Review

Octopus Consciousness: The Role of Perceptual Richness

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Abstract: It is always difficult to even advance possible dimensions of consciousness, but Birch et al., 2020 have suggested four possible dimensions and this review discusses the first, perceptual richness, with relation to octopuses. They advance acuity, bandwidth, and categorization power as possible components. It is first necessary to realize that sensory richness does not automatically lead to perceptual richness and this capacity may not be accessed by consciousness. Octopuses do not discriminate light wavelength frequency (color) but rather its plane of polarization, a dimension that we do not understand. Their eyes are laterally placed on the head, leading to monocular vision and head movements that give a sequential rather than simultaneous view of items, possibly consciously planned. Details of control of the rich sensorimotor system of the arms, with 3/5 of the neurons of the nervous system, may normally not be accessed to the brain and thus to consciousness. The chromatophore-based skin appearance system is likely open loop, and not available to the octopus' vision. Conversely, in a laboratory situation that is not ecologically valid for the octopus, learning about shapes and extents of visual figures was extensive and flexible, likely consciously planned. Similarly, octopuses' local place in and navigation around space can be guided by light polarization plane and visual landmark location and is learned and monitored. The complex array of chemical cues delivered by water and on surfaces does not fit neatly into the components above and has barely been tested but might easily be described as perceptually rich. The octopus' curiosity and drive to investigate and gain more information may mean that, apart from richness of any stimulus situation, they are consciously driven to seek out more information. This review suggests that cephalopods may not have a similar type of intelligence as the 'higher' vertebrates, they may not have similar dimensions or contents of consciousness, but that such a capacity is present nevertheless.

Keywords: consciousness; perceptual richness; octopuses; cephalopods

1. Introduction

Perception can be defined as the reception, organization, interpretation. and experience of incoming information [1]. Given that definition, what is perceptual richness? Clearly it is shaped by sensation and the abilities and limitations of the sensory receptors, yet equally it has to be shaped by the cognitive system's abilities to use such information, including learning capacity. Birch et al. [2] suggest that it should first be looked as within modalities, that richness might be high in one and low in another, so this review will look at different modalities separately. Sensory systems tend to trade off sensitivity (ability to detect a small amount of energy) with acuity (the ability to discriminate fine differences in the energy received) and high acuity would result in richness of information in terms of sensation. Many sensory systems perceive two dimensions of information in a particular sense, such as intensity and wavelength in both vision and audition for humans, and the bandwidth of that second dimension would be another measure of sensory richness. This does not hold for chemical sensing, however, where there is no obvious dimension, and yet chemicals convey a vast amount of information. A third dimension of richness is perceptual, and specifies how sophisticated an animal is in the treatment of the incoming information, what Birch et al. [2] call categorization power. This is not quite the same as learning, though learning specifies how one deals with incoming information, and it does not talk about use. There is a fourth perceptual dimension that this paper will take into

consideration. Mobile animals must be able to situate themselves in space, and even a sessile animal has to locate external items and event with regard to oneself. That capacity is spatial localization. One aspect deals with egocentric information about relationship with regard to one's position in space. Another more complex situation is the construction of a cognitive map, a representation of either the two or three-dimensional world [3]. To gather sensory information even within one sense an animal might have different channels, or receptor systems. One example is distance and contact receptor systems for chemical information—for humans in smell and taste and for octopuses in distance olfaction and sucker surface chemical reception. Perceptual processing can take place in different parts of the brain that function for different cognitive tasks, such as localization and identification in human vision (leading researchers to talk about 'blindsight'), which can lead to different access to consciousness. Although sensory richness is no guarantee of perceptual richness, complex perceptual ability also does not guarantee access to consciousness, but it may be an a priori necessity. For instance, the use of mechanoreception for balance and orientation uses complex parallel systems in many animals [4] yet is fairly automatic.

However, there is an important guide for evaluation of perceptual richness in every animal, including octopuses, von Uexcüll's [5] umwelt or sensory world. It is different for each animal; he says that "there is no real world but as many worlds as species". Despite being aware of this, human researchers tend to be anthropocentric [6], especially focused on vision, and the octopus is very different from us. Hochner [7] talks of 'embedded cognition', as motor and sensory systems are part of a larger interacting system of animal and environment, specifying and controlling cognition, behavior and consciousness [8]. Octopuses live in sea water, an efficient filter particularly of longer wavelength of light but less so of its polarization cues. Water is a good medium for conveying chemical and mechanical cues, which octopuses and other cephalopods rely heavily upon. The nearshore environment is complex and changing, demanding careful assessment of incoming information and quick decision making. The cephalopod movement control system is based on muscular hydrostats, and the resulting complexity of motor output control has led to a low-level system of subroutines controlled in the chains of ganglia that run along the dorsal arms of octopuses. There are more neurons in the arms than in the brain, so octopuses have a distributed nervous system and their decision-making locations are a matter of debate. The sophisticated skin appearance system, paradoxically, is produced by a color-blind animal for color sensitive receivers [9]. Despite the complexity of the chomatophore system [10], skin appearance may be open loop, not monitored by the eyes. Thus, to understand perceptual richness in the octopus (and other cephalopods), we need to understand not just what information is processed to what extent in which sensory modalities, but also which cognitive tasks they are utilized for [11], before speculating to what extent this information is recorded in consciousness. In addition, it is useful to have some idea of the processing center, and the octopus brain is often compared with that of mammals [12], and see Figure 1 in reference [12]. The octopus brain–body ratio is similar to that of smaller mammals [9], it has over 30 differentiated lobes and input is generally to the dorsal brain and output from the ventral. The surface of the large optic lobes has been compared to that of the fish deep retina, the peduncle lobe to the cerebellum, and the vertical lobe the seat of learning and memory, to the limbic system. The extensive arm brachial cords together make a parallel to the mammalian spinal cord.

2. Vision

The striking resemblance of the cephalopod eye to that of vertebrates, particularly mammals, is often pointed out as a fine example of convergent evolution, that the lens eye of these groups is the 'one best way' to process incoming light information. However, this resemblance is only partially true, and to understand the perceptual richness of cephalopod vision, we must know the capacities and limitations of their visual sensory system; Hanke and Kelber [13] have a good recent review. This section of the paper will examine how visual information is used to guide octopod behavior in several different situations,

including recognition and processing of visual stimuli in learned tasks, communication with conspecifics particularly with sexual signals, orientation within the environment, and self-recognition. In addition, visual information is used to guide the separate complex skin appearance system [10]. Although this review will focus on the eyes as receptors, one part of the octopus appearance system is not controlled by light entering the eye, as a modulation of chromatophore expansion is controlled in the skin itself [14]. For octopuses, opsins within the skin with a maximum sensitivity of 480 nm, close to that for the eye, are automatically triggered by higher light intensity to cause a general darkening of the skin, which is particularly useful in countershading camouflage. This is only one of the sources of information for the skin system, but it is one that is not processed by the 'normal' visual system route through the eyes.

For all other visual behavior, the receivers are the paired eyes, and they have a strong external resemblance to the vertebrate eye [13], and see Gleadall and Shashar [15] for a comparison of the visual processing. The octopus has a lens-type eye, with a similar cornea, iris, lens, and retina to that of mammals. It has light–dark adaptation of the retinal receptors, though by a different mechanism than that of vertebrates, pigment migration rather than pigment bleaching and regeneration. It has a variation of receptor density across the retina so that a particular region produces high acuity vision, but instead of the pinpoint fovea of humans there is a horizontal visual 'streak' matching the horizontal slit pupil [16] and fitted for a benthic animal that scans the horizon. The octopus has a maximum visual acuity of around 9.7′ of arc [17] similar to that of a cat or a chicken, so its spatial resolution is fairly good. For humans there are two dimensions of visual information processing: wavelength or color, and brightness or intensity [1]. We have a maximum wavelength sensitivity at about 555 nm, and octopuses' is similar at 475 nm, shifted to shorter wavelengths to match the available light. Cephalopods are not 'red blind' but red insensitive, and their bandwidth or sensitivity range is similar to that of most vertebrates. Chung and Marshall [18] found small variations of the maximum sensitivity in difference cephalopod species in different marine environments, but less for octopods, as vision is less critical to them. However, in addition humans have three separate photo-pigments in the eye, and comparison of firing of receptors containing these pigments allows us to discriminate between peak input of them and to receive what we call color. The comparisons can be mapped on 'color space' [1]. Hummingbirds have four photopigments, a wider bandwidth and, thus, a larger set of comparisons and a parallel but richer visual view of the world [19]. Mantis shrimp have a phenomenal 10–15 types [20], as well as discriminating the plane of polarization of light. This apparently high diversity producing a wider bandwidth may not translate to perception. Mantis shrimp appear to perform color recognition by scanning, rather than making comparisons and discrimination. The result is a crude color perception, and the lesson that good sensory acuity or range may not necessarily lead to perceptual richness. The less acute comparisons for sensory aspects of human visual information are dealt with by complex cognitive and affective mechanisms in the brain, clearly entering our consciousness. For instance, we identify hearts as red, even though the human heart is purple-grey [1]. Cephalopods do not experience this accompanying dimension we call color. Instead, the rhabdomes that are receptor cells in the retina are arranged geometrically, aligned in two dimension perpendicular to each other (as in insects). Octopuses process polarization plane in two channels, allowing them to discriminate the plane of polarization of light, the two-dimensional vibration of light waves [21]. We can ask how octopuses process this dimension and what perceptual richness it offers.

What richness do the cephalopods have in a sensory dimension that humans do not? Polarization acuity is measured in angle of polarization (AoP). Polarization range is unaffected by water depth, where the long wave lengths of light (red) are effectively cut off within 5 m, but since light comes through the water surface, it is often linearly polarized. There may be parallel dimension to color, in angle of polarization, linear polarization background, and intensity. Polarization sensitivity is attenuated at distances more than 12 m, so they are relatively short-range cues but this is quite a distance for

animals who generally weigh less than 1 kg in weight. According to Temple et al. [21], octopus polarization sensitivity is good because it is received in these retinal cells oriented in two dimensions 90 degrees from each other. They tested by projecting a looming stimulus onto a viewing screen and noted that the sensitivity to angular polarization (AoP) depended on a background of linear polarization (DoLP). At their best, octopus discrimination of polarization difference (PD), which would be similar to the visual frequency discrimination in color perception, was one degree of radius. This suggests acuity although we have no comparison. Luminance and polarization contrast sensitivity peak at the same spatial frequency and both decrease at low spatial frequency, which suggest that they are processed via similar pathways [22]. What is the function of this polarization sensitivity? Use of light polarization has been tested mostly in cuttlefish, but there is no reason to think that it would be different in octopuses. Polarized vision allows them to detect an object, such as a potential predator, more effectively in turbid waters [23]. In addition, both polarization and visual landmarks can be used as guides for Y-maze navigation, so the combination of two types of visual information suggests good localization acuity. However, when faced with conflicting information, the majority of animals followed the e-vector. This use in navigation is perhaps not surprising when one considers the well-known dependence on polarization cues by bees for navigation in flight, communicated by dance [24], a similar task. However, the cues available for navigation likely have to be learned by octopuses and see that ability later in this discussion. Perception of light polarization is known to 'break' the camouflage of shiny reflective fishes [25], and transparent prey [26]. This aids in predation for cuttlefish [27], though likely not much for octopuses except as paralarvae. Although it has not been tested, these cues to prey identity need not be available to consciousness. Lastly, polarization patterns appear on the arms of cuttlefish, though Mäthger et al. [28] speculate that in them and in squid, this may be a 'by-product' of iridescence, so their communicative function remains unproven. However, cues to identity of sex used in reproduction may be more automatically processed [29].

Another way in which octopus vision differs from humans', although not from that of other vertebrates such as birds, is that they have laterally placed eyes and thus monocular vision. Information from one eye feeds only into one half of the brain. When visual information feeds into bilateral brains, lateral separation of visual specialization is common for animals across many phyla. This means that different kinds of information are primarily processed by one or the other half of the brain, which might lead to better categorization power. It also touches on the debate of brain lateralization as to where consciousness is 'located' in the brain, particularly as birds have separate processing of different types of information in the two halves, and no cross-transfer [30].

There are several consequences for octopuses to have monocular vision. Cuttlefish, who have some frontal binocular overlap of the two eyes due to convergence, do have stereopsis and can use information from both eyes to judge distance and depth. When stereopsis is used, both time and distance to prey capture by tentacular strike are shorter [31], indicating improved predation efficiency and thus likely better three-dimensional spatial localization. However, no such overlap of the visual fields is apparent in octopuses [13], who have, so to speak, traded off a wide field of view for less acute location information. As a result, when octopuses crawl across the sea bottom, they are predominantly guided by one eye, and the modal heading is 45% to right or left of straight ahead [32]. Monocular vision is widespread in vertebrates and insects and to make up for this localization deficiency, many animals with lateral eyes use motion parallax, shifting the position of the head or the eyes to achieve different sequential rather than simultaneous views of a target location [33]. When arboreal species come to a location for jumping to a new target, they often stop, make lateral head movements and then execute the jump. Such a sequence of actions must be guided by consciousness and a knowledge of the necessity to gain more information about the environment and is a case where lessor sensory acuity is compensated for by behavior. Vertical 'head bobs' are commonly produced by octopuses, but as they do not normally use visually guided prey capture, these head movements are performed more widely in a

number of situations. In parallel with those of other animals, octopus head bobs must be consciously initiated. They appear to be produced in 'situations of interest' [29], including viewing one's reflection in a mirror (Mather et al. in sub). Although more investigation is needed to explore exactly what cues trigger this action, knowing that one 'needs' more information in a given situation, taking action to obtain it and only then acting on it must be guided by awareness [34,35].

Another consequence of having lateralized eyes and monocular vision is that information is delivered to two separate brain locations. How is it dealt with, and how might this affect where and how conscious decisions are made? Lateralization of allocation of information processing has been extensively studied in humans, who have binocular vision [30]. For body self-consciousness, Ionta et al. [36] concluded that there is a bilateral network but a right hemisphere dominance. Although bilateral brains seem to allocate specific cognitive processing specialties to one side or the other, might this be more likely if the visual input was divided? The avian brain is a good 'test case', as each lateral eye sends input to the contralateral hemisphere and there is little callosal transfer [30]. Indeed, the left hemisphere attends to routine repetitive stimuli, and the right is more vigilant and attends to novel stimuli. Early researchers found that octopuses that learned visual shape discrimination using one eye had not stored it so that they could access it with the other [37]. However, they could do so the following day when the information storage had crossed to the other side of the brain. These researchers also did not appreciate that octopuses were functionally monocular. Initially, this lack of binocular vision hampered octopuses' ability to follow detours in a maze task [38], although after being 'trained' by the sight of a crab stimulus being pulled down the detour corridor they could perform the task. They were often confused if they had been blinded in one eye and switched head position and thus eye use. If the optic commissure was cut, the octopuses could only perform a detour task if they did it quickly [39], because later they could not rely on the stored memory trace. What we might call their categorization power was better than that of birds but lesser than that of binocular animals.

Initially it was thought that lateralization of function was true only for vertebrates and was connected to sociality and the necessity of keeping contact with the group. However, Byrne et al. [40] found that asocial octopuses would preferentially track a plastic model of a crab moved outside their tank with one eye. Later investigation [41] with the same task showed that nearly all octopuses had a side preference for viewing, but that it could be either left or right. When octopuses were given both a prey recognition task and a t-maze to solve, there was no asymmetry in maze exploration, so lateralization appeared context-dependent [42]. The brain lateralization seemed clearer for cuttlefish. Juveniles tested in a t-maze gradually developed a left turning bias, but only when shelter was provided at the end of the maze arm [43]. This preference was modulated by pre-hatching experience, as it only developed in cuttlefish exposed to predator odor before hatching [44]. More extensive testing revealed that the same species had different lateralized preferences in predatory and anti-predator situations [45]. These studies suggest that cephalopods have the same lateralization preferences and thus the same brain lateral specialization as vertebrates, but the preferences does not depend on monocular vision or lateralized information storage. The question remains the same one as for vertebrates—is there unity of consciousness, and where is it 'located' in the brain?

The ability of octopuses to process visual shapes, a test of categorization power, was evaluated in Naples in the 1950s and 1960s in a situation which was not ecologically valid for them [6] but normal for mammals. Octopuses were rewarded for contacting the positive one of a pair of shapes and given a small shock for contacting the other [37]. Sutherland found that they were able to discriminate between a vertically and a horizontally aligned rectangle, though less able to discriminate between obliques (as are mammals). He theorized that these extents were cues used to encode differences, then tried other shapes. Octopuses were able to discriminate a W shape from a V one, and a square from a circle [46]. Muntz and Gwyther [47] found these animals could distinguish circles

of different sizes, including when they were placed at different distances. So they had some depth perception to combine with the visual encoding. The authors theorized that octopuses must be monitoring accommodation in the eye, though this has not been tested. It became apparent that an octopus could use several different cues, depending on which was rewarded, and, thus, were learning what to learn. When they were given two different cues, brightness and shape orientation, for the same discrimination, they learned faster than with one, and subsequent testing revealed that some mostly used one of the cues and some the other. A separate group trained to use one cue and then switched to another one took longer to 'unlearn' the first cue and learn the second. When an orientation cue was too difficult for discrimination, octopuses could be trained to use it by being given easy contrasts and then finer and finer discriminations [37]; acuity could be trained. Subsequently researchers found that octopuses could use conditional discrimination with these cues, when it was positive during one environmental situation, aeration on, and negative when the aeration was off [48]. Octopuses could also learn these visual cues to perform reversal learning, when the positive choice was well learned it was switched so that it became the negative, and so on [49]. Finally, cuttlefish could use visual cues associated with a preferred prey at a particular time (What, where, when), which is considered to be episodic-like memory [50]. Although memory per se does not prove an animal has consciousness, clearly the flexibility of assessment and use of these visual spatial clues supports the idea. Although this discrimination between shapes gives a clue to visual spatial learning, a different task, finding out what smaller cues support reconstruction of a whole figure, gives parallel results. When background matching, cuttlefish match skin patterns equally well to completed circles and to fragmented ones [51], though not to scattered components. Lin and Chiao [52] showed that cuttlefish could transfer learning of prey images to one that was reduced in size or contour, to a sketch or a silhouette, and, again, when it was partly occluded. Images did not need to be faithfully matched but the whole could be recognized from its parts, another proof of categorization power and suggesting Gestalt perception.

Vision is often used by vertebrates for a different task, self-monitoring, and Gallup's [53] mirror task was once considered an important one for evaluation of animal cognition and awareness. He used the recognition of oneself and of a mark on one's body surface in the mirror as a sign of intelligence. Yet, animals that failed the mirror test could use the visual reflection to perform mirror-guided behavior in navigation tasks. Self-recognition in a mirror clearly discriminates on the basis of the likelihood of self-grooming and dominant use of vision [54]. The ecological situation of the species involved is important [7]. Many intelligent species 'fail' the mirror test, and wrasse fish which groom ectoparasites from other species may pass it [55]. Octopuses do not recognize themselves in a mirror (Mather et al., in prep), and their self-recognition may be chemical [56]. Instead, octopuses perceive that the situation is abnormal and attempt to 'make the animal move' with directed 'passing cloud' skin pattern displays [57], which appeared to attempt to startle prey in another species. Again, the animals seem to know that more information is needed and behave in such a way that might provide it. The lack of visual self-recognition is an obvious limitation in the octopus' use of vision, yet the moving skin display shows a parallel with the head bob, the apparent recognition of lack of information leading to an attempt to gain more.

The limitation on visual self-monitoring brings up a problem. Given the large proportion of the nervous system in the arms, does the computation power of the many ganglia and arm-arm connection by the supra-brachial commissure mean that the brain does not 'know what the arms are doing' and they are instead a separate decision-making system? Grasso [58] produced an elegant model of the possible computation by the interacting ganglia that would produce such control, and Carls-Diamante [59] philosophized what such a separate system might be doing to program decisions. Researchers [60] have not been able to find a somatotopic body-centered 'map' in the octopus brain. Yet, cephalopods can use visual information about the arms. Cuttlefish position arms in appropriate positions to camouflage against the background, extending their arms parallel to nearby lines [61] and

raising papillae when they are on rough surfaces [62]. Octopuses [63] and squid [64] weave arms into a tangle that mimics algae. There is no reason to suspect that consciousness is necessary for camouflaging imitative behavior, however. In fact, cuttlefish skin displays were not altered by the placement of a 'cuff' behind the head so that the animal could not self-monitor its camouflaging appearance [65]. Still, octopus arm choice in a reaching task is strongly influenced by eye use, suggesting visual guidance [66]. Gutnick et al. [67] showed that octopuses can learn to visually guide an arm through a Y-maze. Additionally, when an octopus has learned a kinesthetic cue for arm guidance in a similar task, other arms that have not been used in learning can perform the appropriate movement [68]. Thus, it is the central brain and not the arm that has learned the choice. These results predict that the visual monitoring of guidance of arm movement is possible but not essential, that the brain is guiding task learning, but also that conscious monitoring of the details of output is not much involved.

What of the rich and complex skin appearance system [10], how is it perceived by the octopus visual system? Packard [9] was the first but not the last to point out that it was aimed at and shaped by the vertebrate, particularly the fish, visual system. The cephalopod skin system is apparently tuned to the color sensitivity of vertebrates [65] although the octopus camouflage system picks out features of the background and not its general appearance for matching [69]. Only a few octopod species use visual signals on the skin to communicate to conspecifics. One directs raised white papillae on a dark brown background to females, with the area of the display correlated to amount of arousal [70]. Species of the genus Abdopus have a male longitudinal stripe display both to females and to rival males [71] but there appears no sophistication in its use, and sexual signals are generally likely to be automatic. The situation is quite different in cuttlefish and squid, although Sepia apama cuttlefish have conspicuous sexual displays and inconspicuous camouflage ones [51]. Most of the reports of squid displays are repertoires, although Mather [72] has a detailed report of the use of sexual displays in the Caribbean reef squid. Different displays are conspicuously different, especially seen in black and white. However, the squid have excellent modulation of display intensity. The agonistic Zebra can vary in intensity of the expansion of the dark areas, of expansion of other chromatophores as background and spatial extent of the display itself, as well as other components such as 'accessory' fin base stripe and spread of the arms. Intensity of Zebra is cued to the situation of male–male encounters, and there is also a ritualized Formal Zebra with predictable amount of display and relative position of the opponents [72]. Squid here reveal the bilateral control of motor output, as a display can be made on one side of the animal only, and a sexual display can be shown to a female on one side when an agonistic one is being given to a male rival on the other; also see Brown et al. [73] for cuttlefish. However, there is no evidence that consciousness in involved despite the production richness, as sexual signals are usually fairly automatic.

For a more ecologically valid situation in which visual information is important, it is useful to look at monitoring one's position in space. The distribution of the soft-bodied octopuses is limited by shelter availability and, perhaps as a result, they are central place foragers. This is true to some extent for the cuttlefish Sepia apama as well [74]. Although long distance movements may be more dependent on perception of temperature differences or other cues about the water, or on day–night cycles [75], short distance navigation depends more on visual information. Direct observation of movement [76,77] or sonic tracking [78,79] was necessary to confirm how the animals moved in space. Such fine-grained analysis was particularly true for Mather [78]. Octopuses moved out from their 'den' after a pause for orientation and in many cases moved out of sight of the den. Surface chemical cues would be used if octopuses returned along their outgoing path, but they jetted mantle-first in the water and returned from a different angle than they had left from. When displaced, octopuses did not retrace to the nearest segment of the path but often returned directly home, which suggested they had some kind of cognitive map of the occupied space, demonstrating categorization power. Further, both Mather [78]

and Forsythe and Hanlon [77] noted that octopus did not hunt in the areas that they had visited over the last few days. They were win-switch foragers, and had built up a working memory of where they had hunted and avoided these locations in the short term.

Laboratory testing for visual direction of movement, to confirm these abilities, also used cuttlefish as subjects. Mather [76] found octopuses in the laboratory could learn to go to visual landmarks for a food reward and followed the landmark when it was displaced. Boal et al. [80] gave octopuses the opportunity to explore a novel arena and to visually locate an open escape burrow. They remember its location for a week and were able to learn a reversal to use a previously blocked borrow more quickly. Cuttlefish [81] were able to solve a similar problem and learn the same reversals, using visual cues. Both species could conditionally discriminate, solving two mazes with different choices by the guidance of disparate visual cues [82]. Again, cuttlefish could be trained to use place or either proximal or distal visual cues to direct their choice in a t-maze [83] and were capable of both strategies. Cuttlefish, who are predominantly but not exclusively benthic, could learn to take a more direct path to shelter that involved moving over a vertical barrier [84] and preferred vertical rather than horizontal information when it was available [85]. These studies emphasize the flexibility of use of visual landmark information, important in the complex changing marine environment. However, Cartron et al. [86] found that cuttlefish could also use information about the polarization of light to navigate. In fact, when given a conflict, they preferred to follow the e-vector of the light. Although this ability has not been well investigated, we can see that there is indeed a rich set of visual information available to use for location in space by the octopus. However, these situations in testing are very simplistic, and see Cheng and Newcombe [3] for far more sophisticated models and directed testing.

What of brain involvement in this perceptual task? The vertical lobe of cephalopods is recognized as the area controlling visual memory acquisition. In cuttlefish, lesions in the ventral vertical lobe led to reduced acquisition of spatial learning, and in the dorsal lobe to excess motor activity and poorer long-term retention of spatial information [87]. Jozet-Alves et al. [88] found a difference between the sexes which might be the result of anatomy and which could be linked to visually guided mobility and range size. Mature male cuttlefish travelled further in an open field test than immature ones, and when tested in a t-maze were more likely to use visual cues for orientation than females and immatures. This dichotomy may be more general amongst the cephalopods. At maturity, female octopuses begin to restrict their movement, and males move towards them to attempt to initiate mating (using chemical cues? See the next section). This is paralleled by Caribbean reef squid; as females mature they become more place faithful. In contrast, males compete for access to females, and leave to monitor other groups if they lose or even, after a day or two, if they win the consortship of a female and mate with her [30]. Again, male–female differences in perceptual abilities maybe be the result of embodiment [7] of the octopuses and other cephalopods in their life history strategies.

3. Chemical Sensing

Octopuses likely have acute sensitivity to a variety of chemical cues, but the information from research about their chemical sensing is scattered and often simplistic. Chemicals are delivered to octopuses both from a distance as water-borne and by contact with the sensors in the suckers, where there are estimated to be 10,000 receptors in each sucker. Water is a good carrier of chemicals and also, because of its relatively high specific gravity, of mechanical cues. Although air is thought of by humans as an 'empty' space between items, water is an excellent conveyer and modifier of information. What is impressive about this sensory system is the variety of chemicals and the variety of types of information that are conveyed, probably at the same time, that must be sorted out and that need different, often very quick responses. Additionally, contrary to humans' impression, many animals not only receive directional information from and also navigate by odor plumes [89].

Water-borne chemicals such as predator cues and chemical from damaged tissue can have a negative affect. This is particularly true for neritic squid, who 'have nowhere to hide'. Chemicals are assessed by the paired olfactory organs in squid [90] and are often cues for escape reactions. Chemicals such as paraben and K+ blockers, and also squid ink, caused strong escape jets when they were passed over an olfactory organ, but when the organ was anaesthetized, no escape occurred. The use of ink is an interesting system. Ink, which contains melanin, is an alarm cue causing antipredator behavior and flight in squid [91] but is also an antipredator repellent against fish [91,92]. In pygmy squid, blobs of ink are released as decoys and the squid turns pale, changes direction sharply and escapes [93], but ink can be used by the same species as a 'smoke screen'. Boal and Golden [94] found cuttlefish increased their ventilation rate to conspecific ink as well. Still, chemicals are documented as alarm cues in squid and cuttlefish and the effectiveness of the olfactory organ been proven, but this has not been true so far for octopuses even though they eject ink.

Polese et al. [95] studied the structure of the octopus olfactory organ and identified olfactory sensory receptors within it. They also [96] suggested that chemicals received by the olfactory organ could control reproduction. Given that octopuses mostly do not have visual cues to sex and that males are attracted to females from a distance, the presence of pheromones is likely true but has not been definitively proven. Water from tanks with conspecifics can increase arousal, as blue-ringed octopuses exposed to water from different-sex and same-sex conspecifics had different responses [97]. Females increased their ventilation rates to males but not females, males initially showed no response but significantly increased their ventilation rate over time. Walderon et al. [98] found females increased ventilation rate to water from males, but the results were mixed for males. When given the opportunity to move, both sexes oriented on the side of a Y maze where same sex conspecifics had been. Since they did not orient to locations with food odors, their situation may not have been straightforward. Boal and Golden [94] also found that cuttlefish increased their ventilation rate to water from conspecifics' tanks, yet Boal and Marsh [99] found that they did not move up a Y maze to this cue. The link between mechanism and behavior seems obvious, however has clearly not yet been made. However, cognition might not be involved in such vital and automatic reproductive behaviors.

Researchers also delivered a variety of water-borne chemicals that should be associated with food to cephalopods. Boyle [100] found that Eledone responded with increased ventilation rate to some but not all food-related chemicals, and Lee [101] that octopuses oriented to a variety of food-associated chemical cue in a Y maze, though not to betaine and taurine. These are simplistic situations for odor responses, but fortunately that is not all the research on exposure to chemicals. Darmaillacq et al. [102] studied the long-term effect of exposure to cuttlefish even before hatching, mostly to visual stimuli but sometimes to chemicals. Guibe et al. [103] found that early exposure to potential prey odor changed prey preference, and Jozet-Alves and Hebert [44] that exposure to predator odor changed lateralization to form a left-turning bias. Such long-term memory needs to be studied further.

Studies of the chemical sensitivity of the suckers are similarly scattered. It is only recently that van Giesen et al. [104] looked at the anatomy and physiology of sucker chemoreceptors. They found that octopuses had evolved a set of chemotactile receptors that detected chemicals that were poorly soluble in water. They are both diverse and used in combination, and account somewhat for the diversity of contact chemical signals that octopuses can respond to. Long ago, Wells [105] produced behavioral data about this expertise. He trained octopuses to discriminate cylinders soaked in a variety of solutions, such as sea water, hydrochloric acid, sucrose, and quinine, and diluted the solutions until they were 100 times as dilute as humans were supposed to be able to discriminate. The octopuses' consistent correct discrimination meant that this was well above their threshold. They were also able to discriminate between 'normal' sea water and both diluted and concentrated solutions. This is the only study that gives us an idea of the very high acuity

of this receptor system, though it is logical given the necessity of recognizing potential unseen food chemically [106]. Additionally, while quinine may not occur naturally in the cephalopod's habitat, cuttlefish quickly learned not to attack preferred prey on whose exoskeleton quinine had been 'painted'. Their attack latency increased considerably, but they also approached tentatively with a single arm contact and tried to 'wipe' or 'blow' the chemical off the carapace of the prey. Such rejecting behavior was also true for octopuses encountering stinging sea anemones [107] and scallops with encrusting sponges [108]. This variety of responses reminds us of the behavioral flexibility of octopuses, who might have encountered many different encrusting organisms and may use categorization power to discriminate different ones and choose a variety of appropriate actions.

4. Mechanoreception

The high specific gravity of water suggests that mechanical deformation will be more easily conveyed than it is in air, and that marine animals will use it often and in diverse situations. Mechanoreception is used in the balance system, reception of water deformation, contact touch cues and internal proprioception. The specialized receptors of animals on land receive and transform sound, and we call these hearing systems. A fundamental misunderstanding of this transformation led to Moynihan [109] to suggest that cephalopods might be 'deaf' as if they needed to be functional in air, and Hanlon and Budelmann [110] replied with a better description of the sensory systems involved in the animals' medium. Squid and cuttlefish, though not octopuses, have lines of ciliated receptors on the head, which are sensitive to water movements [111,112], and years later Mooney et al. [113] demonstrated that squid do respond to sounds and habituate their response to them. Both vision and mechanoreception are used by squid in predator evasion [114] although different 'tactics' are used by paralarvae and juvenile/adult stages. The variety of responses tuned to different sounds is similar to those produced to chemical cues of predators and clearly demonstrates categorization power. Some kind of statocyst system receiving distance mechanical cues about the forces exerted by gravity and one's movement are almost universal in mobile animals. Cephalopods have evolved a three-dimensional balance system that is very similar to the inner ear of vertebrates [4], yet in both phyla the responses are automatic movements of body muscles or eye position, only monitored in case of failure.

The Naples research team used contact tactile stimuli in parallel with the studies on vision. Initially they believed that octopuses could not integrate touch information from the suckers with proprioception measuring muscle stretch and would, therefore, not discriminate textures but rather measured the amount of sucker surface area that contacted the test cylinders [37]. Octopuses 'scan' surfaces by moving suckers along them, which might also eliminate orientation cues. This was not strictly true, as octopuses could learn to tell a square from a cube, apparently by the sharp change in angle of the figures at the corners. A lack of integration of proprioceptive and tactile input would also account for their inability to discriminate object weights [37]. Additionally, Grasso's [115] observational study of sucker-arm coordination talks of close and further-away sucker–sucker coordination, as well as attachment patterns he describes as arm walk, arm lift, and octopus lift. Octopuses can use arms as a suction surface for grasping but equally, each sucker can fold to form a pincer grasp, resulting in their ability to untie knots in surgical silk. Neighboring arms can be recruited to aid in a reaching task [66] or different arms can perform complimentary actions to move while maintaining camouflage [63]. All this coordination may easily be controlled below the level of the brain, so that the richness of the tactile-motor-proprioceptive coordination is monitored at the local level and is not available to the brain and, thus, to consciousness.

5. Conclusions

In addition to the fact that perceptual systems are complex and (equally importantly) that cephalopod such as the octopus are poorly known, there are four conclusion that emerge from this exploration of their perceptual richness:

(1) Perception and cognition must adapt to the environment, and Hochner's [7] embodied cognition gives us a place to start when we evaluate a marine animal . . . or one that is terrestrial or even airborne. It is not a dictum, though. Cetaceans and cephalopods live in the same ocean and they differ very much in sociality, mechanoreception, movement coordination, and even what medium they use for respiration. However, they have nevertheless adapted their perceptions, actions and even life history to the medium;

(2) Complexity and access to consciousness is likely system or even task specific. Octopuses fail the mirror test because their source of self-recognition is not visual but probably chemical; we have been testing the wrong sense for the situation. P-richness [2] can vary within as well as across modalities. Even though the visual system is important for skin pattern camouflage, its production does not appear to be monitored and the output is not accessible to the animal's senses. Conversely, two different visual cue types, geometric use of landmarks and plane of polarization of light, make a rich source of visual information for navigation. Where to go in space is learned and may be consciously monitored;

(3) Sensory richness does not guarantee perceptual richness, and even a rich perceptual representation, as measured by acuity or bandwidth, may not be accessible to consciousness. Thus the sophisticated arm movement system combines touch and chemical sensors, muscular allocation and sucker and even arm movements, but although arm position can be monitored by the brain, it does not normally receive close details of arm actions, which are, thus, not usually available to consciousness;

(4) Flexibility is a major characteristic of the octopus, and its drive to gain information shapes its actions. Some of these are consciously monitored, at least in allocation of attention, as in Baars' [36] global workspace. Not enough information from the lateral eye causes the octopus to use a head bob to gain more depth cues. The fact that most benthic marine animals are in hiding leads it to a two-step foraging strategy. First the octopus goes with visual guidance to where prey are likely to be and then finds them with the flexible arms through chemical cues, even though they cannot be seen. Later, the animal remembers where it found them [105]. The pressure of many predators leads to a many-step set of reactions as the threat gets larger and perhaps generates the octopuses' mantra: If at first you do not succeed, get some more information and try something else.

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