright white light, causing the expansion of chromatophores while the skin is still attached to the whole animal, as demonstrated by Packard and Brancato, could contribute to the differences in speed. The authors suggest that the action spectrum of LACE in the eyes of *Octopus vulgaris* has a maximum sensitivity λmax at 474 nm, which aligns with the peak they observed in their analysis specifically, the shortest wavelength of blue light with a λmax of 480 nm. This similarity suggests that opsin phototransduction, a process involving light-sensitive proteins (opsins), is responsible for the expansion of chromatophores in response to light.

Ramirez and Oakley (2015) identified ciliated peripheral sensory neurons in the hatchlings which are similar in terms of morphology and position to the mechanoreceptor cells described in cuttlefish and squid. Similar findings were observed in squid *Doryteuthis pealeii* and cuttlefish *Sepia officinalis* and *Sepia latimanus* whereby full-length transcripts encoding rhodopsin and retinochrome are found in the skin and Gqα mRNA transcripts are identified surrounding the chromatophore components (Kingston et al. 2015). Williams et al. (2019) found distinct clusters of iridocytes positioned beneath the outermost layer of chromatophores in *Doryteuthis pealeii*, showing that the reflective colour of each chromatophore is linked to its changing shape. The synchronisation between the iridescence and chromatophore shape occurs at a precise and rapid rate with a temporal resolution finer than one second. Contrary to previous studies that induced changes in iridophores through electrical or chemical means which typically occurred over seconds or minutes. The findings suggest that chromatophore organs possess structural reflectivity due to proteins such as reflectin and crystallin, indicating unique optical capabilities in squid.

The rate of adaptation to the surrounding is demonstrated by Squid *Sepioteuthis lessoniana* which exhibited consistent rapid colour changing between two distinct background substrates at the shortest duration measured around one-third of a second (Nakajima et al. 2022; 3.1). These colour-changing events lasted approximately 2 s on average. While there were significant variations in the duration of body transformation across different experimental conditions, the findings revealed no significant differences between individuals with an average velocity of approximately 0.16 ms. Nakajima et al. (2022) further observed that swimming orientation could affect the changing process as some colours were relatively short (0.3 s) and four times longer on average. Hadjisolomou et al. (2021) used a non-invasive, light flash startle stimulus to quantify body patterning temporally in living squid, *Doryteuthis pealeii* in the areas of the head or arms, mantle, and fin. The expansion of chromatophores resulted in an average increase of 155.06% across the body, while retraction led to an average decrease of 40.46%. It is noteworthy that, before flash stimulation, the chromatophore state is expanded or retracted at exposure to ambient light and visual environment. The stimulation could elicit a jet-escape startle response and transient chromatophore expansions. The duration of light flashing was ~100 μs with an illuminance of 12,500 lx for even lighting provision from a distance - chromatophore responses to the stimulus were however unequally distributed, yet their temporal dynamics at the peak for both expansion and retraction appeared between the range 100-150 ms. This indicates the speed was nearly similar independent of the magnitude of the stimulus with those chromatophores on the head or arms responding fastest.

In other studies, squid *Dosidicus gigas* exhibit synchronised flashing patterns involving rapid closing and opening of chromatophores over the whole body at 2-4 Hz in 3 s from one end to another end of its body, upon seeing similar species in

the vicinity indicating intraspecific communicating (How et al. 2017; Rosen et al. 2015). Rosen et al.'s (2015) findings revealed that two dynamic displays were shown by squid *Dosidicus gigas*. Flashing is characterised as a rapid oscillation of body colour between white and red occurring at frequency 2-4 times per second upon the squid seeing another squid species nearby, suggesting a form of intraspecific signalling among individuals of the same species. The amplitude and frequency of flashing could be adjusted and the phase relationship with another squid could be rapidly changed. In contrast, flickering is characterised as involving irregular wave-like activity in neighbouring patches of chromatophores and the patterns mimic the down-welled light in the water, suggesting a dynamic form of camouflage in blending in the surrounding.

3.3 Which cognitive mechanisms affect how cephalopods solve a task?

Studies centred on cephalopods have illuminated their aptitude for learning. In laboratory settings, associative learning commonly encompasses classical conditioning or discrimination learning, along with instrumental or operant conditioning involving trial-and-error processes (Hanlon & Messenger 2018). Cephalopods have demonstrated a propensity for adaptability within their social interactions, indicating a degree of flexibility in responding to various situations and their behavioural repertoire extends to encompass future-oriented actions illustrated notably through instances of tool utilisation (Scheel et al. 2017; Finn et al. 2009). Recently, a set of behavioural tasks have been designed to evaluate the variations in *Octopus vulgaris*'s predatory behavioural responses. Borrelli et al. (2020) suggest that several aspects of cognitive abilities could be measured such as the ability to acclimatise, reaction to novel stimuli (neophobia), social learning capability, problem-solving ability, and response to artificial stimuli (individual learning, preferences). Previously, octopuses have demonstrated spatial memory and navigational skills in optimising foraging strategies. For instance, Mather (1991) conducted 60 field analyses of young *Octopus vulgaris* foraging behaviour within the Bermuda environment. These longitudinal investigations revealed that these animals could recall their routes or employ alternate pathways to their dens, traversing an average distance of 9 m within 55 min, without necessitating the deployment of chemical cues. This supports the findings of Forsythe and Hanlon (1997), whose field study involving *Octopus cyanea* Gray 1849, on a Polynesian coral reef illustrated an average journey length of 81 m over 118 min in a single trip. Notably, these octopuses occasionally exhibited unexpected stops, subsequently executing a 'bee line' swims to their dens.

Comparable tendencies emerge within cuttlefish where specific foraging incidents are recollected based on consumed prey ('what'), consumption locations

('where'), and the temporal interval ('when')—the what-where-when (WWW) components since the event (Jozet-Alves et al. 2013). Schnell et al. (2021b) investigated whether *Sepia officinalis* episodic-like memory deteriorates as they age. The findings revealed that episodic-like memory is not susceptible to aging-related factors. Essentially, the WWW components were retained, and information was used to make subsequent decisions. According to Jozet-Alves et al. (2013), this aptitude enables cephalopods to retain the WWW components of previous foraging encounters, thus facilitating rapid adjustments in response to prevailing prey conditions. The same strategies may not apply to octopuses. Poncet et al. (2022) studied episodic-like memory in 7 *Octopus vulgaris* and found that they adopted less cognitive demanding strategies to forage, and interestingly each presents variation to their preferred method, suggesting interindividual differences. But one out of seven octopuses learned to keep track of the time the food replenishes, suggesting like cuttlefish, octopuses might also possess neural prerequisites for episodic-like memory just that in this context, it matters less to adopt episodic-like memory strategies, the goal is attained if their need is satisfied. The findings showed insight into the differences between interspecies and intraspecies. Notably, cuttlefish demonstrated a lower level of interindividual differences under the same experimental conditions (Poncet et al. 2022). This indicates variations in interindividual differences within each species in learning and memory abilities.

Variations in interindividual differences are shown in cephalopod's behaviours related to cognitive mechanisms such as inhibitions, planning, processing, and decision-making. In Josef et al.'s (2015) (See also 3.1) novel experiments, their finding suggested that the gradual transition of *Sepia officinalis* mantle may serve as a cue for processing, planning, and anticipation of upcoming events. The experimenters were able to provide information concerning the percentages of change as the animal crosses between the contrasting backgrounds, as well as the time lag the mantle reflectance changes in seconds. In Schnell et al. (2021a), the enquiry into whether cephalopods could possess the capacity for delaying gratification was raised. The authors investigated cuttlefish *Sepia officinalis* self-control using an inter-temporal delay maintenance task and learning performance using a reversal-learning task in which the results are analysed for their association with learning performance. The findings revealed that cuttlefish could delay their gratification up to 50-130 s for better food choice, like the results found in mammals and birds, the animals are susceptible to choosing a less preferred food choice when the waiting gets longer. The authors posit an ability for future planning and inhibition to immediate impulses. Further suggests delayed gratification could be associated with phenotypic traits i.e., camouflage, relative to the experimental design. The authors suggest that the duration they remain motionless might have arisen as 'by-product' acting upon camouflage abilities. The findings further suggest associations between faster discriminating brightness, a longer delay to

gratification, faster learning of the reverse reward-related contingency, and a longer delay to gratification.

Learning and memory are affected by context. Bublitz et al. (2017) replicated the traditional visual reversal learning methods on *Octopus vulgaris* and found varied results with one octopus completing the learning criterion, but not the other three. Bublitz et al. (2021) suggest that the success of learning in octopuses is highly influenced by the experimental conditions and learning context. For instance, in their reversal spatial task, learning signals were perceived by the octopus (exhibited Mottle Display) rather than because they had extensive training so the authors could conclude that learning is positively affected by context namely, the signals directly indicated an incorrect response. Their findings highlight that octopuses performed better in visual discrimination than spatial discrimination tasks contrary to the theory that good spatial skills indicate good spatial discrimination abilities. Further led the experimenters to conclude that spatial serial reversal learning could not be effectively tested using positive reinforcement alone, making it difficult to compare reversal performance based on spatial versus visual cues. Despite differences in experimental design, most octopuses successfully reversed multiple times in succession with a minimum number of errors per reversal that differed across studies. The octopus' response was positively influenced by the associative process and not by the training phase. This further underscores the significant role played by contextual variables. Recently, Kawashima et al. (2020) have expanded the enquiry into cephalopod cognitive dynamics by focusing on octopus *Abdopus aculeatus*. Their study showed distinctive variations in terms of speed and reaction towards learning conditions. A compelling aspect of their findings lay in the gradual and adaptive changes observed in the expression of specific body patterning. This observation prompted the researchers to suggest a potential link between the manifestation of dark colouration and positive emotion as they become sensitive to the conditioned stimulus i.e., active mode, faster reaction, and more learning. In contrast, pale colouration seemed aligned with inactive or silent mode. This was substantiated by their comparatively slower reactions to the stimuli and diminished learning capacity (less learning) within such states.

The potential influence of living conditions and environmental factors on cognitive abilities was the subject of an investigation by Yasumuro and Ikeda (2018). The authors investigated the ontogeny of learning and memory, as well as the dimension of depth perception in *Sepia pharaonis* by employing the 'prawn-in-the-tube' paradigm. Central to their enquiry was the hypothesis that cuttlefish raised in an enriched environment would acquire normal cognitive abilities more than those raised in an impoverished environment. In the context of learning and memory, distinct patterns emerged based on the environmental context. The cuttlefish from the isolated environment were able to memorise the task at an early age but failed to recall at a later age; those from the poor environment were not able

to memorise the task at any age, those from the standard environment were able to memorise the task at later ages and those raised in the enriched environment showed an ability to memorise task at all ages. In depth perception, cuttlefish from an isolated environment consistently maintained a distance from their prey and demonstrated the lowest success hunting rate across all ages; in contrast, those raised in an enriched environment demonstrated the highest success hunting rate. As such, living conditions have an impact on cognitive performance in cephalopods.

3.4 Which neurophysiological properties in cephalopods drive learning and memory?

Cephalopods have exhibited learning and memory abilities comparable to vertebrates (Williamson & Chrachri 2004). The authors suggest two central memory systems: one for visual associated with optic lobes (OLs) and another for tactile or taste involving the median superior frontal lobes (SFL) and the vertical lobe (VL). Lesions to specific lobes disrupt learning, with the OL linked to visual learning and the SFL and VL associated with tactile learning. Visual memories are bilaterally transferred between OL via the central commissure, with potential predator-related inputs (escape) communicated via pathways to the magnocellular lobes and motor responses, while inputs related to potential prey (attack) are communicated via separate pathways to the peduncle and basal lobes which involve complex motor sequences. Cholinergic system disruption in the vertical and frontal lobes of the CNS affects learned behaviours and memory recall, while long-term potentiation (LTP) in the octopus' VL suggests structural similarities to the vertebrate hippocampus. According to the authors, this theory highlights the existence of distinct central memory systems and separate visual and tactile-taste memory systems in cephalopods, contributing to their cognitive functions.

Recent studies have revealed a connection of fibres between both the OLs and the peduncle lobe and those fibres that run from the anterior basal and the magnocellular lobes which connect the outputs with the oculomotor (Chung et al. 2022). This associates the OL and VL which in turn supports the capacity for visual memory (Shigeno et al. 2018). With its layered structure, the OL plays a major role in visual learning and coordinates behavioural responses e.g., escape (Yoshida et al. 2015; Marini et al. 2017). The lobes also collaborate with the vertical and superior frontal lobes to respond to pain (e.g., deciding to retreat or attack) (Hanlon & Messenger 2018).

Byrne et al. (2017) suggest that *Sepia officinalis* and *Octopus vulgaris* can be trained to perform vertebrate-like learning and memory tasks. Removal of the VL, involved in visual information and higher functions, did not affect general behaviour but impaired learning of new tasks. The VL and the median of the SFL

may form an associative network for learning and memory, similar to the mammalian hippocampus and insect mushroom body (See Table 1). There is evidence (Moser et al. 1998) to suggest that artificial electrical saturation of hippocampal LTP impaired spatial learning in rats, thereby supporting the association between LTP and learning. Furthermore, Shomrat et al's (2008) experiments demonstrated that *Octopus vulgaris* shows different sites for short- and long-term storage, whilst the short-term memory (STM) is consolidated within the behaviour-controlling circuitry, the long-term memory (LTM) is retained in the VL system. The VL modulates short-term learning rate through activity-dependent LTP, while inhibiting behaviours associated with aversive experiences (Byrne et al. 2017). Byrne et al. (2017) suggest that memories acquired before transection or tetanisation remain intact, supporting the role of LTP in mediating long-term behavioural memory similar to mammals and humans with hippocampal lesions.

Marini et al. (2017) suggest that the octopus' learning system adheres to an associative learning model, involving interstitial neurons called amacrines and the synapses. Amacrines and large efferent neurons are present in the VL with the VL receiving input from the median part of the SFL where visual and taste information integrates (Shigeno et al. 2018). The VL neuropil connects to the outer cell body layer, establishing *en passant* synapses with the amacrine neuron-like dendrites of pyramidal cells in the CA1 region of the mammalian hippocampus innervated by the Schaffer collaterals (Shomrat et al. 2015; Byrne et al. 2017). Shigeno et al. (2018) suggest that repeated stimulation of certain synapses strengthens the signals, and this enhanced connectivity may account for the short fluctuation of memory recall and long-term cumulative changes, consistent with Hebbian theory namely, 'cells that fire together wire together', implying that how LTP or long-term depression (LTD) is generated depends on the timing between the arrival of synaptic input and the postsynaptic action potential (Abraham et al. 2019).

Abraham et al. (2019) suggest that synapses serve as the primary site for storing information underpinning the processes of learning and memory. They suggest that the octopus's sub-vertical lobe and amacrine cells share functional similarities with insect premotor centres and honeybee Kenyon cells (Shigeno et al. 2018). Shomrat et al.'s (2008) experiments showed the involvement of LTP in the pathway between SFL-to-amacrine-cell for long-term associative memory. Abraham et al. (2019) suggest that the glutamatergic synapses between SFL neurons and amacrine cells show two different forms of LTP when subjected to high-frequency stimulation of the SFL pathway. Interestingly, it is observed that LTP does not occur in the synapses between amacrine-to-large efferent neurons in octopuses. In contrast, there is evidence suggesting LTP in cuttlefish, high-frequency stimulation does not potentiate the SFL-to-amacrine-cell synapses (Abraham et al. 2019). This suggests similarities between vertebrates and cephalopods in terms of LTP and LTD concerning learning and memory systems. These forms of synaptic plasticity are

'evolutionarily highly conserved', suggesting important roles in learning and memory in the invertebrate nervous systems (Abraham et al. 2019).

The octopus CNS is structured in a circum-oesophageal manner to accommodate its complex visual system and limb-based tactile capability (Chung et al. 2022; See 3.5). It has been suggested that it functions as an embodied organisation integrating a decision-making unit that integrates multimodal sensory information and coordinates with motor commands executed by the periphery (Amodio et al. 2019). The organisation of the VL along with its network connectivity, neuromodulation, and LTP, suggests the involvement of neuronal mechanisms in mediating behaviours related to learning and memory (Shomrat et al. 2015). Octopus and cuttlefish share similar neuronal elements with comparable connectivity networks with the same neurotransmitters involved in synaptic transmission. Specifically, the connection from the SFL to amacrine interneuron (AM) is glutamatergic while the connection from AM to the large efferent neurons is cholinergic (Shomrat et al. 2015; Katz 2016). Nevertheless, their plasticity mechanisms differ. Octopuses exhibit both short- and long-term synaptic plasticity networks localised at the glutamatergic synapses, including serotonergic neuromodulation in the connection between superior-frontal lobe-to-cholinergic AM in the VL. In contrast, cuttlefish show no plasticity at these synapses but rather show LTP at cholinergic amacrine to efferent large neuron synapses (Shomrat et al. 2015). This indicates distinct locations (diametrical) of plasticity but shared similar circuitry, contributing to their visual system (Katz 2016). Shomrat et al. (2015) suggest that although there is no indication of the neuromodulator 5-HT having a modulatory effect on the cuttlefish, intracellular whole-cell recordings from the large efferent neurons or extracellular recording of the spiking activity from the axons of the large efferent neurons indicate LTP. Plasticity happens at the cholinergic fan-in synaptic connection in cuttlefish, suggesting different strategies for learning and memory storage (Shomrat et al. 2008; Shomrat et al. 2015).

Shigeno and Ragsdale (2015) studied *Octopus bimaculoides* hatchlings and adults and revealed that the VL gyri consists of five distinct lobules. The neuropil receiving input from the SFL exhibited intrinsic neurochemical organisation and heterogeneities in the distribution patterns of neurotransmitters. Specifically, 5-HT was present in the two lateral gyri, while octopressin was present in the three medial gyri. The complex anatomy of the constituent lobes of the SFL-VL system suggests the presence of functional subsystems within the learning circuitry. Chung et al. (2022) showed that the number of gyri in a species may indicate its learning and memory abilities—possibly explaining the interspecific collaborative hunting behaviour documented between the *Octopus cyanea* and reef fishes (wrasse, coral trout) with octopus leading the hunt (Bayley & Rose 2020; Chung et al. 2022; Vail et al. 2013) contrary to previous findings that octopuses do not collaborate (Hanlon & Messenger 2018).

Meanwhile, habituating the late embryo stage of cuttlefish *Sepia officinalis* (*in ovo*) to sensory experience concerning tactile, chemical, and visual stimulus modalities, could influence its postnatal behaviour (Romagny et al. 2012). This further taps into the question of cephalopod memory storage. The role of the VL of the supraoesophageal nervous mass in *Octopus vulgaris* was investigated by removing 50% of the VL of the observer octopus and testing them on their discriminatory performance by observational learning paradigm (Fiorito & Chichery 1995). Their findings revealed that such octopuses showed a deficit in their learning, but their learning level improved after 24 h as demonstrated in the observational phase, whereas those that did not have their VL tissues removed showed no impairment in discriminative performance, suggesting removal impaired short-term (STM) recall but not retention of 'observational' long-term memory (LTM). Similarly, support for STM and LTM suggests they shared the same entry but have independent stores, which is demonstrated in *Sepia officinalis* by way of the 'prawn-in-the-tube' paradigm, an associative learning task in Dickel et al. (1998). It is worth mentioning that Dickel et al. (1998) found that cuttlefish could learn to inhibit their predatory behaviour and have good retention for this learning for 2-8 min, and their predatory responses recovered in 20 min after training, suggesting a separate STM and LTM stores. The retention performance not to attack prey was examined during the post-embryonic stage corresponding to STM rate (5 min) and LTM rate (1 h). Their findings revealed STM was fully operational as early as 8 days post-hatching, whereas 1h retention performance progressively increased between 15-60 days post-hatching, suggesting the existence of a time lag between establishing STM and LTM. To investigate such differences in a time lag, a cellular and molecular study by Agin et al. (2003) investigated the LTM of *Sepia officinalis* of their feeding motivation and revealed that if administered a *de novo* protein synthesis inhibitor, cycloheximide within 1-4 h before associative training, it intervened the formation of LTM in line with studies in other animal species. This suggests the production of new gene products that are expressed in a time-dependent manner is critical for LTM formation (Agin et al. 2003).

Additionally, learning and memory abilities are closely linked with neurotransmission, specifically, the serotonin system, in regulating social behaviours in octopuses. For instance, when the animals are engaged in mating activities, their aggressive or competitive behaviours towards each other are suppressed. This suggests that the neural pathways or mechanisms in the brain that are responsible for promoting social interactions, such as aggression or competition, are inhibited or less active during mating and this phenomenon allows the animals to focus on mating and reproductive activities without the interference that might hinder successful mating (Mohanty et al. 2014). Molecular studies have confirmed the functional role of 5-HT neurotransmission in regulating prosocial behaviours in *Octopus bimaculoides* is evolutionarily conserved (Edsinger & Dölen 2018;

Bacqué-Cazenave et al. 2020). Edsinger and Dölen (2018) findings revealed that exposure to (+/-)-3,4-methylenedioxymethamphetamine (MDMA) resulted in enhanced prosocial behaviour in octopuses, manifested by increased time spent in social contexts compared to other places. The inhibition of neural mechanisms associated with promoting social interactions during mating suggests a dynamic interplay between neural pathways governing social behaviours and those involved in other aspects of behaviour, potentially including learning and memory processes. Furthermore, the genome sequencing of the serotonin transporter gene revealed similarities between octopuses and humans. MDMA administration was also linked to heightened social interaction time and qualitative behaviour. These findings shed light on the molecular underpinnings of learning behaviour.

To recap, the cellular properties of cephalopod VL in learning and memory systems appear to align with those of vertebrates and insects. Molecular mechanisms that mediate neuromodulation and synaptic plasticity in the VL are highly conserved and extensively adapted across the cephalopod species (Shomrat et al. 2011, 2015). The connectivity networks in cephalopods appear to have evolved to facilitate various learning and memory processes that are specific to their unique lifestyles. From an evolutionary perspective on the organisation properties of circuitry involved in learning and memory, cephalopods may have converged with insects and vertebrates, despite potential intra-phyletic differences (Chung et al. 2022).

3.5 Which physiological properties in cephalopods contribute to their body patterning?

3.5.1 Brain and Central Nervous System

Cephalopods have similar body plans namely, highly evolved large brains with different lobes linked by neural connectives and tracts with the lobes in the ventral area of the brain separated partially from those in the dorsal area by the oesophagus (Williamson & Chrachri 2004). Figure 3 depicts the anatomy of the octopus's brain: Visual stimuli received from the environment enter a visual system that works concurrently with the central nervous system (CNS) in a hierarchical fashion with the highest level of control in processing visual information from the optic lobes (OLs)(William & Chrachri 2004; Hanlon & Messenger 2018). OLs send signals to peduncle lobes, then project to the lateral basal lobes of the brain which in turn project to the anterior and posterior chromatophore lobes where the majority of the chromatophore neurons are found. The additional tracts and interconnections proceed to other brain regions and back to the OLs and the peduncle lobes (PLs). In turn, these pathways evoke localised skin colour changes and partial patterns. Figure 4 depicts the concept underlying the chromatophore control mechanism to

clarify the connection between the major lobes in the CNS, and the pathway of the chromatophore system by William & Chrachri (2004) and Dubas et al. (1986).
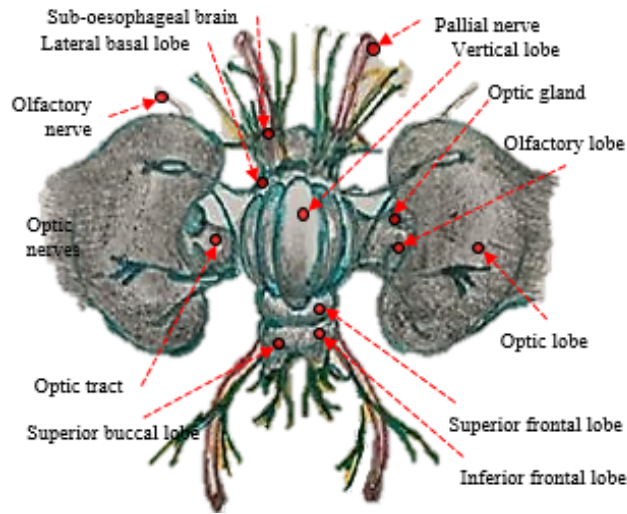

Figure 3 The structure of Octopus vulgaris central nervous system in the brain (adapted from Hanlon & Messenger, 2018).
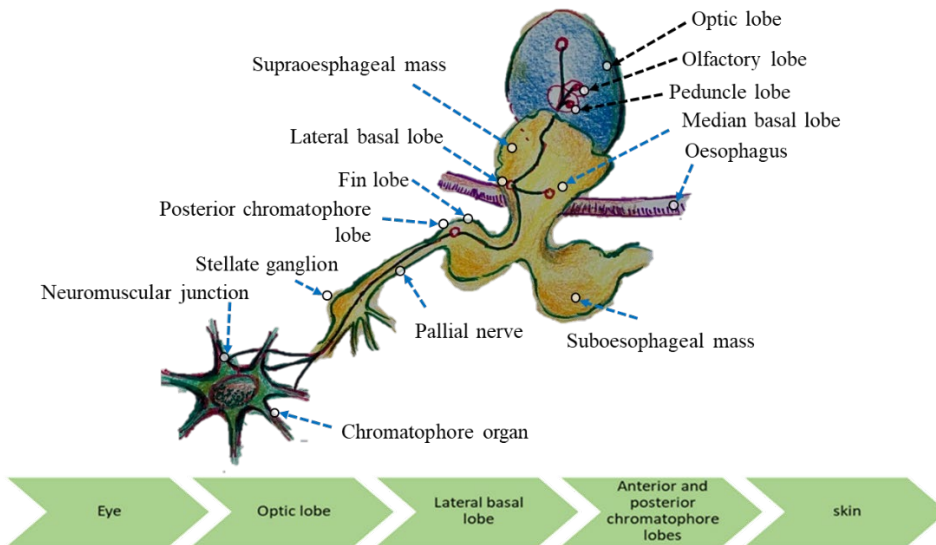

Figure 4 A simple illustration underlying the chromatophore control mechanism (adapted from Dubas et al. 1986).

OLs serve as a visual analyser, motor centre, and visual memory (Hanlon & Messenger 2018). This organisation is similar across cephalopods. The OL is equated with the vertebrate tectum or superior colliculus (Shigeno et al. 2018; See Table 1; Figure 4)—Vertebrate tectum receives inputs from retinal ganglion cells which already processes the spatial visual world before any tectal processing (Isa et al. 2021). Williamson and Chrachri (2004) suggest that the OL consists of an outer cortex comparable to the ganglionic layer of the vertebrate retina for visual processing and input classification, and a central medulla for visuomotor functions

and memory. The retina's photoreceptors interact like basal processes and form 'on-off' receptive fields, terminating mainly in the outer cortex. These receptors synaptically interact with amacrine neurons (AM) in the inner granule cell layer, which in turn are organised in specific planes to extract visual information orientation. Secondary-order visual neurons receive inputs from the AM, and lateral interactions might occur in the medulla. Discriminating visual image takes place in the cortex of the OLs where the photoreceptor cells synapse with second-order neurons (Williamson & Chrachri 2004). Chung et al.'s (2022) analyses of the size and anatomy of four different octopuses relative to total CNS volumes revealed that their OL range between 60% to 80% substantially larger than the coastal species.

The PL is a candidate analogy for the cerebellum as there are traces of parallel fibres originating from the spine cells in the neuropil of the lobe that looked like the granule cells and serial synaptic relays in the vertebrate cerebellar (Shigeno et al. 2018; See Table 1; Figure 3). Evidence of the organisation of the chromatophore control system has led researchers to construct a hierarchical system comprising the chromatophore lobes, with the chromatophore motoneurons underpinning the lowest level (Figure 4). These motoneurons receive inputs from the lateral basal lobes, in which signals come from the OL at the highest level or the PL. The visual, statocyst, and proprioceptive information converge in the peduncle and basal lobes (Hanlon & Messenger 2018). The statocyst plays a role in eye muscle control for equilibrium, visual stabilisation, oculomotor control systems, and maintaining countershading and keeping the ventral surface pale and dorsal surface dark (Gleadall & Shashar 2004; Marini et al. 2017).

The vertical lobe (VL) is represented by 14% of the volume of the supra-oesophageal mass (octopus) with over 25 million nerve cells, making the VL system the largest learning and memory centre in cephalopods and invertebrate neural structures (Shomrat et al. 2011; Shomrat et al. 2015; Marini et al. 2017; Shigeno et al. 2018). Octopuses have multiple gyrifications with functions comparable to vertebrates (Shomrat et al. 2008). Chung et al.'s (2022) findings revealed that contrary to some social cuttlefish and squid that have lissencephalic vertical lobes, octopus' multi-gyri VLs notably, *Vampyroteuthis infernalis* (an ancestral form), mesopelagic octopus *Japetella diaphana* (3-gyrus), coastal octopuses (5-gyrus) and their examined species (7-gyrus), suggesting more gyri is associated with adaptation to their ecological environment. Although cephalopods lack neural structure (just like the mammalian cortex or thalamus), some structures execute functions analogous to the thalamus namely, the suboesophageal mass that functions like a relay centre (Shigeno et al. 2018; Ponte et al. 2022). Furthermore, Shigeno et al. (2018) consider the giant fibre system of squid *Doryteuthis pleii*, the magnocellular lobe of cuttlefish and octopus have similar functions as those of Mauthner cells found in teleost fish, agnathans, and some amphibians. They account for escape behaviour and rapid change in directionality.

Octopuses are found to possess a large and complex CNS, consisting of six functional regions namely, VLs, OLs, inferior frontal lobes, PLs, supra-oesophageal mass, and suboesophageal mass with body movements and locomotor activity mediated by the hierarchical organisation of muscle control, which in turn mitigates the CNS processing the controlling of their appendages (Chung et al. 2022). Shigeno et al. (2018) suggest that there are striking similarities between cephalopod and vertebrate brains concerning both function and organisation (Table 1). In particular, OLs are comparable to the vertebrate tectum, VLs to the vertebrate cerebral cortex (palium), and PLs to the vertebrate cerebellum. This organisation may be linked to a theory suggesting that the brain inhibits the peripheral nervous system through a gating mechanism (Zullo & Hochner 2011). The human CNS consists of the brain and the spinal cord, while the peripheral nervous system (PNS) comprises nerves (axons and glial cells) and ganglia (clusters of nerve cell bodies) (Gazzaniga et al. 2019). The CNS acts as a centre for command and control while PNS transmits signals from sensory inputs and in turn executes the motor command from the CNS (Gazzaniga et al. 2019). Recent studies have revealed intriguing findings in cephalopods (Sakaue et al. 2014; Bellier et al. 2017, See Shigeno et al. 2018):

- Two types of cholinergic nerves have been identified—acetylcholine synthetic enzyme choline acetyltransferase (ChAT) has cChAT-positive fibres from the brain ganglia possibly relate to brain efferents, and pChAT-positive nerves intrinsic to the arm and possibly relate to the sensory system.
- Two types of serotonin-like innervation were found in the arm: one from the brain innervating the periphery via the cerebro-brachial tract and another found in the axial nerve cord at the cellular layer.

In sum, cephalopods such as octopuses, possess complex nervous systems with evolved large brains consisting of different lobes connected by neural pathways. While the human CNS and PNS serve distinct functions, recent indications have suggested different systems might be in place for cephalopods' appendages and the underlying mechanisms associated with the chromatophore systems.

3.5.2 Chromatophore and reflecting cells systems

The ability of cephalopods to rapidly change their body pattern in milliseconds to match their environment is facilitated by the synchronised regulation of chromatophores in the skin (Williamson and Chrachri 2004; Hanlon & Messenger 2018). This regulation is centrally controlled by the stellate ganglion and chromatophore lobes, which are regulated by motor neurons (Williamson and Chrachri 2004). The physical texture of the skin can be altered by the dermal muscle, allowing for instant transitions from rugose to smooth or highly papillate (Messenger 2001). One hypothesis suggests that the myogenic control, induced by muscular units outside central control, leads to the expansion of individual

chromatophore sacs (Messenger 2001). However, How et al. (2017) support the findings of Laan et al. (2014), proposing that oscillatory neurons are responsible for passing wave patterns (See Rosen & Gilly 2017). Dubas et al. (1986) found no evidence for direct inhibitory innervation of the chromatophore muscles in the squid, *Lolliguncula brevis*, suggesting that muscle fibres are innervated by excitatory motor fibres only. However, Williamson and Chrachri (2004) do not rule out the possibility of the presence of interneurons, which may render chromatophores unresponsive to electric stimulations.

Chromatophores, found in the outermost layer of skin, consist of pigment cell that displays red, brown, or yellow colours and is surrounded by neuronal, sheath, and glial cells (Hanlon & Messenger 2018; Guidetti et al. 2021). Unlike other animals, cephalopod chromatophores are neuromuscular organs under direct neural control, not hormones (Dubas et al. 1986; Messenger 2001; Mäthger et al. 2009a; Hanlon & Messenger, 2018). Chromatophores possess pigment-containing sacs surrounded by radial muscles allowing for the rapid expansion and retraction of the cells, leading to changes in skin pattern, texture, and colour (See Figure 5).
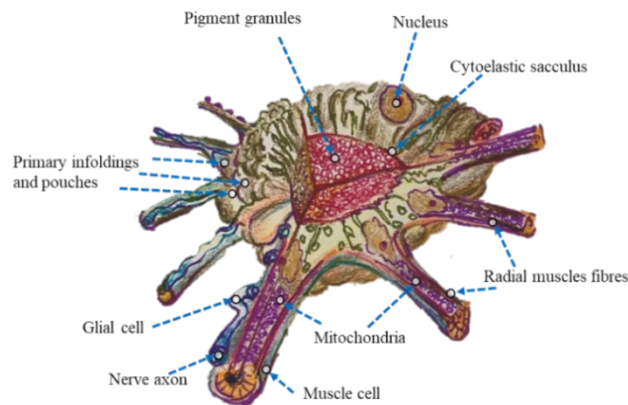

Figure 3 Schematic view of chromatophore organ (adapted from Cloney & Florey, 1968 in Hanlon & Messenger 2018).

Other components of the colour system include iridophores, leucophores, and photophores (Kelley & Davies 2016; Hanlon & Messenger 2018; Ikeda 2021; Guidetti et al. 2021). Iridophores produce iridescence and silvery colours, whilst leucophores function as diffusers of light (Mäthger et al. 2009b; Mäthger et al. 2013; Ikeda 2021). In squid *Doryteuthis pealeii,* gradational colour change in iridophores could be activated via neuronal control involving acetylcholine (Ikeda 2021). The patterns in the skin and body are further supported by muscle elements called papillae which form textural units (Mather & Alupay 2016). Photophores are luminescent organs that enable the control and production of light visible in species found in shallow waters (e.g. Japanese bobtail squid *Euprymna morsel*) and deep-sea waters (e.g., firefly squid *Watasenia scintillant*) (Ikeda 2021).

Rosen and Gilly (2017) compared the chromatophore activity of squid *Dosidicus gigas and Doryteuthis opalescens* and found notable differences in

innervation patterns and connectivity. They suggest that these wave-like activities are myogenic, originating from within the muscles. Additionally, 5-HT was found to inhibit electrically stimulated responses and spontaneous chromatophore waves, with variations in inhibition observed in denervated *Doryteuthis opalescens* compared to intact individuals (Rosen & Gilly 2017). The colouration system in cephalopods is mediated by a combination of pigmented chromatophores and structural reflecting cells (Williams et al. 2019; Cai et al. 2019; Guidetti et al. 2021). This system generates colour through pigmentation, chromatophores, and interference with visible light by leucophores and iridophores. Multispectral analysis and mapping of *Octopus bimaculoides* skin support the notion that colour is produced through the interplay of these chromatic elements (Mäthger & Hanlon 2007; Mäthger et al. 2009b; Mäthger et al. 2012; Williams et al. 2019; Guidetti et al. 2021). Vertical arrangement of chromatophores and iridophores in squid leads to a spectral shift and broadening of the reflectance signal (Mäthger & Hanlon 2007; Williams et al. 2019). The blue iridescence observed in the blue-ringed octopus, *Hapalochlaena lunulate*, and *Octopus bimaculatus* is attributed to multilayer constructive interference involving densely packed reflective plates with specific thicknesses (Mäthger et al. 2009b).

Kingston et al. (2015) found evidence of opsin transcripts including rhodopsin, retinochrome, G_{qx}-proteins, and squid transient receptor potential transcripts in the retinas and skin of Squid *Doryteuthis pealeii*. Different levels of rhodopsin gene transcripts were observed in cuttlefish *Sepia officinalis* and *Sepia latimanus*. Manipulating these components affected pigment dispersion, indicating their role in controlling colour change. These photosensitive components reflect different colours of light and are found in radial muscle fibres, sheath cells of chromatophore organs, and folded membranes. They also support extraocular photoreceptors and phototransduction in the retina, potentially duplicating the functions of retinal photoreceptors. Reflectin gene, uniquely cephalopods and hierarchically organised, can self-assemble into higher-order structures and is sensitive to environmental conditions such as pH and temperature which can induce reversible changes in the protein structure and optical properties (Guan et al. 2017).

From an evolutionary perspective, Guan et al. (2017) revealed that the origin of the reflectin gene can be traced to a 24-bp transposon-like DNA fragment from the bacterium *Vibrio fischeri* symbiotic with marine animals or vice versa from ancient cephalopod to *Vibrio fischeri*. Reflectin's self-assembly is triggered by aromatic interactions, and acetylcholine (ACh) modulates the reflection platelet properties through protein kinase-mediated phosphorylation, affecting hierarchical assembly and altering reflectin spacing and thickness, thereby influencing light properties. The authors employed spectral scanning and nuclear magnetic resonance to observe and analyse colour differences. In line with early studies that suggested reflectin has multifaceted features *in vivo* and *in vitro* and is expressed exclusively in

cephalopods and that structural colours are mediated by multilayer interference interacting with incident light at the cellular and protein levels (Crookes et al. 2004).

Cephalopods that have fewer and larger chromatophores have simpler and bolder body patterns, in contrast, those with densely packed and small chromatophores have more subtle and refined body patterns e.g. *Sepia spp.* *Octopus spp.* (Messenger 2001). *Octopus vulgaris*' chromatophore density is approximately 230 per mm^2 compared to those of cuttlefish, *Sepia officinalis* (50 per mm^2) or squid, *Doryteuthis Pleii*)(8 per mm^2), and the more complex patterning repertoires, the higher densities of chromatophores (Packard & Sanders 1969 cited in Hanlon & Messenger 2018). Hanlon and Messenger (2018) suggest that the skin of octopus (and cuttlefish) has a more complex combination of pigment and structural colouration because there is a layer of leucophores underneath the iridophores in addition to interactions between chromatophores and iridophores. As the body pattern is made up of all the chromatic, postural, textural, and locomotor components (Hanlon & Messenger 2018), the exact arrangement of elements can appear different in different cephalopods. For instance, squid generally has iridophores but no reflecting leucophores as found in octopus and cuttlefish, making it simpler skin elements and body patterning (Mäthger et al. 2009b). The pattern arrangement of iridophores and chromatophores in *Doryteuthis pealeii* is more abundant while the majority of iridophores are observed externally adjacent to lightly pigmented chromatophores (Guidetti et al. 2021). Relative to the Loliginid squid and octopuses which developed only very few chromatophores at hatching, *Sepia officinalis* already developed the adult body patterns repertoire at hatching (O'Brien et al. 2017).

3.5.3 Visual-Skin integration

Cephalopods possess eyes with primary structures similar to vertebrates (Hanke & Kelber 2020; Ogura et al. 2004; See Figure 6), except for the following.
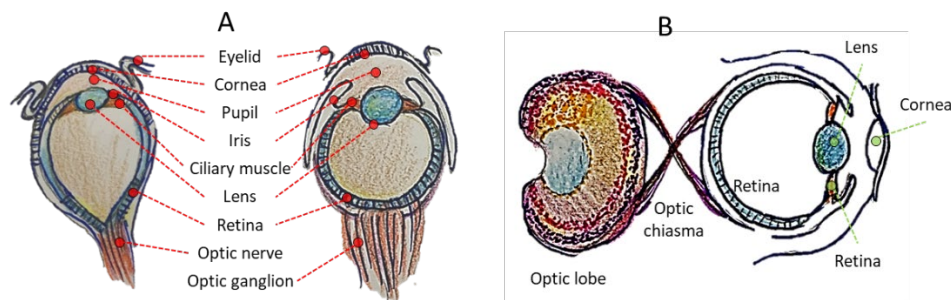

Figure 4 Structural comparisons between human (left) and octopus (right) eyes (A, adapted from Ogura et al. 2004); Schematic view of octopus' visual system (B, adapted from Yoshida et al. 2015).

Most cephalopods exhibit quick pupil constriction in response to light with exposure of t_{50} values ranging from 0.3 to 3 s (Hanke & Kelber 2020). *Nautilus*

pompilius takes 90 s and the deep-sea octopus, *Japetella diaphana* have slower constriction times (Hanke & Kelber 2020). Differences in eye structure are likely responsible for these variations, with nautilus having pinhole eyes and simpler OLs contrary to octopuses and squids (Yoshida et al. 2015). Pupil dilation is more variable and externally influenced possibly serving functions such as camouflage to merge with the substrate, dilate to signal, or communicate to threaten others, which can occur laterally with only one eye (Hanke & Kelber 2020). In terms of size, most evidence is derived from the nocturnal European *Octopus vulgaris* with eyes positioned laterally on the head with about 20 mm in diameter for a 250 g size except for *Architeuthis* and *Mesonychoteuthis*, the giant squid and colossal squid measured around 270 mm (Hanlon & Messenger 2018). Cephalopod eyes differ in certain aspects, like having rhabdomeric photoreceptors that do not result in a blind spot and monochromatic vision because there are only rod-like photoreceptors sensitive to a restricted range of wavelengths. Polarised vision and visual information are speculated to be processed in the OLs via photoreceptors which are connected to other brain areas via optic tracts (Williamson & Chrachri 2004). In vertebrates, visual information is processed in the inner retina before being transmitted to the brain via the optic nerve (Morshedian & Fain 2017; See Figure 6). In contrast, cephalopods have everted retinae, where photoreceptors project directly to the OLs for visual processing (Hanke & Kelber 2020). The OLs and eyes of octopuses and squids are connected by a chiasm (Yoshida et al. 2015).

Cephalopods are considered colourblind due to having only one visual pigment in their retinas, unlike humans with three photoreceptors for colour perception (Messenger 2001; Hanlon & Messenger 2018). Contrary to Kawamura et al. (2001) findings that octopus *Amphioctopus Kagoshimensis* could discriminate colour, earlier studies suggest that the retinas of most cephalopods cannot discriminate wavelength, supporting the hypothesis of colour blindness (Hanlon & Messenger 2018). There is evidence to suggest that cephalopod have polarised vision in detecting silvery fish, and transparent organisms, and avoiding predators within a short distance (Mäthger et al. 2009b; Hanlon & Messenger 2018; Nahmad-Rohen and Vorobyev 2020). Mäthger et al. (2006) showed that cuttlefish changes its body pattern and elicits Disruptive patterns when there is sufficient contrast of colours on the background but the same does not occur when the animal is placed on a yellow-blue chequerboard. The similarity in their body and colour in the three different colour conditions implies that the cuttlefish perceives the background as identical. Experiments with cuttlefish *Sepia officinalis* could achieve camouflage using a form of luminance by matching the brightness and contrast of their body patterns to the background rather than relying on colour information (Marshall & Messenger 1996; Chiao et al. 2015). The evidence suggests that cephalopods achieve camouflage through visual perception rather than colouration.

Octopuses lack blind spots, possibly because their retinal axons transmit information by travelling over and behind the retina to reach the optic nerve (Mather

& Dickel 2017). The pupil structure of octopuses is unique and characterised by several features. According to Hanke & Kelber (2020), one feature is the presence of an iris that forms a lobe, which contributes to the unique shape of the pupil. Within the iris structure, there are different cell layers, including the chromatophore and iridocyte layer which are involved in controlling the pigmentation and colouration of the iris. What sets octopuses apart from vertebrates is their mechanism for focussing their vision. While vertebrates adjust the shape of their lens to achieve focus, octopuses achieve focus by moving their lens. This allows them to rapidly adjust their focus to respond quickly to changes in their visual environment. Furthermore, octopuses exhibit myopia at rest, but their moveable lens enables them to maintain sharp vision and track objects while in motion (Hanke & Kelber 2020). Stubbs and Stubbs (2016) conducted a numerical simulation and suggested that cephalopods could perceive the spectral composition of objects on non-flat backgrounds through a mechanism involving chromatic aberration and pupil shape. Their findings revealed that when stimuli have different chromatic aberration coupled with elongated pupil shapes, chromatic blurring is formed on the retina. This chromatic blurring provides an additional visual cue to use alongside other sensory information, to enable perceiving colour variations.

Cephalopods show variations in visual acuity and different degrees of binocularity (Messenger 2001). Octopus lacks rods and cones and colour vision and absorbs at shorter wavelengths 470-475 nm (Hanlon & Messenger 2018; Hanke & Kelber 2020; Guidetti et al. 2021). For instance, cuttlefish's visually driven camouflage is associated with their large eyes which offer $360°$ of the substrates (Mäthger et al. 2013). They perceive shapes from shading alone and use pictorial depth cues to improve accuracy (Zylinski et al. 2016). Zylinski et al. (2016) showed that cuttlefish use shading as a cue for 3-dimensional form and adjust their skin colouration to match shading and illumination conditions. They rely on multiple visual cues, such as edge fragments and texture-defined features, to infer the background and resemble 3-dimensional objects. Further suggest that cuttlefish employ depth perception, including stereopsis and motion parallax, along with pictorial depth cues to recognise contours, sense texture gradients, and enhance disruptive patterns.

The differences in vision bias can be attributed to their early developmental stages according to O'Brien et al. (2017). O'Brien et al. (2017) suggest that polarisation sensitivity and contrast vision improve with age in *Sepia officinalis*, which occurs around 7 days post-hatching, and much like squid, they can visually detect prey and quickly attack when the prey reflects polarised light rather than luminescence. Around stages 20-21 of the organogenesis stage, the OL and lens of the cuttlefish embryo mature. In the final stages of development, cuttlefish egg absorbs seawater to increase the perivitelline fluid volume which causes it to expand its size twofold from its original size (O'Brien et al. 2017). The inner layers of the egg membrane of *Sepia officinalis* become thinner and translucent partially

as it is digested by the epidermis, while octopus eggs remain constant throughout (O'Brien et al. 2017). The size of *Octopus vulgaris* hatchlings (paralarvae) is between 1-2 mm and transparent and goes through a planktonic phase typically in pelagic (shallow) waters for weeks and months before settling on the sediment (Hanke & Kelber 2020). *Sepia officinalis* does not exhibit this behaviour, after hatching, they do not spend time as plankton like the octopuses. Rather, they are found in the sand, or attach motionlessly to an object or substrate with their ventral arms and mantle to stabilise their position (O'Brien et al. 2017).

Vision has important implications for camouflage, involving pupil dilation and screening pigment retraction to enhance visual perception. Octopuses exhibit visual adaptations specific to their light environment, with some retaining their eyes for task-specific reasons (Chung et al. 2022), which in turn influence their behaviour (Hanlon & Messenger 2018). For instance, bioluminescent light is prevalent in the mesopelagic habitat (NOAA, 2023; Wagner et al. 2009), which serves various functions including camouflage, mimicry, communication, and defence (Widder 2010). The firefly squid *Watasenia scintillans*, a bioluminescent species has multiple pigments which may have enabled it to dissociate between downwelling lights and light produced by a conspecific (Matsui et al. 1988; Ikeda 2021). Chung et al. (2022) show that *Vampyroteuthis infernalis* has bioluminescent organs and extremely large eyes for tasks that require bioluminescence, improved lens, elongated and large diameter photoreceptors, minimal screening pigment granules, and no corneal membrane. They suggest that these show an adaptation to increase sensitivity to detect bioluminescence from a long distance while monitoring for prey and mate.

However, limited behavioural data exists for *Vampyroteuthis infernalis* but Chung et al. (2022) suggest their unique specialisation is likely related to having sub-oesophageal mass that resembles a squid-like structure that is elongated and positioned similarly, and the supra-oesophageal mass that resembles an octopus-like structure consists of a subdivided frontal lobe system and a superior buccal lobe located near the anterior region. Deep-sea cephalopods and nocturnal species e.g., the Australian *Sepia apama* demonstrate camouflage adaptation to its environment during moonless nights fitting in with the surrounding substrates (Hanlon et al. 2007). *Sepia officinalis* adapt their camouflage patterns in response to the visual environment even in dim light conditions, suggesting the perceptual capability to alter camouflage patterns at light levels of .003 lux photopic units i.e., reaching the starlight level (Allen et al. 2010). This adaptive camouflage provides a deceptive advantage in hunting and avoiding predators. Dana squid, *Taningia danae* have large occludable photophores on the tip of the dorsolateral pair of arms that flash brief blue-green bioluminescence light in a synchronised manner before an attack or escape (How et al. 2017). Similar flashing pattern, using arm-tip photophores were observed in deep-sea squid *Octopoteuthis deletron*. Additionally, *Vampyroteuthis infernalis*, and *Stauroteuthis syrtensis* emitted light lures with

asynchronous blinking (0.5-1 Hz) from small bioluminescent photophores on the underside of their eight arms to trap the planktonic crustacean prey.

Read together, these studies suggest a link between biochemical markers associated with phototransduction and chromatophore activity that contributes to the rapid change of body patterning (Deravi 2021). It is noteworthy that although both *Octopus vulgaris* and *Octopus bimaculoides* belong to the same genus, the two species go through different life cycles given that there is no paralarval stage in the latter species, suggesting two species represent "different biological and physiological adaptations" (Sweeney et al. 1992; Zarrella et al. 2019, p. 2).

Discussion

4.1 Which cognitive processes are associated with changes in body patterns in cephalopods?

The results presented in 3.1 elucidate that cephalopods' body patterns are multifunctional and context-dependent, reflecting their cognitive processes and interactions with the environment and conspecifics. Essentially, cephalopods employ a diverse array of sexual and foraging strategies, encompassing activities such as searching, handling, and processing food. These strategies are adapted to their ecological niches and survival requirements. Interactions amongst conspecifics, whether for food, territory, or mates, exhibit a spectrum of aggressiveness, manifesting through behaviours that include body displays, vocalisations, and physical contact. Nevertheless, there are various matters necessitating resolution. Firstly, from cephalopod literature, one may argue that the attainment of a unanimous interpretation concerning the implications of body pattern manifestations and their concomitant cognitive depictions seems to pose a formidable task. To discern whether an organism is engaging in background adaptation, assuming the guise of a distinct organism, or employing singular versus multiple strategies appears to be a notably intricate challenge. This is exemplified in a field recording provided by How et al. (2017). Upon examination of the recording that documented the body exhibition of the Broadclub cuttlefish *Sepia latimanus*, my interpretation diverges from that of the authors, who construed it as an adaptation to a context of prey. As the cuttlefish approached the camera head-on, it displayed conspicuous Passing Cloud patterns, with the beak and arms tucked in and both ventral arms splayed outwards. As the distance decreased, the wave signals and passing intensified, spreading rapidly from the head to the arms and across the body. The animal's appendages extended and thrust forward into the shape of a cone while the chromatophores intensified with a sudden contraction of the muscles, the spots intensified, expanded, and changed from whitish to yellow and brown. The eyes changed shape, the arms curled backward into a web, revealing the inner underside resembling a siphon, and speedily swam away from

the camera. In seconds, the animal transformed its shape and colours, possibly mimicking the surrounding environment. The authors omitted an examination of the accompanying audible vocalisation during the morphing process, in my view a crucial contextual aspect particularly when distinct from sounds originating from the oxygen tank or diver. Rather than deception, one may argue that the transition from primary defence (e.g., threat or fear) to secondary defence through warning colouration and signals is also a plausible theory.

Secondly, several studies (Nakajima et al. 2022; Hanlon & McManus 2020; How et al. 2017; Sato et al. 2016; Brown et al. 2012; Norman et al. 2001) have demonstrated remarkable and sophisticated behaviour in cephalopods, including the use of body patterns to deceive predators, prey, and conspecific. For instance, How et al. (2017) examined the Passing Cloud behaviour within a specific context and deemed it a form of deception namely, to deceive prey animals to move rather than convey a message. This does not align with Packard and Sanders's (1969) conjecture cited in Mather and Mather (2004) that the Passing Clouds observed in *Octopus vulgaris* appear to communicate 'Move, you other animals!'. How et al.'s (2017) footage recordings of *Octopus laqueus* align with Packard and Sanders' (1969) description, albeit the authors opt to term it 'chromatic pulse' over Passing Cloud without specifying the functional mechanism. Despite the variations such as *Octopus cyanea*'s inconsistent engagement during camouflage, with rates falling below 31% (Hanlon & Messenger 2018), the nocturnal *Octopus laqueus* prevalent in tropical ecosystems displays Passing Clouds while foraging. How et al. (2017) have suggested that these patterns might serve as warning signals, contribute to motion camouflage, or even facilitate prey flushing. From my perspective, it becomes increasingly clear that delineating cephalopod behavioural strategies into distinct categories such as antipredatory, signalling, or agonistic are challenging and to a significant extent, an apprehensive endeavour. Further necessitates a critical analysis to delve into the nuanced advantages and trade-offs associated with camouflage during foraging activities.

Moreover, the intricate nature of cephalopod communication strategies is evident through various examples. Notably, the rapid transformation of *Octopus vulgaris* in 0.2 s in the presence of a diver predator in a sit-and-wait type of motionless behaviour (Hanlon 2007), could be interpreted as agonistic relative to the warning signal. Studies (Messenger 2001; Hanlon & Messenger 2018) suggested that cuttlefish (*Sepia officinalis*, *Sepia latimanus*) and squid (*Sepioteuthis lessoniana*) alter colouration, use arm swaying and body posturing to manipulate prey perception. They rely on visual manipulation to avoid detection, while octopuses shape their soft and flexible bodies to achieve Disruptive patterns to hinder predator recognition. *Octopus cyanea* exhibited various forms of masquerades such as resembling a moving rock or algae, adapting to the dappled sunlight from the waves to masquerade as inedible objects (Hanlon 2007; Hanlon

& Messenger 2018) or *Thaumoctopus mimicus* mimic dangerous species as their arms were drawn close into a leaf-shaped wedge (flatfish mimicry) moving with jet propulsion; upon attacks by damselfishes *Amphiprion spp*, transformed into sea-snake appearance to deceive others as dangerous (Norman et al. 2001; Hanlon et al. 2010; Hanlon et al. 2011). Additionally, the Mottle Display and dark blush, as well as Passing Clouds exhibited by male cuttlefish during encounters with larger mate-guarding males are indicative of combative or aggressive signalling and territorial rivalry. Recently revealed LPSO's body patterns during repeated mating, food, and den sharing including Passing Clouds, is interpreted as interspecific communication signalling rather than common behavioural pattern reported in previous studies (Caldwell et al. 2015). All suggest multifaceted behavioural strategies, indicating communication signalling at various cognitive processing levels.

Concerning a specific type of behaviour i.e., multidirectional passing wave displays observed in the Flamboyant cuttlefish, *Metasepia pfefferi,* and the *Paintpot* cuttlefish, *Metasepia tullbergi* while stalking small fishes and crustaceans – How et al. (2017) suggested that these displays involved rapid changing their body patterns to create high contrast patterns of white, yellow, red, and dark brown, in which the patterns resembled those of the Caribbean two-spot octopus *Octopus hummelincki* and the Caribbean reef *Octopus briareus*. Earlier studies of algae octopuses suggested that they display versatile and adaptable mating tactics aimed at enhancing their chances of success in aggressive encounters (Huffard et al. 2010). This aligns with the tertiary contention that, whilst not overtly articulated within the discourse of How et al. (2017), there exists a plausible basis for asserting that these behaviours could encompass elements of learning, memory, and complex sensory processing as these are essential processes to allow adaptation to their environment, remember their past experiences, and modify their behaviours accordingly. In particular, Hough et al.'s (2016) findings are indicative of acquired learning in cuttlefish, thereby implying that the innate nature of their body patterning ability is subject to adaptation through learned experiences. Critically, this may appear contradictory to the notion of body patterning as hard-wired, which is shown by cuttlefish embryos where sensory information shaped their development, enhancing their perception and interpretation of their surroundings, and in hatchlings that possessed all the body patterning repertoires observed in adulthood (O'Brien et al. 2017; Romagny et al. 2012). These embryonic studies demonstrated the presence of mature body pattern repertoires in hatchlings, and that cuttlefish embryos could already increase their ability to perceive information from their environment as they are progressively shaped by the sensory information in the organogenesis stages. It is plausible that some learning took place in Hough et al. (2016), further indicative of greater flexibility inherent in the behavioural responses. However, the studies did not rule out the possibility of sensitisation. Additionally, cephalopods exhibit species-specific body patterns. In my view, the colour and pattern changes observed in response to specific stimuli, like the

anticipation of a food reward, were not consistently maintained over time. This implies that these changes may not be solely driven by direct communication between the individuals, but rather influenced by factors beyond communication, such as environmental context, internal state, or other variables. In essence, the observed variations in colour and pattern changes indicate that these changes might not always convey a consistent and specific form of communication amongst cephalopods. As the experiment has not been replicated nor has it been conducted in octopuses or squids, we should be cautious in interpreting such findings.

Fourthly, given cephalopod's inherent flexibility as expounded in Hough et al. (2016); Nakajima et al. (2022) are aligned with studies (Amodio & Fiorito 2013; Amodio et al. 2019) that have linked the cognitive abilities of cephalopods to their flexible behaviour to emphasise the complexity of their cognitive processing. Some researchers argue that although phenotypic mismatches can occur, *Thaumoctopus mimicus* relies on specialised chromatophores for rapid and reverse changes to mimic the behaviours of others are considered high-level cognitive processing (Hanlon et al. 2007; Hanlon et al. 2010; Tan & Elgar 2021; Postema et al. 2023). However, a notable challenge arises in perceiving cognitive processing as intricate and indicative of high-level function, a perspective problematised by the insights put forth by Blumberg and Wasserman (1995). They highlighted a significant instance in the studies by Griffin (1984) wherein the portrayal of the behaviour of a camouflaged assassin bug to lure and capture its prey as a complex and adaptive manifestation indicative of intentional thinking, was critiqued as being premature and lacking empirical evidence as well as consideration for alternative explanations. This observation underscores the importance of considering the underlying stimuli that might contribute to the exhibited behaviours. Furthermore, it warrants attention to the selective emphasis on the complexity of behaviour and raises enquiries into the impartiality of such an analytical approach.

In my perspective, most cephalopod species in nature are mobile and interact with dynamic environments with movements as complex to serve multiple functions. These movements can also impact the ability of receivers to detect and interpret signals, with varying degrees of movement potentially altering the quality of information conveyed. One perspective is colour defences albeit an effective strategy may entail associated costs. This is accentuated by Lind et al. (2022) that remembering the specific stimuli and events for making efficient and accurate decisions could potentially be demanding considering the aspects of memory storage and learning time. They emphasised the complexity of efficient decision-making involving readily accessible information as recalling every single experience can be computationally demanding. The ability to remember sequences of events is beneficial if the information conveyed is genuinely informative. This implies that natural selection favours memory systems that strike a balance between the costs and benefits associated with remembering information. Additionally, hypotheses concerning the evolutionary trajectory of the memory system should be

in place to incorporate an assessment of the potential learning costs linked to memory formation – an area of knowledge that currently remains relatively constrained in cephalopod literature.

Fifthly, studies have shown that cuttlefish and octopuses have exhibited camouflaging abilities enabling them to match backgrounds and adapt to substrate variations during movement (Josef et al. 2012; Josef et al. 2015; Skelhorn & Rowe 2016; Mather & Dickel 2017; Hanlon and McManus 2020; Nakajima et al. 2022). This finds support in earlier studies, indicating the association between body patterning and cognitive capacities. For instance, *Sepia officinalis* employ diverse defensive responses based on predator types, including flight responses when encountering cruising predators and cryptic body patterning with dark Mottle patterns to match substrates against ambush predators (Staudinger et al. 2013). Laboratory studies on longfin squid *Doryteuthis pleii* have exhibited various tactics such as inking or fleeing in response to different predators (Staudinger et al. 2011). Although the results seem to contrast Hanlon and Messenger's (1988) field study where predator size relative to the animals yielded differing body patterning results, juvenile *Sepia officinalis* use false eyespot signals and selective responses based on the perceived level of threat from predators (Langridge et al. 2007). Furthermore, earlier cuttlefish studies suggested context-specific patterns during the motion to avoid high-contrast ones (Zylinski et al. 2009), indicating support for the argument that animals utilise both signals and cues for communication. This aligns with Tan and Elgar's (2021) analyses of visual signals and cues in which they proposed that motion is a conduit for conveying signaller information, capturing attention, and revealing attributes. On one hand, the reliability of protection camouflage offers varies given the impact of motion camouflage involves speed, orientation, and consistency. On the other hand, the notion that animals use dynamic patterns to confuse predators (e.g., motion dazzle) which have not consistently yielded the intended results – one possible explanation could be due to a lack of knowledge concerning receiver perceptions. This has been shown in Mäthger et al. (2009b) in which defining a specific appearance as a visual signal that carries information and that is received by the opponent or intended receiver is challenging, especially when the sender is motionless or camouflaged. This entails the receiver's role and perspectives i.e., how moving animals' colour patterns and signals are perceived and comprehended, should be investigated.

Sixthly, Amodio and Fiorito's (2022) initial investigations into mirror self-recognition in *Octopus vulgaris* indicated a level of self-awareness discernable through observable responses and marked body appearances. Additionally, they suggested the presence of dominant-subordinate relationships within social groups. Although dominance-subordinate relationships or territoriality have been observed in laboratory studies amongst certain octopuses, Hanlon and Messenger (2018) suggested that the evidence for such behaviour in the wild is not apparent but associated with den defence rather than intraspecific aggression or territoriality. My

view is unlike certain squid species where shoaling seems to be a common behaviour beginning after hatching, the social and mating behaviours manifested in octopuses have emerged as a result of the process of natural selection. These behaviours are believed to be influenced by evolving environmental conditions and shifting social dynamics over time. Consequently, this raises questions regarding the previously documented asocial nature of octopuses (solitary creatures) and their learning abilities. Further prompts examination of their potential for social behaviours and the capacity for social learning. Essentially, octopuses might have developed these strategies in response to the challenges and changes they experienced in their environment and interactions with conspecifics. Not only that the association between den utilisation and dominance rank in the same species as previously shown by Cigliano (1993) should be investigated and clarified, but it is also important to consider the potential impact of laboratory adaptation and size disparities on social behaviour.

Finally, visual information is primarily processed in the OLs as explained in the results. For instance, the decision-making in cuttlefish is influenced by their visual guidance (Panetta et al. 2017) and cuttlefish may utilise visual cues such as shading to adjust body patterns for camouflage namely, possess the ability to derive shape and form information from visual cues (Zylinski et al. 2016). My perspective is these findings have potential implications for Marr's (1982) theoretical framework, which emphasises both biological and machine vision systems should operate on the same fundamental principles with a focus on the scene as whole and individual objects within the scene. These systems should rely heavily on bottom-up processing, with internal representations of visual information tailored to the specific visual environment in which they operate. However, it is unclear from the studies whether the process of interpreting visual cues like shading is based on low-level retinal input or higher-level cognitive and cortical processes. Furthermore, Zylinski et al. (2016) found that cuttlefish exhibit up to 37% lateral asymmetry in camouflage. However, it remains unclear how this asymmetry is perceived in the wild, particularly by fish or during predation. This study suggests that, like humans, cuttlefish utilise pictorial depth cues in visual images, but their response is not consistent with the illumination. This discrepancy may be attributed to environmental factors. Unlike humans who experience varying lighting conditions due to the sun's movement, underwater lighting geometry is different. As distance increases, pictorial relief loses directionality, and specular highlights may influence the response to visual cues. In this context, it is important to generate precise and contrasting hypotheses to ascertain whether cephalopods depend on distinct visual cues or alternative mechanisms to perceive object shapes and to explore the underlying reasons for the observed asymmetry. A step forward is to recognise the diversity of behaviour and strategies across different species and not generalise findings under a broad class of 'cephalopod'.

4.2 How fast can cephalopods change body patterning in response to stimuli in their environment?

The results presented in 3.2 elucidate the intricate mechanisms governing chromatophore function, the specific involvement of specific opsins, variations in the rates of expansion and retraction across various species, resulting in rapid and precise alterations in colouration, and their interrelation with processes of visual learning and memory. This thesis identifies several aspects related to the rapid alteration of body patterns that necessitate further investigation. First, questions remain concerning the opsin-expressing cells found in octopus hatchling skin. Specifically, the extent to which these cells function as mechanoreceptors, light sensors, or both, or the level needed for detecting these stimuli, warrants meticulous investigation. Notably, Ramirez and Oakley (2015) did not investigate whether these peripheral sensory neurons are functionally analogous. Similarly, the intricate connection between the light sensors, the chromatophores, and the CNS in the context of LACE methodology, necessitates elucidation. The hierarchical organisation of the chromatophores system within octopus' skin, both in its nascent (fresh) state and as it ages have been established in a manner that remains not contrasted with the equivalent systems within cuttlefish and squid. This underscores the urgency for comprehensive research into the kinetics of the system encompassing the temporal duration, velocity, and synchronicity of colouration alterations during the rapid transition (polyphenism), particularly when it concerns a cognitive task. Similarly, the optical attributes inherent to octopuses, which might parallel those observed in squid, remain enigmatic. Whether octopuses possess analogous optical functionalities, akin to the squid or cuttlefish capacity to activate and deactivate iridophores (passive or inert) just as what is uncovered in squid that can turn on and off their iridophores for a few seconds to minutes due to acetylcholine responding to muscarinic receptors as suggested by Mäthger et al. (2004), remains a point of uncertainty. Further systematic investigation is warranted in these directions to deepen our comprehension of the mechanisms governing cephalopod body patterning dynamics.

One may critique that while the attainment and distinction of the rates of cryptic patterns remain pending in terms of predator and prey visions, most substantiating evidence originates from studies involving nocturnal and asocial species (Hanlon and Messenger 2018) possessing 5-gyrus VLs (Chung et al. 2022) exemplified by *Octopus vulgaris* and *Octopus bimaculoides*. Consequently, it becomes imperative to undertake investigations to ascertain whether analogous outcomes would be observed in species characterised by 7-gyrus VLs or prosocial behaviours within the cephalopod domain. Furthermore, the existing body of knowledge regarding squid species remains limited, despite their distinct life histories and social behaviour – in light of the revelations put forth by Hadjisolomou et al. (2021) that the response rate exhibited minimal variability (remain constant) irrespective of the

strength of the stimulus, with a particularly noteworthy observation being the heightened reactivity of chromatophores situated on the cephalic region or appendages. Consequently, this observation raises the need for additional investigation, and caution should be exercised when interpreting these findings as they do not provide direct causal evidence for uniform programming in all cephalopods or suggest identical light sensitivities. Nonetheless, they enhance our understanding of the intricate nature of colour alteration in cephalopods.

4.3   Which cognitive mechanisms affect how cephalopods solve a task?

The results presented in 3.3 explore a perspective on cephalopod cognition, underscoring the intricate interplay between physiological responses, body patterns, cognitive processes, and environmental context. The intricate association between colouration expression and emotional disposition further underscores the multifaceted nature of cephalopod behaviours and cognitive modulation, elucidating a nuanced interrelationship between visual cues and cognitive responses. According to cephalopod studies, octopuses have shown extraordinary spatial navigation abilities and a diverse array of learning capacities, encompassing simple sensitisation, associative learning, and problem-solving. The expression of these abilities is species-specific and can vary amongst individuals. Certain behaviours indicative of these skills may be underpinned by cognitive attributes akin to those observed in vertebrates (Schnell & Clayton 2021). For instance, the ability to exert self-control through an associative process is an integral facet of learning and conditioned reinforcement (Lind 2018). This concept finds support in the work of Schnell et al. (2021a), where a demonstration of delayed gratification in a self-control task serves as an illustrative form of cognitive ability. Nevertheless, it is noteworthy considering that factors such as camouflage and the 'sit-and-wait' behavioural traits adopted by octopuses could conceivably exert influence on this particular ability (Schnell et al. 2021a; Hanlon et al. 2007). In their study, Schnell et al. (2021a) acknowledge certain limitations inherent in their experimental design, particularly concerning their omission of assessing the sustained inhibition of impulsive responses. In my view, despite these limitations, their findings underscore the presence of adaptable and flexible cognitive ability and implications for the understanding of cognition and self-control. This underscores the necessity for rigorous evaluation of behaviour's significance in animal cognition.

Schnell et al. (2021a) pointed out that the presence of a training phase could have potential limitations to associative learning as it could complicate the interpretation of results and the establishment of true associations between variables being measured in cephalopod studies. In my perspective, while recognising the complexities introduced by incorporating a training phase, the integration of such a

phase within experimental paradigms involving non-verbal organisms offers notable advantages. Given the divergent nature of cephalopod behavioural strategies across distinct species, establishing a baseline becomes essential to facilitate precise evaluations of their cognitive capabilities. Furthermore, the introduction of the tasks helps mitigate the impact of extraneous variables that could lead to fluctuations in performance metrics, thereby augmenting the quality of the signal-to-noise ratio inherent in the collected data.

Critiques may question the sufficiency of associative learning for acquiring complex behaviour such as tool use, self-control. However, Enquist et al.'s (2016) studies revealed that the act of waiting can be reinforced when associated with stimuli that have acquired conditioned reinforcement value. Their model simulation showed that a correct sequence of behaviours (waiting followed by taking action) is initially executed by chance, leading to the intermediate state acquiring the value of conditioned reinforcement. Consequently, the act of waiting becomes reinforced, and the inclination to immediately seize a smaller reward diminishes progressively over time. On the other hand, 'wait' behaviour could also be reinforced through a chaining process. Animals might fail to develop self-control if struggle to differentiate between situations or when the benefits of waiting are not experienced (Enquist et al. 2016). Interestingly, their chaining model suggested that animals could learn through associative learning to achieve optimal behaviour in a wide variety of ecologically relevant circumstances. Specifically, self-control, and forming expectations about future events could be learned, challenging the notion that animals are limited to react to present needs and stimuli. Nevertheless, it is important to note that cephalopods lack typical behaviours associated with habitual tool use, food caching, or sociality commonly observed in birds, corvid, or mammals (Poncet et al. 2022), consequently, these cannot be considered as driving forces behind their cognitive capacity.

Schnell et al. (2021b) suggested that older cuttlefish maintained their episodic-like memory, demonstrating intact recall of event details and utilising this information for decision-making. Poncet et al. (2022) replicated the study with octopuses and suggested individual variations in foraging strategies, with some employing less cognitively demanding approaches. Lind et al. (2022) suggested that animals exhibit inconsistent performance in general-purpose short-term memory tasks, specifically in accurately remembering and retrieving sequential information. Humans outperform other animals in sequence discrimination, indicating potential quantitative differences in cognitive abilities. Animals exhibit episodic-like memory tied to their past experiences and learning, which differs from human episodic memory. Human episodic memory possesses unique characteristics, such as the ability to mentally travel back in time and recall contextual details associated with past events (Tulving 2002). Lind et al. (2022) suggested that human episodic memory has two distinct features that are intractable in animals: First, it has a general purpose, allowing for the encoding of almost any episode without relying

on biologically significant stimuli; Second, it enables the recollection of contiguity occurrence rather than just single events. No evidence has firmly demonstrated that animals could precisely recall sequences of events, and their limitations in sequence memory, as well as in general-purpose short-term memory suggest that their episodic memory might not be as accurate as that of humans, but rather a form of specialised memory as suggested in Lind et al. (2022). This further infers that any episodic-like memory observed in cephalopods would be a specialised form of memory rather than a general-purpose episodic memory.

The criticism is that the presence of WWW components is elusive, let alone interpreting cephalopod behaviour solely based on human-like categories might lead to misleading conclusions, as cognitive processes might differ fundamentally. Our understanding of both cephalopods and human cognitive abilities is incomplete, which could limit the accuracy and generalisability of conclusions drawn from the comparison. Moreover, to directly compare cephalopods and humans oversimplify the complexities of cognitive abilities, given the vast differences in brain structure, sensory systems, and evolutionary backgrounds. Nonetheless, the evidence suggesting a similarity to episodic memory between cephalopods and humans challenges Macphail's claim of humans' cognitive superiority. One acknowledges the significant contributions stemming from the identification of episodic-like memories in cuttlefish, which in turn signifies their adoption of diverse foraging strategies, such as the more complex time-tracking method (Schnell et al. 2021b; Jozet-Alves et al. 2013) juxtaposed with the comparatively simpler foraging strategies in octopus (Poncet et al. 2022; Hanlon & Messenger 2018). In particular, Poncet et al. (2022) argued that time perception in octopuses differs from humans, as humans perceive time in terms of distance, elapsed time, spatiotemporal relationships, and relative sequences.

The absence of these factors in octopuses should not dismiss the possibility of episodic-like memory. I concur that dismissing episodic-like memory solely based on the absence of time perception criteria would be unwise. This resonates with Rescorla's (1988) perspective positing that the concept of contiguity between two events (forming associations) implies that an organism's behaviour is not random but driven by a purposeful search for information. The organism actively engages in making connections between stimuli based on logical and perceptual relationships. This perspective implies that the organism is not merely passive but actively constructs a mental representation of its world by incorporating expectations, beliefs, prior experiences, and knowledge into the learning process. Based on this argument, the findings from Poncet et al. (2022) would support a form of cognitive processing—The varied strategies engaged by different species indicate that cognitive processes in cephalopods are not simple – that strategies might compensate talents.

This finds resonance in Heyes (2012b) and Amodio and Fiorito (2013) who questioned the dichotomy between social and individual learning, arguing against

the assumption of two distinct and parallel learning mechanisms. They proposed that social learning abilities are not limited to social species and can be observed in solitary-living animals. Case in point, evidence of learning and memory mechanisms has been established in the past in species such as *Octopus vulgaris*, *Sepia officinalis*, *Octopus cyanea*. Further calls for a more nuanced perspective that acknowledges the occurrence of social learning in solitary-living animals and its diverse manifestations across species and individuals.

Furthermore, body patterning in juvenile cuttlefish may not be a simple stimulus-response process, but as suggested by Darmaillacq et al. (2017) likely involves a complex integration of visual information and could vary between individuals. Josef et al.'s (2015) experiments suggested the gradual transition served as a cue for processing, planning, and anticipation of upcoming events. There should be a period in which crypsis is compromised as the gradual change only occurred after the animal had arrived in the new background (Pembury Smith & Ruxton 2020; Josef et al. 2015)—One should nevertheless be cautious when interpreting the results. On one hand, behaviour like *Thaumoctopus mimicus* that adopts other organisms' body form in their environment as they move faster to capture their prey (or escape), could be due to the limited success in matching their background as its speed increased (Pembury Smith & Ruxton 2020). In Josef et al. (2015), the artificial grey and black background yielded a limited Uniform pattern with incomplete adjustment to either pattern reflectance. The findings from Alfakih et al. (2022) showed that a rapid colour change from seconds to minutes (*acute*) incurs higher costs compared to the slower transition over days to weeks (*chronic*). One may critique that different outcomes can arise because the transition phase involving interactions with complex backgrounds in the natural habitat with richer and shallow waters is presumably more sophisticated.

On the other hand, variations in cognitive abilities may be influenced by contextual factors (motivation, stimuli type) rather than assuming poorer cognitive performances. It is reasonable to assume that the experimenters would have limited control over the animals' motivational aspects, which in my view is a potential bias in assessing cognitive performance. For instance, young cuttlefish prefer crab over shrimp once they are exposed to the choices, and preference is distinct and greater when they are exposed to visual and chemical cues. Josef et al. (2015) did not rule out the possibility that post-hatched young cuttlefish are plastic, and their individual experience can be shaped as unveiled in Darmaillacq et al. (2004); Darmaillacq et al. (2006). No doubt it is a novel technique in terms of test design, it is quite difficult to detect variation in individual cognitive performance without addressing ceiling or floor effects – this was not addressed by Josef et al. (2015). The failure to address ceiling and floor effects can lead to several significant consequences including limitations in generalisability. Although insightful, the correlation between the animal's velocity and their camouflage properties was not investigated. Moreover,

this type of background matching may be explainable in most observers but likely different in the eyes of predators or prey.

Although the results strongly indicate cephalopods' aptitude for conditional learning to navigate their surroundings and their ability to tailor cognitive skills to specific ecological niches, there are still unresolved issues requiring further investigation. First, whether the same is applicable in both sexes, which is an important biological variable in cognitive function and learning, specifically with cephalopods having the largest and most complex nervous system of invertebrates. Previous studies (Jozet-Alves et al. 2008) compared both cuttlefish sexes before and after achieving sexual maturity and found cognitive dimorphism between sexes essentially, mature male cuttlefish travelled further, had greater mobility, and used visual cues in line with a range expansion theory. It is also unclear whether the same results can be said unequivocally about octopuses and squid. Further research is needed to determine whether the reproductive period, which leads to a decrease in mobility in females and an increase in mobility in males, has an impact on the observed differences.

Second, concerns emerge regarding the contextual variables and methodological variations in assessing cephalopods' episodic-like memory. This encompasses the difficulties of establishing objective criteria, such as time indicators or the number of trials, to ascertain or identify recall elements within associative learning. These challenges were acknowledged by Schnell et al. (2021b) and Poncet et al. (2022). The establishment of satisfactory criteria for cognitive performance becomes daunting due to variations across contexts and species. For instance, the diverse food preferences and strategies employed by octopuses and cuttlefish can influence their motivation and responses to reward stimuli. Likewise, monkeys excel in pairwise tests, showing linear processing and mental representation of order, while pigeons rely on simpler behavioural rules and struggle with internal pairs but when such changes are minimised, pigeons demonstrate a rudimentary understanding of order (Scarf & Colombo 2010 cited in Colombo & Scarf 2020).

Furthermore, the omission of contextual variables can introduce confounding factors and contribute to behavioural differences between species (Colombo & Scarf 2020). For instance, Bublitz et al. (2021) recognised the challenges of controlling and accounting for all the factors and conditions in their experimental settings that could potentially influence the outcomes. They found out that octopuses were not perceiving the incorrect signal accurately, and in this context, the octopuses exhibited a positive reversal learning effect which was not primarily due to extensive training but rather to the associative processes involved. The authors observed that the octopuses' change of body pattern to Mottle Display supported their conclusion, highlighting the impact of different stimuli that can affect learning speed. Borrelli et al.'s (2020) experiments were directed towards the establishment of a standardised battery test across cephalopods, further exemplified

how contextual learning processes can manifest and differ between individuals, often become apparent with characteristics of receptiveness to stimuli-induced learning such as 'readiness' to learn. In Kawashima et al.'s (2020) research on cognitive dynamics, distinct variations in learning speed and reactions were documented, and the authors found a link between distinct body patterns and emotions. These studies contribute additional layers of complexity to the understanding of cognitive functionality and processing. They underscore the significance of emotions, a less explored biological factor, and crucially, body patterns, a frequently overlooked indicator in the interpretation of cognitive abilities.

This thesis proposes that to enhance the accuracy of comparative cognitive research, it becomes evident that contextual repeatability, a challenge due to the lack of replication, and internal task validity are pivotal for ensuring reproducibility and consistency in studying cognitive phenomena in non-verbal animals. In human studies, Schubiger et al. (2020) emphasise that cognitive test batteries are subject to regular evaluation for construct validity and test-retest reliability. The emphasis placed on internal task validity assumes importance as it aids in discerning whether a measure truly captures individual and species differences in terms of cognitive abilities rather than representing variation in factors other than cognitive nature (Schubiger et al. 2020). A proposal put forth by Heyes (2012b) advocating for the comparisons and testing of both hypotheses enabling the assessment of whether behaviour is shaped by associative processes or higher cognitive processes is worth considering. Heyes (2012b) contends that achieving this objective necessitates detailed specifications for both hypotheses, facilitating the formulation of distinct predictions about behavioural or neural outcomes. By observing and conducting experiments based on these predictions, it becomes plausible to ascertain the hypothesis that is more likely to possess accuracy.

4.4 Which neurophysiological properties in cephalopods drive learning and memory?

The results presented in 3.4 elucidate that learning and memory are regulated by neural circuits and neurotransmitters. The insights gained from these studies contribute to a broader understanding of the neural mechanisms that influence not only cognitive functions, potentially including learning and memory abilities but also social behaviours. The results revealed unresolved differences have existed at cellular, molecular, and neurophysiological levels in cephalopods (See also 4.5). Critically, synaptic plasticity's involvement in learning and memory mechanisms differ. Octopuses exhibit both STM and LTM synaptic plasticity, while cuttlefish exhibit LTP at specific synapses. Although squid is less studied, they have LTP at cholinergic synapses. Despite these variations, both cuttlefish and octopuses share

similar circuitry and neural elements, indicating different strategies for learning and memory storage (Shomrat et al. 2015). In the context of Shigeno and Ragsdale (2015), the identification of distinct lobules with different neurotransmitter distribution patterns indicates functional subsystems within the learning circuitry in *Octopus bimaculoides* hatchlings and adults. Similarly, evidence from Chung et al. (2022) indicates a potential correlation between the number of gyri and learning and memory abilities differentiating cephalopod species. In my perspective, these findings do not imply that one species has less memory storage than the other. Rather, they highlight the likelihood of distinct strategies and learning mechanisms employed by different species. The results from Boal (1996) cited in Hough et al. (2016) demonstrated that octopuses can retain short-term, long-term, and sensory memory while learning complex tasks over five weeks to two months. This indicates their considerable capacity for various forms of learning (Zarrella et al. 2015; Marini et al. 2017; Hvorecny et al. 2007). Except for the earlier studies noted in 3.4, there is a lack of recent data to corroborate the same on cuttlefish or squid. Dickel et al. (1998) by using the 'prawn-in-tube' paradigm, found that cuttlefish learn to inhibit their predatory behaviour and their retention for this learning ranged from 2-8 minutes with their predatory responses recovering after 20 min of training. The cuttlefish studies showed that learning and memory have already begun during embryonic stages.

This thesis has identified several aspects that require further clarification. For instance, the implication of similarities with teleost fish and others when compared to their magnocellular lobe, the cholinergic nerves, and serotonin-like innervation in the arm remains unclear. Although both octopus and cuttlefish demonstrated brain lateralisation (Byrne et al. 2004), their performances are likely shaped by the nature of task demands (O'Brien et al. 2017; Güntürkün et al. 2020). While various evidence and hypotheses exist concerning the role of synaptic plasticity and memory storage mechanisms (Abraham et al. 2019), this thesis has primarily delved into a limited discussion of these topics. Exploring the initiation of these mechanisms during the embryonic stage is worth considering. Further investigations are necessary to understand the potential impairment of visual processing and related functions caused by disruptions to the dopamine concentration involved in modulating synaptic activity in the OLs as earlier suggested (Bidel et al. 2016; Williamson & Chrachri 2004). To gain further insights into the roles of dopamine and ACh in synaptic modulation, obtaining high-quality behavioural data is imperative given cephalopods' relatively short lifespan, and as revealed in Schnell et al. (2021b), the absence of degenerative diseases, as well as the sexual signalling at the end of their life evidenced by their pronounced body patterns.

4.5 Which physiological properties in cephalopods drive body patterning?

The results in 3.5 elucidate three main parts of cephalopods' physiological attributes that drive the change in their body patterns. The studies suggested that cephalopods exhibit intricate nervous system organisation characterised by an evolved large brain with distinct lobes interconnected by neural pathways, a complex system of chromatophores in their skin that allows rapid colour and texture changes for camouflage and communication, and a unique visual system which operates in tandem with the CNS, with the highest visual processing control occurring in the OLs. The coordination of the nervous system, effector organs in the skin, and photoreceptors enable cephalopods to achieve camouflage, mimicry, crypsis, and polyphenism. These adaptations are crucial for their survival and are utilised through their interaction with the environment. Except for a few unique species, all cephalopods possess these mechanisms, giving them diverse strategies to ensure their continued existence.

This thesis has identified several areas that require clarification. Firstly, there appears variation in estimated neuron numbers in cephalopods, and the implications of certain neural structures remain unclear. For instance, some suggest around 200 million and others 500 million neurons in the CNS (Chung et al. 2022; Amodio et al. 2019; Hanlon & Messenger 2018); In the OLs, 65 million (Hanlon & Messenger 2018) compared to 128,940,000 neurons (Yoshida et al. 2015) have been suggested. Addressing these discrepancies is imperative due to the potential influence of brain sizes, neuron counts, and gyri variations on the differentiation of learning and memory capacities. This need for clarification is pertinent in light of Chung et al.'s (2022) findings, which revealed that relative to bean-shaped OLs, the croissant-shaped with its larger OL volume and medulla might be associated with the higher spatial resolution to integrate, store, and retrieve information from PLs, and VL. In turn, it enables camouflage during the day observable in dynamic body patterns in *Octopus cyanea* and *A. aculeatus*, and courtship patterns in *A.capricornicus.*

Secondly, the notion that body pattern is a simple stimulus-response, may be an incorrect assumption. The evidence suggested that the skin of octopus and cuttlefish have a more complex combination of pigmentary and structural colouration relative to the squid. Ramirez and Oakley's (2015) evidence revealed an additional light pathway in the skin found in the octopus that induces chromatophore expansion, mediated by r-opsin, the visual pigment. Kingston et al. (2015) identified that squid has certain proteins, including rhodopsin, retinochrome, G_{qx}-proteins, and transient receptor potential transcripts in the retinas and skin, but the extent of these phototransduction proteins in cuttlefish varied. While squid has iridophores but no reflecting leucophores like those found in octopus and cuttlefish (Hanlon & Messenger 2018; Mäthger et al. 2009b), the activation of chromatophores could occur simultaneously on the mantle, head, arms, and fin in squid (Hadjisolomou et

al. 2021). On one hand, these studies suggest simple stimulus-response, but molecular studies (Sakaue et al. 2014; Bellier et al. 2017; Shigeno et al. 2018) identified two types of cholinergic nerves from the brain ganglia intrinsic to the arm and two types of serotonin-like innervations from the brain and in the axial nerve cord. This implies that attempting to equate the overall arrangement and functions of cephalopods and their arm-nerve cord with the human PNS would be overly simplified. Rosen and Gilly's (2017) findings support myogenic control rather than oscillatory neuronal control and their findings of 5-HT having an important neuro-modulatory role in inhibiting spontaneous chromatophore activity are not in line with Messenger (2001). Mäthger et al. (2009b) showed that ACh could induce colour change in *Doryteuthis pleii*, resulting in a shift towards a shorter wavelength in the spectrum. Messenger (2001) suggested that the substances responsible for controlling the chromatophores are L-glutamate (L-glu)–neuromuscular excitatory transmitter, FMRFamide-related peptides, and serotonin (5-HT)–retraction. Further indicated that 5-HT did not function as a neurotransmitter in the radial muscle but has both presynaptic and post-synaptic effects, particularly in muscle relaxation through interaction with calcium ions Ca^{2+}. 5-HT$_3$-type receptors are not ionotropic on the radial muscle fibres, and the 5-HT system likely involves switching off the excitatory effects of the L-glu. Although there remain questions to be investigated, these studies suggest that the mechanisms underlying body patterning are not simple. The mechanisms of serotonergic inhibition and the precise processes of coordination between vertical and horizontal control of chromatophore activity remain unclear. It is noted that this evidence derives from the loliginid squid's species in which pattern generation namely, to elicit a specific skin pattern, involves overlapping and discrete fields on the skin in coordination. Future studies should aim to clarify the importance and function of 5-HT as a neurotransmitter.

On the other hand, the findings that the opsin in the skin were similar to those occurring in the retina, may imply that visual stimuli that were being processed in the OLs and VL have implications on chromatic control – which may also be regulated by other physiological processes. Although the method by Guidetti et al. (2021) is insightful in identifying the interplay of the chromatophores system, it does not respond to leucophores (possibly others) which by themselves do not generate colouration. It is also unclear whether the skin cells can function as light sensors in a way that parallels the function of their retinal photoreceptors. Similarly, how the phototransduction components interact in sequence with the chromatin-rich environment e.g., the shallow-waters or tropical environments, and how they influence visual processing of the stimuli across cephalopod species, require investigation. It is noted that there is extensive research done on the architecture of cephalopod skin, but there remains a lack of comprehensive understanding concerning these aspects and their sequences.

Thirdly, body patterns are linked to communication signalling. Nahmad-Rohen and Vorobyev's (2020) findings revealed that octopuses occasionally do not

respond to the stimulus but rather show unilateral 'conspicuous' body patterns where one side of the body becomes darkened, and the other side remains pale. The pattern was observed when they did not show a fixation response. Contrary to previous studies, the darkened side was not always the side facing the stimulus, and the colour alteration was causally linked to the sinusoidal grating. The authors suggested that polarisation vision serves similar functions to luminance vision but might not directly identify material properties, potentially explaining the detection of transparent prey with high polarisation contrast. My view is Nahmad-Rohen and Vorobyev's (2020) interpretation of these body patterns and their communication significance was speculative. In particular, discerning a specific appearance as a visual signal that effectively conveys information and is accurately perceived by the intended receiver poses challenges. A wider range of stimuli would be advantageous to explore octopuses' communication signalling and visual capacities.

Despite the prevalent colour blindness amongst most cephalopods, the significance of polarisation sensitivity has been suggested for functions including camouflage breaking, contrast enhancement, object recognition, signal detection, and discrimination (Cronin et al. 2003; Mäthger et al. 2009a). It is noteworthy that, communication signalling through this means has been associated with activity level and body patterns with preliminary evidence indicating polarisation information may be important for female receivers (See Boal et al 2004; Mäthger et al 2009a). The notion is substantiated in Mäthger et al. (2009b) that cephalopods possess a rhabdomeric visual system, enabling the detection of linearly polarised light, and the iridescence aspect of their vision might have a communication function as predators like sharks, teleost fish, or other marine mammals that lack polarisation sensitivity, rendering them unable to perceive the information visually. *Octopus vulgaris* discriminates visual objects based on brightness, size, polarisation orientation, and the plane of polarisation (Messenger 2001; Gleadall & Shashar 2004; Hanlon & Messenger 2018)—Thus, unlike humans, octopus segregates polarisation features in an object and discriminates the different spectral features of similar brightness (Shasher & Cronin 1996).

Nevertheless, Hanlon and Messenger's (2018) analyses suggested that the evidence for polarised vision and its signalling function is inconsistent across cephalopod species. This further prompts enquiries into how cephalopods compensate for their colour perception. Stubbs and Stubbs' (2016) findings suggested that cephalopods could perceive spectral composition through a combination of chromatic aberration and pupil shape. This indicates that cephalopods could perceive colour variations. In contrast, Chung et al.'s (2016) studies showed that the various species they examined possessed a single visual pigment in their experiments and that unless a highly improbably optical solution for colour vision as proposed by Stubbs and Stubbs (2016) can be substantiated, colour blindness remains prevalent characteristic. This discrepancy highlights the

challenges of interpreting experimental results and, questions how closely the simulation results can align with actual cephalopod visual processing. Moreover, while Hanke & Kelber (2020) suggested that the octopus possesses 'pseudo-cornea' i.e., strictly not a component of the eye as it could not be isolated from the ocular structures, an alternative viewpoint suggested that octopuses possess moveable lenses and begin invagination whilst still embryos, and octopuses do not have corneas and that the retina is connected to the optic nerve without passing through a photoreceptive layer at the back of the eye (Octolab 2019). This emphasises the intricate nature surrounding the anatomical and functional aspects of vision, which could potentially influence the approach to simulate and construct a behavioural model.

Fourthly, species-specific variations in body patterning and communication signalling exist within cephalopods. While cephalopods typically use asymmetry in communication, cuttlefish use body shading as a means of evading detection by predators – Their distinct responses to shaded stimuli and sensitivity to the direction of illumination have been observed, with an intriguing behaviour of orienting towards the light source rather than consistently adopting shading of their patterns (Zylinski et al. 2016). The reasons behind this behaviour as well as their divergent responses to 2D and 3D stimuli, remain elusive. Nevertheless, this contrasts with the strategy exhibited by octopuses, highlighting the intricate nature of their visual behavioural mechanisms and suggesting the existence of inter- and intraspecies differences. This notion is supported by the disparities in the chromatophore system. Notably, deep-sea cephalopods displayed reduced reliance on chromatophores, which is evident in the case of the deep-sea cranchiid squid featuring reduced chromatophores with much smaller chromatophore lobes in the brain. Additionally, certain species e.g., *Cirrothauma* lack chromatophores, and there are no chromatophores found in *Vampyroteuthis* (ancient cephalopod) except those that are related to photophores (Hanlon & Messenger 2018). This implies a simpler or non-existing body pattern, suggesting divergent communication signalling strategies or different defence mechanisms. Furthermore, the *Vampyroteuthis,* cirrate octopods, *Thaumeledone, Graneledone,* and *Bentheledone* (incirrate sub-family of Eledoninae) have no ink sac, in contrast to some deep-sea squids (Hanlon & Messenger 2018). These observations suggest a nuanced landscape of species-specific behaviours and adaptations.

Fifthly, the phenomenon of lateralisation in visual processing is evident in both cuttlefish and octopus. While *Octopus vulgaris* displayed a preference for one eye when attacking prey (Byrne et al. 2002; 2004), cuttlefish tended to turn to the left for shelter, suggesting the use of the left eye and left-brain hemisphere (Jozet-Alves et al. 2012; O'Brien et al. 2017; Hanlon & Messenger 2018). This bias is also observable during the embryonic stage when perceiving information from the prenatal environment as suggested by O'Brien et al. (2017). According to Güntürkün et al. (2020), the activation of left- or right-hemispheric loops of

feedforward or feedback projections is contingent upon task demands, potentially dominating a neural process temporarily. This thesis noted that the methodological basis leading to the postulation that *Octopus vulgaris* has sensory asymmetries in the visual system was questioned by Boal and Fenwick (2007). Although lateral asymmetry of eye use was demonstrated at individual octopus (Byrne et al. 2002), there is no systematic bias towards left or right eye use at the population level as the distribution of lateral asymmetry of eye use is best described as anti-symmetrical because some octopuses exhibited no eye preferences (Byrne et al. 2004). Supporting these observations, Darmaillacq et al. (2017) proposed that environmental factors can influence the development of visual lateralisation in cuttlefish because adaptation is advantageous for young cuttlefish to quickly determine which shelter to choose. They suggested that the influence of environmental constraints on the ontogenesis of visual lateralisation emphasises the plasticity of this trait, further suggesting that the development and expression of lateralisation can be influenced by both intrinsic factors namely, eye preference, and extrinsic factors including exposure to predator odours and shelter availability.

Read together, it becomes evident that visual and chromatophore systems are distinct to each species. The synchronised activation of chromatophores in squid suggests a coordinated control mechanism for rapid colour change. In comparison, octopus and cuttlefish exhibit more complex colouration than squid, which could potentially influence communication, camouflage, and other visually guided behaviours. The size and density of chromatophores vary amongst species and are likely influenced by species-specific lifestyles and habits including environmental factors, prey abundance, habitat limitations, den availability, or social organisation. Furthermore, differences in retinal proteins suggest variations in visual capabilities and sensory processing amongst cephalopod species. The processing of visual stimuli within the OLs and VL appears to influence chromatic control and coordination of colouration. These findings underscore the intricate interplay between body patterning and sensory systems, indicating diverse visual capabilities and adaptive strategies within cephalopod groups. As such, body patterning is not a simple stimulus-response process but likely involves complicated processing integration of visual information which could vary between individuals.

The results of the thesis are aligned with Macphail's (1987) claim regarding the challenge of determining whether the variations in performance observed truly indicate inherent differences in cognitive abilities between species or are instead influenced by contextual factors namely, environmental factors. The environment in which cognitive studies are conducted can significantly influence the outcomes and interpretations. Factors such as the presence of predators, resource availability, and social dynamics can impact the performance of cephalopods. Therefore, it is essential to consider contextual factors when assessing and comparing cognitive skills across different species. Macphail's Null Hypothesis (1987) encourages critical analysis of alternative explanations for cephalopods' body pattern

expressions, challenging the notion of high-level cognitive processes as the sole attribution. However, the results in this thesis show variations in cognitive abilities observed amongst cephalopod species, further suggesting quantitative differences rather than qualitative ones, contradicting Macphail's Null Hypothesis (1987) and indicating that cognitive capacities are not uniformly distributed across all cephalopod species. The differences in social behaviour and the cognitive demands associated with these behaviours provide evidence for the hypothesis that cognitive abilities can vary depending on an organism's ecological niche and social context. Octopuses, cuttlefish, and squid exhibit behavioural differences at both group and individual levels, implying that factors such as species-specific adaptations, environmental influences, and individual differences within the same species can contribute to diverse behavioural patterns and outcomes. Body patterning can indicate cephalopod's cognitive processes and functions; however, the data are insufficient to justify cephalopods' cognition as complex, as such a causal link with their body patterning. Overall, this study finds the cephalopod literature contradicts Macphail's Null Hypothesis and highlights the presence of quantitative differences.

4.6   Ethical aspects

In accordance with the stipulations outlined in EU Directive 2010/63/EU and the guidelines on housing cephalopods, experimental protocols must align with ethical standards (Fiorito et al. 2015). The EU directive recognises that cephalopods can experience pain, suffering, distress, and enduring harm. The 3R principles emphasising Replacement, Reduction, and Refinement are established to govern ethical considerations in animal research. Within this framework, specific recommendations pertinent to cephalopods encompass measures, treatment, and disease prevention including the screening of animals entering the facility, quarantine procedures, monitoring, detailed examination of individuals considered as 'abnormal', treatment including dosage, route, duration, and obtaining approval for animal research. Nonetheless, the treatment of the capture, transportation, maintenance, and acclimatisation and wild-caught cephalopods within captive settings remains an under-addressed aspect in much of the reviewed literature. The limited number of subjects involved in the experiments can be attributed to the considerable mortality rate among captured wild cephalopods, both prior to their arrival at the laboratory and shortly thereafter. Although the EU directive recognises the unique characteristics, it did not tailor regulations to their behavioural and physiological needs and is likely inadequate in mandating the use of alternative methods that replace the need for experimentation. This is an important consideration for animal behaviour as the processes can induce stress that might impact their behaviour and responses during the experimental contexts. Furthermore, animal wellbeing should involve assessment of physiological

responses such as changes in hormone levels, acid-base balance, immune system, and oxidative stress system amongst others prior to experiments. However, this is also not addressed in the cephalopod literatures. In my perspective, it is of paramount importance that when cephalopods are removed from their natural habitats, they are afforded the requisite care and considerations. The challenges encountered in this endeavour could partially stem from a limited understanding of cephalopod physiology, including factors such as temperature and pH levels that potentially impact their central nervous system. A noteworthy observation highlighted by Jerez-Cepa and Ruiz-Jarabo (2021) pertains to the deficiency of cross-taxa comparisons, which may contribute to the challenges faced in this context. Furthermore, the concept of refinement is subjective. To address these concerns, Narshi et al. (2022) proposed a formulation of a scoring system tailored to invertebrates. This system aims to furnish a framework for the consistent and validated assessment of welfare and the implementation of necessary interventions within zoological collections, with the overarching goal of mitigating animal suffering.

While the EU directive is a step forward within the European Union, it becomes increasingly apparent that a broader global standardisation of regulations governing cephalopod research is imperative. This harmonisation would ensure uniform and ethical treatment of these animals across diverse geographical regions and research endeavours. This imperative arises from a comprehensive review of the existing literature, which underscores the pronounced variations in animal welfare regulations evident across different countries and regions. The inconsistency is demonstrated in the literature, where certain countries lack provisions for safeguarding the welfare of cephalopods. For instance, the animal protection law in Israel does not include invertebrates, thereby rendering ethical assessment by an ethics committee infeasible. Similarly, the treatment of invertebrates is notably absent from the United States Animal Welfare Act regulation and there is no provision for the care and use of laboratory animals. However, while these disparities persist, adherence to 3R principles is generally followed. My view is researchers should routinely acclimatise their subjects and report the care during transportation and maintenance phases.

In response to the substantial expenses associated with cephalopod research and experimentation, efforts have been directed towards the formulation of a more streamlined and economically viable approach. Notably, the Cephalopod Experimental Projected Habitat (CEPH) was proposed by Josef (2018). The preliminary results showed that the system holds promise in creating a controlled environment that could capture insights into cephalopod behaviour and responses to visual stimuli. However, there are several limitations and potential issues to consider. First, The CEPH system may not fully replicate the natural conditions of the ocean, specifically the lighting, projected images, and tank setup might not accurately simulate the complex interplay of light dynamics, currents, and sensory

cues that characterise the animals' native environment. This disparity between simulated and actual conditions constitutes a fundamental limitation that must be acknowledged. Second, the behaviours and responses observed within the confines of the CEPH system might not necessarily extrapolate (translate directly) to the cephalopods' behaviour in their untamed habitat. The responses to projected stimuli might be different from real-life interactions with live prey, predators, or their surroundings. Furthermore, the study might have neglected other sensory modalities that cephalopods might rely on such as tactile and chemical cues. Third, while the paper mentions compliance with the EU legislation for animal experiments, there might still be ethical concerns regarding the capture and use of wild-caught animals in experiments. In sum, the CEPH system shows promise as a tool for studying cephalopod behaviours, its experimental limitations emphasised the need for cautious interpretation of the findings and consideration of the broader ecological context in which these animals operate.

4.7   Environmental aspects and future research

The environmental impact on cephalopods is a subject of growing concern. The outcomes of Yasumuro and Ikeda (2018) have underscored the nuanced interplay between living conditions, environmental enrichment, and the cognitive faculties of cephalopods, as evidenced by variations in learning, memory, and depth perception abilities across distinct rearing contexts. Similarly, Court et al. (2022) found that water acidification and warming could negatively impact the survival of cuttlefish newborns. Interestingly, these newborns showed enhanced blend capabilities for defence while their mobility, exploration, and predation avoidance abilities were unaffected. This implies a potential resilience in newborns. Evidence has further shown that by embryonic stage 25, cuttlefish eyes have developed enough to perceive light and distinguish stimulus characteristics like shape, movement, and brightness. Furthermore, prolonged exposure to FLX, as highlighted by Bidel et al. (2016), could disrupt the normal functioning of dopamine in the brain, possibly leading to problems in synaptic function, communication between neurons, and consequently abnormal synaptic processes, in turn, contribute to disturbances in neurodevelopment, abnormal growth, and brain function. Their studies also pointed out the role of POs and lysozymes in immune response. Decreased lysozyme-like activity due to FLX exposure could affect cuttlefish resistance to bacteria, aligning with earlier vertebrate studies and indicating potential effects on survival. The results suggested that even low concentrations (1 μg L−1) of antidepressants could alter immune parameters in mollusc haemocytes. However, our understanding of the newborns' state of resilience, their direct response to stimuli and the development of brain structures involved in visual information processing in the optic lobes is limited. In addition, this thesis

emphasises the urgency to understand the interplay between environmental factors and cephalopod biology in particular, the anti-predatory and mating behaviours associated with factors such as handling, noise levels, and season.

Furthermore, the validity of dominance-subordinate relationships and issues of whether octopuses possess the ability to recognise conspecifics and themselves require further investigation. As the behavioural context of agonistic encounters can influence iridescence, through the interaction of acetylcholine reacting to muscarinic cholinergic receptors. However, our understanding of the trade-off between efficient decision-making and the potential costs of remembering stimuli and events is limited, especially in species that employ transparent camouflage. Future research should investigate the effects of confounding variables such as diet, temperature, or water quality, which could strengthen the validity of the results.

Previous studies have suggested that cephalopods have no circadian rhythms, which play a critical role in influencing learning performance (Bradley & Young 1975). However, findings by Medeiros et al. (2021) and Gutnick et al. (2023) challenged this notion (See Appendix 1). In particular, Medeiros et al. (2021) suggested the quiet state with only one eye movement corresponds to a resting behaviour that is not triggered by a reflexive glass tank but could be a response to environmental stimuli rather than resting behaviour; Gutnick et al. (2023) found pale skin colour during quiet sleep and darkened colour upon active sleep transition in octopuses, indicating a potential link between MSFL-VL circuit and vertebrate hippocampal circuits. They proposed the MSFL-VL circuit's role in memory consolidation, aligned with tactile learning and reward circuits. Even in the nocturnal octopus *Eledone cirrhosa*, the evidence seems insufficient to support the absence of circadian rhythms. In cephalopods that maintain a day and night cycle, melatonin levels in the blood, OL and retina fluctuate and peak during the night, indicating the involvement of melatonin in transducing the day-night cycle and regulating rhythmic behaviour (Muñoz et al 2011; Hanlon & Messenger 2018). Studies on sleep patterns and neural activity further hint at potential connections between cognition, memory, and sensory processing. However, the thesis has not explored how these aspects interplay with body patterning and cognitive processes.

Conclusion

The thesis has explored the association between body patterning and cognitive abilities of cephalopods and their implications for Macphail's Null Hypothesis (1987), which proposed that vertebrates possess similar cognitive capacities. The examination of cephalopod literature has revealed remarkable behavioural traits in cephalopods.

First, the thesis has explored the multifaced role of cephalopod body pattern elements which served various cognitive functions involving communication, inter- and intraspecies signalling, predator avoidance, feeding, and mating. The rapid adaptation of body patterns aided camouflage, crucial for survival. In sum, cephalopods' diverse behaviours, from sexual signalling to intricate camouflage mechanisms, underscored their cognitive abilities and adaptability to various ecological niches. Social interactions further highlighted their cognitive flexibility and capacity for communication, cooperation, and learning.

Second, the thesis has explored the temporal perspective of cephalopods. Cephalopods' dynamic chromatophore systems, coordination with structural reflectivity, and response to light stimuli demonstrated their intricate sensory and neural mechanisms. The transition phase involving interactions with complex backgrounds in the natural habitat likely differed from artificial settings in which the cost and speed of colour change could vary. Time perception in cephalopods differed – the absence of certain factors such as perceiving time in terms of distance or spatiotemporal relationships, should include consideration for the driving forces behind their cognitive capacities namely their habitual tool use, food caching, or sociality which differed from vertebrates.

Third, the thesis has explored the cognitive mechanisms that affected how cephalopods solved a task. Cephalopods exhibited diverse forms of learning and memory, such as habituation, associative learning, problem-solving, and learning. Differences in cognitive performance were influenced by contexts and factors such as motivation, and stimuli type, as well as reflected in the changes in their body patterns. Cognitive processes in cephalopods were reflected in various strategies, thus challenging conventional understanding and calling for a nuanced perspective that acknowledged diverse manifestations of learning across species and individuals.

Fourth, the thesis has explored the neurophysiological properties in cephalopods that drove learning and memory. Cephalopods exhibited learning and memory

abilities comparable to vertebrates. Their memory systems involved distinct lobes with OLs linked to visual learning and SFL/VL associated with tactile learning. In particular, cuttlefish and octopuses exhibited considerable capacity for various forms of learning, including short-term, long-term, and sensory memory with variations in synaptic plasticity and learning and memory mechanisms, but both shared similar neurotransmitter involvement. Further explored the environmental factors that could influence the developmental stages of cuttlefish, in turn, affected the intrinsic and extrinsic factors on body expressions.

Fifth, the thesis has explored the physiological properties in cephalopods that drove body patterning, in particular, cephalopods exhibited species-specific adaptations in their visual and chromatophore systems, influencing their behaviour, communication, and camouflage abilities. There were variations in visual adaptations amongst cephalopods, influenced by their light environment and specific species characteristics. The presence of mature body pattern repertoires in hatchlings supported the notion of innate patterning abilities, which could be conditioned to break camouflage.

In sum, the cephalopod studies challenged Macphail's Null Hypothesis and underscored the cognitive sophistication exhibited by cephalopods. The thesis concluded that body patterning could serve as a viable indicator of cephalopods' cognitive functions and capacities, contradicting Macphail's assertion that there were no significant qualitative or quantitative differences in intelligence across vertebrates. Despite limited data on the causal link between body patterning and higher cognitive functions, different species of cephalopods possessed the ability to solve learning tasks, albeit with variations at the individual and group levels. Further identified that the cognitive levels included stimulus-response, dynamic camouflage, and intentional manipulation, and the cognitive processes encompassed sensory discrimination, learning, memory, decision-making, and potentially self-awareness. However, the interpretation of body pattern expressions and their cognitive representations presented challenges, leading to diverse hypotheses and ongoing debates regarding the attribution of high-level cognitive processing to cephalopods' behaviour. Salient factors such as structural adaptation, plasticity, learning mechanisms, ecological niche, and sensory-perceptual abilities likely contributed to the observed variations in cognitive capabilities amongst cephalopods. This thesis has further underscored the importance of contextual factors, including environmental conditions, for a comprehensive understanding of cephalopod cognition, as well as emphasised the limited understanding of the interplay between cognitive performance and individual or species-specific strategies, and their impact on body patterning and decision-making processes.

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Popular science summary

Cephalopods, a group of remarkable marine creatures including octopus, cuttlefish, and squid have captured the imagination of scientists and many nature enthusiasts. When we look at the octopus's eyes, we feel a sense of 'vibe' as if it exudes a sense of being like when you look into the eyes of a dog or cat, or a person. They are nature's true master of disguise. Their camouflaging prowess, coupled with their exceptional problem-solving skills and memory capabilities tell a story of their level of intelligence that leaves us in awe and leaves us pondering the mysteries of their minds. While cephalopods have demonstrated various wonders, it also questions whether the phenomenon of Clever Hans that animals could appear to possess human-like intelligence and abilities (attributes) because they are relying on more simple, associative processes to respond to their environment namely, subtle cues from the humans and not because they have complex minds (Pfungst & Rahn 2010). Some other researchers view that this is not just an innate physiological ability. Rather, the fact that cephalopods can camouflage to blend seamlessly with their environment to avoid detection by predators, as well as to communicate and/or signal other animals, may reflect a level of nature's complexity that awaits our discovery—as we remind ourselves of the vast diversity of life on Earth and the endless mysteries waiting to be explored.

The study is inspired to do just that—uncovering a very tiny piece of the puzzle by exploring whether their remarkable ability in changing body patterning in response to environmental cues and context is the result of their highly developed nervous systems and specialised skin cells interacting with their cognitive functioning. In the mesmerizing world of cephalopods, the mastery of body patterning and remarkable cognitive abilities unfold.

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Appendix 1

Table 3 A selected summary of cephalopod literature

Authors	Species	Methods	Objectives	Key findings
Josef et al. (2015)	*Sepia officinalis* (8)	In situ behavioural experiments	Examined the mantle reflectance when cuttlefish crossed two contrasted backgrounds.	• Camouflage during movement revealed a delayed sigmoidal way of changing colour in a black and grey background. • The animal started changing its mantle reflectance beforehand and completed the adjustment after crossing to a different background.
Kingston et al. (2015)	*Doryteuthis pealeii*, *Sepia officinalis*, *Sepia latimanus*.	Immunohistochemistry labelling, RT-PCR	Identified & localised phototransduction components in cephalopod skin.	• Evidence for the presence and activity of several key components in the chromatophores which include opsins, G-proteins, cyclic nucleotide-gated ion channels. • Manipulation of the components resulted in changes in pigment dispersion – suggesting their involvement in controlling colour change process. Essentially, they are photosensitive and reflect various colours of light – cephalopod dermal tissues, and chromatophores have a combination of molecules that respond to light.
Ramirez & Oakley (2015)	*Octopus bimaculoides* skin, hatchlings (0-4 months old) and adults (11).	Used antibodies against r-opsin phototransduction proteins to identify neurons that express r-opsin in the skin.	Investigated how skin senses light.	• The maximum sensitivity of the light sensors underlying light-activated chromatophore expansion closely matches the spectral sensitivity of opsin from octopuses' eyes. • Generated white light stimulus by fibre optic light source set to maximum brightness i.e. peak intensity: 681 nm, full width at half maximum: 150 nm; Generated action spectrum from the same white light, red LED light to create the light active chromatophore expansion. • Common molecular mechanism for light detection in eyes co-opted for

light sensing in skin and then use for light-activated chromatophores expansion. Octopus skin is intrinsically light sensitive suggesting association with body patterning abilities.

Yoshida et al. (2015)	Molluscs embryonic samples of pygmy squids *Idiosephius paradoxus*, and chambered nautiluses, *Nautilus pompilius* (adult tissues).	Symposium review to report experimental results of the visual system and optic lobes of cephalopods.	Characterised deep sequencing of eye transcriptomes	• Both cephalopods and vertebrates showed similar features in their eyes and visual systems including optic lobes. • Both cephalopods and vertebrates have specialized brain regions e.g., VL for learning and memory functions. • Both cephalopods and vertebrates exhibited unique blood vessel systems that support the complexity of their CNS. • Uncovered 3 types of genomic innovations contributing to their brain and camera eye formation: these included novel genes in the morphogenetic pathways, recombination of different genes' coding and regulatory regions called evolutionary tinkering or co-option, and genes duplication and divergence in function. • The cortical layer organization for both cephalopods and the deeper layer of vertebrate retina appear superficially similar. Cephalopod retina differs from vertebrates' layered retina that has many types of neurons; the cephalopod retina has only a single layer comprising rhabdomeric photoreceptors, and the visual neurons are located outside of the retina. • OL is the first place to process visual information. • Variations of squid's opsins, retinochromes, and arrestins concerned intraocular and extraocular photoreception, suggesting potential differences in how these proteins function and interact with GPCRs.
Caldwell et al. (2015)	*Larger Pacific Striped Octopus*	Laboratory observation & photography	Exhibited photographic and video showing	• Comprehensive descriptions of LPSO behaviour, body patterns, and postures in captivity and contrast with other cephalopod species.

			behavioural patterns and prey capture methods	Specifically, LPSO exhibited beak-to-beak mating and egg-laying akin to decapod squids and cuttlefishes. • LPSO has many similarities with *Octopus chierchiae* in terms of behavioural and biological – they are speculated as close phylogenetic relationships. • Pair bonding previously described was not found. • The generalization that senescence begins shortly after egg laying (e.g., shallow-water females) cannot apply here in which egg laying can last up to 6 months and brooding lasts up to 8 months.
(LPSO) - Live, 24 (13 males)				
Rosen et al. (2015)	*Dosidicus gigas*	Field observation	Studied two displays "flashing" and "flickering"	• Squid flashed its body colour when other squids were visible, indicating a form of intraspecific signalling among the same species. Whereas flickering patterns were a form of camouflage where the animal imitated the light patterns to blend into its surroundings. • Squid could actively control and modulate its colour changing behaviours based on its environment and social context. • There are functional similarities with colour changing behaviours observed amongst cephalopods.
Shomrat et al. (2015)	Cephalopod	Review	Investigated the biological principals for the evolution of mechanisms that mediate complex brain functions.	• Showed intracellular whole cell recording to characterise the VL input and output relationships: - VL connected to other parts of the brain for processing and storing information in coordinated manner. - VL was responsible for learning, memory, decision-making, and coordinating complex behaviours (communication, hunting). - Structure of VL was highly conserved in different cephalopods species. - VL was capable of plasticity.
Zarrella et al (2015)	*Octopus vulgaris*	Overview	Provided overview of the octopus learning abilities to facilitate further	• Highlighted learning and memory observed in all cephalopod species. • *Octopus vulgaris* was asocial with advanced learning capabilities, possessed cellular and synaptic plasticity, and CNS showed complexity akin to vertebrates.

				interpretation of its neurobiology.	• Showed various forms of learning abilities - habituation, classical and instrumental conditioning, spatial learning, and perceptual processes.
Bidel et al. (2016)	*Sepia officinalis*	Lab experiment, videorecording & photography.	Determined the effects of subchronic waterborne fluoxetine (FLX) - SSRI exposure in the last 15 embryonic days relating to neurochemical, neurodevelopmental, behavioural, & immunological endpoints at hatching.	The evaluation of camouflage efficiency of hatchlings to FLX exposure at three different concentrations revealed that FLX: • could enter the eggshell during embryonic development leading to a significant build-up of this molecule in hatchlings. • did not modulate the serotonergic system in the CSN however contradicting evidence from literature suggested different levels in brain 5-HT concentration. • could modulate the dopaminergic neurotransmission system in the CNS. • could modulate cell proliferation in the medulla of the OL and the cortex of the VL underlying learning and memory abilities. • did not influence the volume of brain structure. • did not affect the Disruptive body pattern on the checkerboard background, but the quality of the Uniform pattern was reduced when exposed to low FLX levels. This might be linked to stress response rather than incapacity for Uniform camouflage. Despite neurological changes and visual control over camouflage, the absence of FLX was intriguing which could be due to a time gap between immediate brain impact and behavioural outcomes from the substance. • reduced lysozyme-like activity without impacting PO-like activity.
Thomas & MacDonald (2016)	*Metasepia pfefferi*	Experiment using home aquarium.	Identified the dorsally visible components of the body patterns	• Revealed a combination of 7 textural, 14 postural, 7 locomotors, between 42 and 75 chromatic components yielded 11 distinct patterns. In contrast to other cuttlefish species, this population frequently exhibited displays characterised as travelling waves or blinking spots – Flamboyant Display.

Hough et al. (2016)	*Sepia officinalis* (18)	Experiment - Positive reinforcement was associated with inserting a contrasting-coloured probe (white/black) and causing the cuttlefish to change its body pattern.	Investigated whether body patterning responses can be shaped by learning.	• Cuttlefish broke camouflage to receive food reward within 15 s of probe insertion. The experimental group in the black tank responds faster and more consistently to the probe than control group, implying an occurrence of learning.
				• Both experimental and control groups for the white tank showed no differences, implying an absence of learning. Initially, cuttlefish in the black tank showed Uniform dark body pattern or dark patterns featuring white mantle bar or white squares. Subsequently, a Uniform light pattern, dark pattern with white squares or white mantle bars emerged in response to the presence of a white probe.
				• Body patterning not entirely hard-wired, but shaped by individual experience - implied that antipredatory responses were not solely instinctual but involved learning and decision-making processes.
Scheel et al. (2016)	*Octopus tetricus*	Longitudinal field observation 52.8 hr video recording	Documented the systematic use of signals during agonistic interactions between same species.	• Characteristic revealed agonistic signalling conforming a signalling model (Enquist model).
				• Body patterning plays an important signalling role in mediating agonistic interactions.
				• Mating occurred throughout the year and not seasonal.
				• Social interaction occurred and had important influence on evolution and behavioural trait.
Zylinski et al. (2016)	*Sepia officinalis*	Experiments	Investigated how cuttlefish respond to light and shadow to shade their white square body pattern feature.	• The white square feature is displayed in the presence of pebble-like objects and can shade it to simulate surface curvature. Their shading was most pronounced when on backgrounds of shaded circles and hemispheres. Shading was stronger with light from the lighter side consistent with real convex surfaces. They appeared to perceive surface curvature and consider light direction but tended to orient towards the light source, not background shading.
				• Cuttlefish used shading to create the appearance of 3D form in their skin

				colouration which helped in blending in and avoiding predation.
Stubbs & Stubbs (2016)	Cephalop ods	Experiments – numerical simulations	Tested a model mechanism on visual systems that have a single photoreceptor.	An off-axis pupil and the principle of chromatic aberration can combine to support colour-blind animals in distinguishing colours. This chromatic blurring provided additional cues for perceiving colour variations in shallow water.
Sato et al. (2016)	Japanese pygmy squid *Idiosepiu s paradoxu s* (54)	Experiment & observations	Investigated how inking behaviour affects predation.	- Squid attacked prey successfully after inking in 13 cases with varying success rates. - Inking behaviour during predation occurred 17 times out of 322 trials. 2 categories of ink attacks: - Released ink between the squid and prey before attacking through the ink cloud. - Released ink away from the prey and attacked from another direction. Success rate of ink attacks differed significantly between the two prey species.
Richter et al. (2016)	*Octopus vulgaris*	Learning and problem-solving experiment: trained to retrieve food from an L-shaped container (level 0). They then faced challenges such as retrieving the container through a tight hole (level 1), different orientations (level 2), an opaque barrier (level 3), and randomized	Investigated cognitive and problem-solving abilities in a multi-level learning experiment. Non-invasive operant conditioning task as a new approach for complex cognitive experiments with octopuses.	- Quickly adapted to changes in the puzzle task, including randomisation of the container's orientation in 4 positions. - Demonstrated problem-solving abilities in a series of experiments involving learning and puzzle tasks. - Performance differences were observed between different levels of difficulty with significant differences between levels 1, 2, 3, but not level 4. - Individual octopuses exhibited varied problem-solving strategies indicating the absence of a consistent trial-and-error approach. - Showed high variance in performance during level 0 and level 1 tasks, suggesting individual problem-solving strategies. - Task-solving times differed between individual animals in level 2, indicating a switch from a vision-based strategy to a generalised strategy for some animals. - Reversing the container orientation level 3 led to fast adaptation and improved flexibility but also resulted in increased task duration.

			orientations (level 4).	• Personality traits or cognitive styles might be influential. • Motor learning did not have a major effect on the animals' performance, indicating performance differences relied more on individual strategies than motor learning.
Darmaillacq et al. (2017)	Cuttlefish	Review	Summarised studies of visual development in embryos and young juveniles.	Visual acuity, lateralisation and polarization sensitivity improve as the juveniles grow during the first months after hatching. However, the body patterns production is not a simple stimulus-response process. It likely involves the complex integration of visual information and can vary between individuals.
Rosen & Gilly (2017)	*Dosidicus gigas, Doryteythis opalescens*	Experiments, recording of chromatophore activity & immunohistochemistry analysis.	Provided the first characterization of the chromatophore network in *D. gigas*; compared chromatophore activity with denervated *D. opalescens*	• Differences in motor axon pathways and synaptic connections indicate variations in the neural control of chromatophores between the species. Wave-like activity observed in intact *D. gigas* appeared alongside sparse innervation, while waves in denervated *D. opalescens* appeared after the degeneration of axons associated with radial muscle fibres. • In *D. opalescens*, waves appeared after the degeneration of serotonergic and glutamatergic axons associated with radial muscle fibres. The waves were not affected by tetrodotoxin, nor controlled by the known neural pathway from the brain, suggesting waves like activity are myogenic controlled.
How et al. (2017)	Cephalopods	10 species filed using digital video sequences, 11 from literature and video posted online.	Collated categories of 'dynamic' patterns from public & private recordings	Patterns identified & categorised: • 1. Flashing (*D. gigas*) 2. Flickering (*D. gigas*: Rosen et al. 2015, Stauroteuthis syrtensis: Johnsen et al. 1999) 3. Chromatic pulses/Passing Clouds (*O.laqueus*, *O. hummelincki*, undescribed octopus, *Sepia latimanus*, *Sepioteuthis lessoniana*) 4. Rhythmic passing waves (*Sepia officinalis*, *Sepia apama*, *Sepia bandensis*, *Broadclub S. latimanus*, *Wunderpus photogenicus*) 5. Multi-directional passing waves (*S. apama*, *M. pfefferi*, *M.tullbergi*, *Sepia plangon*, *Sepia mestus*. • *D. gigas* flashes during intraspecific communication (courtship, agonistic

				interaction) flash rate: 3 s at 2-4 Hz end-to-end (Rosen et al. 2015)
				• *S. syrtensis* flicker on and off asynchronously at approx. 0.5 – 1 Hz in the horizontal plane, mouth upwards (light lures to attract planktonic crustacean prey)
				• *Sepia plangon* is slow moving with repeat frequency at 0.3 – 0.5 Hz whereas *Sepia mestus* moves quicker at 1.5 Hz.
O'Brien et al. (2017)	*Sepia officinalis* Hatchlings (<1 week) juvenile (up to 17 weeks)	Review	Synthesised the current developments in the embryonic and juvenile stages concerning sensory experience, learning, habitat, and behaviour.	• While highly stereotyped in expression, different camouflage patterning, posture, and strategies (including inking) are used in predator-specific contexts. • Improved body patterning ie. better background matching is demonstrated in juveniles raised in an enriched and social environment compared with those raised in uniform non-social conditions. • Newly hatched display disruptive patterns on uniform backgrounds and unable to display uniform body patterns. • The tactics and body patterns for primary and secondary defence change as they age and grow larger. • Deimatic Display (paling, freezing, flattening body) with sudden spots on dorsal mantle appear during growth; Zebra pattern appears during the sexually mature stage for social signal and a crypsis form.
Panetta et al. (2017)	*Sepia officinalis*	Use high-speed cameras and spectrometry to analyse the skin changes in the natural habitat.	Determined visual stimuli that influenced camouflage pattern and papillae expression.	• Revealed two-step process: cuttlefish are attracted to a textured rock, then use visual cues to adjust skin texture. In lab tests, cuttlefish were drawn to rocks, responding with skin patterns and papillae. Smooth rocks prompt smooth skin patterns: rocks with shell fragments lead to bumpy mottled patterns. • When masquerading as an object, cuttlefish mimics not only colour and pattern but also physical texture using papillae. Sequential trials confirmed consistent papillae expression matching the rock. • Papillae change rapidly with mean times of 1.17 s for three-step change,

				1.03 s for two-step, and 0.46 s for one-step.
Scheel et al. (2017)	*Octopus tetricus*	Clarification and correction of misconceptions concerning early findings and interpretations.	Differentiated intentional behaviours.	• Prey collection, prey transport, den excavation, and use of non-prey materials at the den are intentional behaviours related to material collection, den maintenance, and aggregation from inadvertent consequences. • The dense aggregation of dens is an inadvertent result of food availability and predation risk. • Addressed the exaggerations and inaccuracies that have been reported in the media regarding the underwater sites inhabited by the octopuses. 'Octopus city' reported by the media was an inaccurate conception.
Bublitz et al. (2017)	*Octopus vulgaris* (4)	Reversal learning experiments – trained using operant conditioning techniques with a secondary reinforcer signalling response correctness followed by primary reinforcement (food)	Revisited serial visual reversal learning.	• Some individuals were able to complete multiple reversals in a visual discrimination task, showing progressive improvement over time. • Individual performance differed with one animal displaying progressive improvement over four reversals, demonstrating a reduced number of errors with increasing reversals, and developed a generalized response strategy. • In contrast, another animal completed only one reversal, while two animals did not exhibit learning to reverse during the initial reversal - indicating certain individuals could learn to reverse in a visual task. • The use of a secondary reinforcer such as a rod that signalled the correctness of a response proved to be useful to train. • Showed behavioural flexibility even under a refined experimental methodology.
Edsinger & Dölen (2018)	*Octopus bimaculoides*	Experiment: Pharmacological manipulation & molecular phylogenetic analysis of the solute carrier	Examined the deep evolution of SLC6A (human serotonin), monoamine transporters, and the SLC6A4 gene	• 2 copies of SLC6A4 found: 1st copy: Slc6a4-(1) (protein Ocbimv22009795m.p; gene model Ocbimv22008529m.g) – in molluscs and *O. bimaculoides*; 2nd copy: named Slc6a4-(2) (protein Ocbimv22009795m.p; gene model Ocbimv22009795m.g) belonging to fly and worm (Unknown; No

		(SLC) 6A subfamily of neurotransmitter transporter proteins and blasting a reference gene set.	family across the animal tree of life and diverse animal genomes. Quantified social behaviours.	mammals, vertebrates or other deuterostomes) • Phylogenetic analysis: (1) clear orthologs of human SLC6A4 in octopuses. (2) high conservation levels in the transmembrane domain and amino acid region essential to MDMA (phenethylamine (+/−)-3,4-methylendioxymethamphetamine) binding. • Behavioural analysis: Exhibited: (1) no preference for social approach to novel male conspecific (2) both male and female show social approach to a novel female conspecific. • Neural mechanisms promoting social behaviour existed in *O. bimaculoides* and the role of 5-HT in regulating this behaviour was evolutionarily conserved despite anatomical differences in brain organisation between vertebrates and invertebrates. • Higher dose range of MDMA induced severe behavioural changes with hyper or depressed ventilation and colour waves across skin or blanching, catatonia, or hyperarousal or vigilance – excluded for analysis.
Shigeno et al. (2018)	Cephalopod	Review: molecular markers & axonal tractography to analyse key brain regions.	Assessed the likelihood of evolutionary convergence.	• Consolidated molecular, anatomical, and developmental findings in the neural organisation. • Provided hypothesis-driven research into the evolution of cephalopod neural systems.
Josef, N. (2018)	*Octopus vulgaris (7)*	Experiments	Proposed an experimental design - Cephalopod Experimental Projected Habitat.	• Suggested reliability of the projected visual stimuli: average reaction (latency) to projected prey crab was 2.9 ∓ 1.5 s relative to live crab 2.3 ∓ 1.3 s. • Suggested perception via video of shark projected: escape response was evoked in 4 out of 9 octopuses. • Spatial and directional stimuli elicit skin colouration and behavioural response.
Amodio et al. (2019)	Cephalopod	Review	Discussed evolution of intelligence;	• Loss of protective shell led to (i) increased predatory pressure, preventing the emergence of slow life

			shed light on the fundamental aspects leading to the emergence of intelligence and highlighted the convergent and divergent aspects between cephalopods and large-brained vertebrates.	histories, and (ii) exploitation of new niches, promoting the evolution of intelligence. • showed that the evolution of intelligence might not be confined to a singular evolutionary trajectory by examining commonalities and differences between cephalopods and large-brained vertebrates. • The convergent aspects included the presence of a sophisticated nervous system that resembles vertebrates in relative size and complexity, and the ability to exhibit flexible behavioural repertoires. • The divergent aspects included the lack of complex social bonds and their fast life histories, shorter than 2 years lifespans, and no parental care - challenged the hypotheses on the evolution of intelligence, suggested coevolution of intelligence with slow life histories and complex social environment.
Abraham et al. (2019)	Cephalopods	Review	Addressed key findings from the synaptic plasticity underlying learning and memory.	Outlined mechanisms underlie persistent activity-dependent synaptic change-activation of NMDA receptor, context and challenges and problems, as well as introducing synaptic plasticity and epigenetics synthesis, ncRNA in memory. • The concept of synaptic plasticity and memory hypothesis suggested that experience-dependent synaptic changes were fundamental mechanisms of learning and memory retention. • Experimental evidence of activity-dependent LTP and LTD supported the link between synaptic change and memory storage. • Overall, highlighted the dominant view that synapses were the principal site of information storage, and also acknowledged the emergence of alternative mechanisms for further research.
Williams et al. (2019)	*Doryteuthis Pealeii*	Experiment Using proteomic and microscopy	Identified biochemical components at the reflective colouration	• Showed structural colour linked to expanded pigmented chromatocytes. • Reflectin proteins in sheath cells, along with Ω-crystallin and pigment

				molecules, contribute to this reflective colouration. • Revealed the interplay of pigmentary and structural coloration in the same flexible organ, suggesting the potential for innovative colour-changing materials.
Nahmad-Rohen & Vorobyev (2020)	*Octopus tetricus*	Psychophysic experiment: Used LCD screen with sinusoidal gratings (based on reflex response) to contrast sensitivity to both luminance and polarisation - around the eye.	Investigated whether the processing of polarisation signals is similar to the processing of chromatic signals.	• *O. tetricus* could detect and respond to polarised light, indicating polarisation vision, and their luminance and polarisation contrast sensitivity declines at low spatial frequency and peak at 0.3 cpd spatial frequency - suggesting both polarisation and luminance signals are processed via same pathways. • Processing of polarisation and luminance signals is largely similar contradicting the hypothesis that polarisation is processed as a distinct channel of visual information. • Displayed unilateral body pattern with one side dark and another pale when not responding to fixation stimulus – dark side not facing stimulus. This pattern was observed when not showing a response to a stimulus. • Colour change was not frequent and linked to sinusoidal grating – most octopuses showed this pattern during polarisation and only one during the luminance experiment.
Bayley & Rose (2020)	*Octopus cyanea,* grouper *cephalopholis argus*, brown-marbled grouper *Epinephelus fuscoguttatus*, gold-saddle goatfish *Parupeneus*	Field observations, video recordings. Substrate composition measured using overlapping images.	Documented co-operating hunting behaviour between the diurnal octopuses and fish species.	• Octopuses signal towards the fish through posturing with skin colour and texture changes, suggesting cooperative rather than opportunistic scavenging. • Fish captured the prey when octopus groped; octopus captured prey when pounced – suggested collaborating to trap and extract prey. • Octopuses were observed exhibiting behaviours such as pouncing (lightening their body and extending arms to envelop rocks or coral and explore underneath), groping (extending arms into cracks and crevices to search for prey), sitting, crawling, forward swimming, and rapid backward swimming.

				Simultaneously, fish lunged forward into holes and crevices.
Borrelli et al. (2020)	*Octopus vulgaris* (55: 22 males)	8 consecutive experiments lasting 12 days	Assessed variations and measured predator behavioural responses to acclimatisation, neophobia, social learning, problem-solving, individual learning & preferences. Standardised battery of behavioural tests.	• Demonstrated both positive and negative learning processes could occur, and inter-individual variability in predatory behavioural response was assessed. • A 5-day acclimatization period was identified as optimal to adapt to captive conditions, allowing for consistent experimental comparisons. • Displayed low levels of neophobia, indicating generalist and opportunistic predator behaviour. • Demonstrated observational learning, as those exposed to a trained demonstrator exhibited improved performance in a task involving manipulating objects. However, integrating visual and tactile information from vicarious experience posed challenges due to parallel neural processing. • Solved a task involving manipulating plugs to access prey, showcasing their ability to apply known sensory modalities to novel contexts. • Showed a marked preference for a red than white ball, could be attributed to both stimulus generalisation and contextual learning (discriminate based on its brightness). • Learned to avoid attacking artificial stimulus associated with negative reinforcement – showcased negative and positive learning processes. • Demonstrated potential for inter-individual variability in behaviour, learning and responses to different stimuli.
Kawashima et al. (2020)	*Octopus Abdopus aculeatus* (30)	Operant conditioning learning tasks: 1st experiment - learning real object; 2nd experiment - Stepwise conditioning from real to	• Investigated whether tropical octopus can learn to respond/ recognise symbolic object in real or virtual form.	• Octopuses consistently touched or grasped white ball after more training. • Like *Octopus vulgaris*, *A. aculeatus* could learn specific object at similar speed. • The number of trials required to condition an octopus depends on the age, size of octopus relative to the size of the object, which influences their speed and reaction time to touch or grasp.

cyclostomus

		virtual objects. 3rd experiment - learning a virtual object.	• Examined the applicability of computer screen for learning tests.	• Might be able to discriminate shape in the selectivity test (ball v. cone). • Could be operant conditioned to virtual object on computer screen, and some did not require training - suggested possibility to generalise with different visual features. • Contrary to earlier studies, as task increased difficulty no tactile feedback observed - lack tactile information to match virtual objects to real objects. • Successful response and display of body pattern was set at 0.1 s resolution. • 3 categories body colouration recorded: pale, ochre, and dark brown. • Colour turned dark brown as task progressed – suggested positive emotion as octopuses sensitised to the conditioned stimulus, in turn increased colour change frequency. • Pale colour indicated inactive or silent mode towards the stimulus whereas dark brown indicated active mode and fast reaction towards the stimulus and more learning.
Hanlon & McManus (2020)	Cuttlefish *Metasepia pfefferi*	2 Field studies (2002; 2019), video recordings.	Determined behavioural ecology in natural settings	• Display unique mating system - Male species that were much smaller in size than the female species, performed 'Flamboyant display' which could last a long time. • Males showed unilateral signalling in competing for a female i.e., white facing the male performing courtship; occasionally extended its arm to 'touch' while simultaneously exhibited elaborate behaviour which included Passing Clouds (waves) for an extensive duration. • Camouflaged most of the time except during courtships and in short secondary defence. • Major discrepancies between body patterns in captivity v. wild. • Aggression and cannibalism could occur when two male sizes were similar.
Ikeda, Y. (2021)	Cephalopods	Review	Outlined current contexts and	• Detailed colour-changing abilities are achieved via specialised chromatic

			findings of colouration change in cephalopods.	and reflecting cells linked to a neural system. • Showed ecological importance of colour and gradational change of body patterning in time course.
Schnell et al. (2021a)	*O. officinalis* (6)	Experiments: Delay maintenance tasks & reversal-learning task	Investigated self-control and learning performance	• Showed self-control by sustaining delays for better rewards (50-130 s) and exhibited better learning performance with longer delay tolerance. • Suggested that cuttlefish, like certain vertebrates, can endure delays for higher-quality rewards.
Schnell et al. (2021b)	*O. officinalis* (24) – 2 cohorts (10-12 months & 22-24 months)	Experiments: WWW tasks for semantic- & episodic-like memory.	Investigated whether episodic-like memory system is vulnerable to age-related impairments in cuttlefish that lack a hippocampus.	• In the semantic task, cuttlefish learned that food location depended on time of day, with consistent performance across age groups. • In the episodic task, cuttlefish retrieved WWW information about past events. Performance was similar across ages, but aged adults achieved the success criterion faster than sub-adults. • Episodic-like memory preservation in aged cuttlefish contradicted typical memory decline—delayed deterioration in this species.
Hadjisolomou et al. (2021)	*Doryteuthis pealeii* (7)	Experiment, high-speed video microscopy.	Exploratory pilot study: the measured speed of chromatophore activity in response to the light flash stimulus.	• Identified 4,065 chromatophores from 185 trials with surface changes during expansion and retraction. • Chromatophores responded within 50 ms, with expansions lasting 217–384 ms and retractions reducing area by 40.46%. Expansion yields an average increase of 155.06% (4000 chromatophores) across the body with the mantle having the highest and fin the lowest percentage, retraction yields an average decrease of 40.46% (65 chromatophores) across the body with the fin slightly highest and head or arm slight lowest percentage. • While not all squid have all the body regions that responded to the stimulation, chromatophore activation occurs not only on the mantle but also, on the head, arms, and fin. • Synchronous expansion and retraction can happen on different parts of the mantle in the same trial. • Speed varied depending on the type of cell and location.

Bublitz et al. (2021)	*Octopus vulgaris* (7)	Reversal learning experiment – one group trained with positive reinforcement alone, another trained with an incorrect-choice signal to indicate they made a wrong choice.	Revisited experimental design to train individual octopuses to discriminate between 2D stimuli presented on a monitor in a simultaneous visual discrimination task.	•Initially, when using positive reinforcement alone, most octopuses did not learn the original task. •Learning improved significantly when trained with incorrect choice signals which were visually indicated – Octopuses learned quickly and completed several reversals with fewer errors. •Exhibited successful performance and progressive improvement in spatial discrimination-based reversal experiment, indicating behavioural flexibility beyond simple discrimination learning contingent on experimental conditions.
Guidetti et al. (2021)	*Octopus bimaculoides*	Multispectral analysis and mapping to analyse the skin. Used calibration curves to semi-quantitatively map the pigments' density.	Presented detailed analysis of the identification of the spatial distribution of pigmented and structural elements. Characterised spectral response and spatial localisation of the interaction of chromatophores and iridophores.	•Identified chromatophores based on their high circularity and pulsing elements whereas the iridophores have strong reflecting and size-invariant elements. •A hierarchical arrangement is observable by the peak and dip in reflectance at certain wavelengths for the iridophores and chromatophores respectively. •Confirmed prior findings, iridophores ($2–20$ μm^2) were smaller than chromatophores ($900–12000$ μm^2) regardless of chromatophores expansion. Suggested body patterns likely arose from the skin's hierarchical organisation combining the optomechanical response of organs and cells to create texture and colours. •Majority of iridophores in octopus were found externally adjacent to lightly pigmented chromatophores - a common pattern in *D. pealeii*. •Overall, provided insights into the complexity and behaviour of the chromatic elements in the skin, which could generate rapid colour patterns for camouflage and communication.
Medeiros et al. (2021)	*O. insularis* (4)	Experiments include visual stimulation and vibration	Studied sleep behaviour and patterns and quantified different sleep	•2 distinct sleep states were identified: Quiet sleep characterised by pale skin, closed pupils, and long episodes (median 415.2 s). Active sleep is marked by dynamic skin patterns,

		tests, video recordings, and an ethogram.	and waking states.	rapid eye movements, and short episodes (median 40.8 s).
				• Active sleep occurred periodically, mostly following quiet sleep (60% recurrences between 26-39 min) mainly after Quiet sleep (82% transitions).
				• Both states were unresponsive to sensory stimulation – indicating a decreased level of arousal compared to the alert state.
				• Suggested that cephalopods followed an ultradian sleep cycle akin to amniotes.
Chung et al. (2022)	*Vampyrot euthis infernalis ,Hapaloc hlaena fasciata, Abdopus capricom icus* and *Octopus cyanea.*	MRI brain imaging techniques and phylogeneti c analysis.	Compared phylogenetical ly diurnal and nocturnal coastal and deep-sea species in neuroanatomic al adaptations linked to behaviours, different habitats, and ecological niches.	• Found distinct brain structural folding in the CNS – indicated different species have different brain structures.
				• The differences between solitary and social life are reflected in the brain structures, including cortex-like formations - Differences were linked to the habits and habitats e.g., enlargement, division, and folds in the optic lobe were associated with behavioural adaptations such as diurnal v. nocturnal activity, social v. solitary behaviours.
				• Neuroanatomical changes linked with ecological niches – reef habitats v. deep-sea.
				• Found parallels between cephalopods and vertebrate brain structures and offered a robust foundation for cognitive comparisons steering away from anthropomorphic interpretations.
Court et al. (2022)	*Sepia officinali s* hatchling s	Open-field and camouflage tests	Investigated the impact of ocean acidification and warming on hatchlings' physiology, camouflage performance, and exploratory avoidance behaviour in different substrates.	• Hatching success decreased under acidification and warming combined.
				• Acidification and warming caused delayed camouflage response in the gravel substrate compared to warming alone.
				• Displayed higher contrast and more pronounced Disruptive pattern, while background matching remained unchanged under warming.
				• Despite the challenges posed by climate change, cuttlefish camouflage and mobility remained intact – suggesting potential resilience in such conditions.

Nakajima et al. (2022)	*Sepioteuthis lessoniana*	Laboratory experiment, recordings, image analysis.	Investigated adaptation of camouflage to substrate	• Showed that squids also used chromatophores to adjust their colour based on the substrate they are on – which could alter their appearance to blend in with different surroundings. • While squid might possess distinct neural pathways controlling chromatic patterns on different body parts, a strong positive correlation existed between head and mantle colouration in camouflaging squid. • Adaptation of chromatophores to substrate reflectivity i.e., moved between substrates with varying reflectivity - their body patterning changed to match the new substrate was a significant finding. • Their defensive strategies changed as they grew and faced different predators. • Colour-changing duration of white-squid events could be relatively long. Although squids anticipated the background, the final colour was determined once they crossed the divider between substrates. • Duration of colour-changing events might be influenced by external factors like stress, feeding, weather, lighting, temperature, and interactions with other squids.
Godfrey-Smith et al. (2022)	*Octopus tetricus*	Field recordings 21 hours, 7-minute video recorded with 13 hour and 29 min captured – interactions between 4 to 8 individuals and 1543 interactions.	Provided first report for species showing throwing or projection of debris in social interaction and other contexts.	- Expulsion named 'throws' observed in frequently expelled shells, silt, and algae by releasing them from their arms and generating a forceful jet using the siphon positioned beneath their arm web - served various purposes, including interactions with fellow octopuses. - Interactions encompassed fights of varying intensity, matings, and instances where one octopus approached or reached out to another eliciting reactions such as colour or posture changes, additional reaches, ducking, or retreat. - Certain throws seemed to aim at specific individuals, supported by multiple observations: Throws made during interactions were more forceful than others and tended to involve silt rather than shells or algae.

				Throws with higher force were often accompanied by uniform or dark body patterns. Throws directed from beneath the arms had a higher chance of hitting other octopuses. - The behaviour showed a rare example of nonhuman projectile use.
Amodio & Fiorito (2022)	*Octopus vulgaris* (8: 5 males)	Experiment in 2 phases: familiarisation (exposed to mirror and control stimulus i.e., non-reflective panel or sight of conspecific) & mark test (marked with non-toxic nail polish near frontal white spots were expressed).	Preliminary investigated Mirror self-recognition to acquire data on behavioural responses towards mirror and 3 control stimuli (self-aware), and to evaluate a method, Mark test (Mirror self-recognition).	•Reaction to the mirror was not consistent among individuals: The panel group (familiar with the non-reflective panel) was more curious and exploratory towards the mirror than towards the non-reflective panel. Aggressive behaviours were only seen when the mirror was present. The social group (familiar with sights of other octopuses) exhibited similar curiosity and aggression toward both the mirror and the conspecifics. •Displayed grooming and attempts to remove the marks both without the presence of a mirror and in sham-marked individuals. Proprioceptive stimuli relative to visual stimuli triggered mark directed behaviour, suggesting performing mark-directed responses and the Mark test is a suitable paradigm. •Exploratory and agonistic responses in social groups were comparable between conditions and in some cases, consistent at the individual levels. This might indicate the establishment of a dominant-subordinate relationship within pairs of octopuses.
Poncet et al. (2022)	*Octopus vulgaris* (7)	Experiment: episodic-like memory task	Investigated if episodic-like memory ability is common across all cephalopods or species-specific.	•One octopus learned the replenishing rates during training and exhibited episodic-like memory ability. Others favoured simpler foraging strategies – avoiding familiarity, alternation, using a win-stay strategy, and being sensitive to risks. •Significant variability in the use of strategies between and within individuals during training. •Octopuses that face different environmental pressure compared to cuttlefish, might not rely on episodic-like memory for foraging optimisation. •Highlighted the different use of cognitive abilities between cuttlefish

				and octopuses, potentially influenced by varying environmental and predatory factors.
Gutnick et al. (2023)	*Octopus cyanea (3 living)*	Experiments recording the extracellular brain activity in the median superior frontal lobe and vertical lobe complex, the supraoesophageal lobe for a period of up to 12 h	Showed the feasibility of recording brain activity non-invasively from untethered, live, and larger octopuses, further providing insights into the relationship between visual learning, memory, and the MSF-VL function.	• Octopuses exhibit distinct skin colour changes during different sleep modes: pale skin colour during quiet sleep and dark colour with chromatophores on the right side during active sleep. • colour changes occur within 210 seconds, suggesting a rapid transition between sleep modes. The observed skin colour patterns suggest a connection between the cellular organisation of the MSFL-VL circuit in octopuses and the hippocampal circuits in vertebrates. • Proposed the MSF-VL circuit's function is crucial for memory consolidation, particularly in relation to tactile and chemo-tactile learning. • Reward circuits are identified with sensory inputs from arms and mouth, which provide feedback to sensory organs and subsequently to the VL system. • The suboesophageal lobes contain primary sensory input areas and lower motor control areas that are linked to the body, arms, and chromatophores.

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