

Review

The Case for Octopus Consciousness: Unity

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Abstract: Birch et al. suggest that consciousness in any animal group must involve four aspects—perceptual richness, evaluative richness (affectivity), integration at one time (unity), and integration across time (temporality). This review will evaluate integration at one time in cephalopods, an area that offers many challenges. First, like most animals with a bilateral nervous system, cephalopods have laterality of brain function, and this challenges unity of function. Second, unlike most mammals, cephalopods have a heavy allocation of both neural and behavioural control to the periphery, especially in the case of octopuses. Third, like all animals, cephalopods gather information through several senses and there can be both unity within and competition between such information, challenging unity. Information gained across all these areas needs to be evaluated both in terms of the methodology used to gather information and the results of the investigation.

Keywords: consciousness; unity; octopuses; cephalopods

In an evaluation of the evidence for consciousness in animals, Birch et al. [1] have argued that an approach examining the biological competence of an animal group can lay the foundation for assessing a unitary consciousness. Thus, he proposed that we should evaluate perceptual richness, unity of function, temporality of use of information across time, and affective assessment of information. The present paper presents information about the unity of handling of information in the octopus, both in terms of lateralization of brain use of sensory information and of central control of peripheral input. One of the important concepts that needs to be evaluated when we are looking for consciousness in any animal is that of unity. Is there one locus at which information is generally assessed and at which decisions are made and output planned? In the case of octopuses, there is both lateralized and central-peripheral allocation. Additionally, how much is the incoming information integrated before decisions are made? This paper addresses these three areas of functioning.

1. Lateralization of Control of Learning

1.1. Task Specific Lateralized Performance

The study of lateralization of brain control has a long and wide history of investigation in many species and groups, which must be a background for investigation in any single group. Gunturkun [2] provided a comprehensive review of this area of functioning, both historically and in terms of topic areas. He points out that early investigation included non-human animals, but that later, anthropocentrism narrowed our investigation to humans and particularly to the study of those with the corpus callosum split, leading to an apparent division of consciousness. Within the last 50 years, research targets for laterality have spread to other animal species, particularly those who have monocular vision from lateral eyes and especially birds, with limited callosal transfer across the brain [3]. One of the central questions about the development of lateralization is that of evolutionary advantage: what value would there be in specializing? Another major area of research is ontogenetic: how might specialization be genetically programmed and what environmental influences might trigger its development? As usual for the cephalopods, studies addressing these questions are few and scattered. Birch et al. [1] suggest that for evaluation of unity across



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the two halves of the brain, we should look at the tasks of interocular transfer, visuospatial biases, cross-modal integration, and multi-tasking. To review such specialization, see below.

By definition, research on the lateralization of animal brains attempts to find the opposite of unity, which is that control of at least some functions of the brain are separate from each other spatially [3,4]. It was originally argued that lateralization of function separated responses to social stimuli from those to non-social, but this division was not inclusive, as solitary animals also have lateral preferences. A second suggestion was the separation of control of different cognitive tasks, so that each could be more efficiently carried out by one brain half. Yet a third suggestion was that there was an evolutionary advantage to being able to use one eye and brain half for routine tasks and foraging, while the other was keeping track of novel stimuli, such as predators and perhaps conspecifics and social situations. Both octopuses and cuttlefish have been studied for such a division, the second with more success. However, it should first be mentioned that the midwater jewel squid because of its array of photophores, has a clear lateralization of visual structure and function [5]. The left eye is large and sensitive, the right one much smaller and more 'normal' for cephalopod eyes. In the midwater dim-light environment, there is a large advantage to picking up the small amount of light filtering down from the surface, but many species in the deeps produce their own light as bioluminescence so there is also an advantage to being able to pick up the light from them. The eyes of jewel squid serve the two separate functions. In their natural environment, jewel squid orient obliquely head-downward so that the left sensitive eye picks up downwelling light and the right less sensitive one is able to look for signals about prey and conspecifics, a dual specialization at the same time. The array of small photophores also matches the downwelling light for visual camouflage. Unfortunately, there is no assessment of either behaviour or the brain allocation to these different processing tasks.

Lateral dominance of one side in response to a visual task was first studied in octopuses by Byrne et al. [6–8]. They noticed that octopuses were normally monocular and tested them in a situation that might have mimicked prey recognition. With an octopus sitting in its aquarium, they moved a small plastic model of a crab outside the glass side of the tank (the first of the paired tasks suggested above) and noted the choice of eye with which the individual octopus tracked its motion. Most of the animals preferentially tracked with one eye [6] and the authors subsequently found that the laterality allocation followed an antisymmetric distribution [7], with equal numbers of octopuses showing left or right eye dominance for the task. Subsequent studies showed that arm use was also specialized, and that frontal arms were predominantly used for a reaching task [8], even though arms were structurally equipotential. During this task, arm choice for reaching into the water followed visual gaze, though not for locations along the substrate. However, Frasinelli et al. [9] did not find a similar pattern of lateralization and argued that lateral functional allocation might be task specific. They used a prey capture paradigm, but with the crab within the octopus' tank, not moving outside. They also tracked octopuses moving in a T maze with two sequential turn choices but no reward, again finding no side turn bias. Since octopuses are known and tested for such biases in standard situations, the difference here might have been that there was no reward in the test, but the particular set of variables that triggers different choices needs more study.

In terms of ecological validity, octopuses are not the best cephalopod choice to study visual lateralization. Although they have been studied for their responses to visual stimuli for decades, they find prey by chemotactile search, initially orienting to likely sites by vision [10], so lateralization of the use and storage of sensory stimuli might need to be evaluated in more than one sense (see the discussion below). Cuttlefish (see studies starting with Messenger, 1968) have visually guided prey capture and are a better model for studying task-specific dominance of lateralized visual fields for different situations, although they also have binocular vision. Such a strong allocation of information processing to the visual modality allowed researchers to study the aspects of laterality discussed by Gunturkun [2], including developmental influences and evolutionary advantage. Unusually

for cephalopods, the cuttlefish has relatively large eggs and hatchlings, and influences on behaviour can be studied not only in very young individuals but also on the embryos [11]. Thus, Jozet-Alves et al. [12] tested the turning preference of cuttlefish in a T-shaped apparatus over the first 30 days of life and found that they gradually developed a left turn bias but only when shelter was placed at the end of the two arms of the apparatus. This bias was present at age 30 days if the cuttlefish was exposed to predator odour as well [13] and was also present three days after hatching if the cuttlefish had been exposed to the predator odour as embryos. Cuttlefish also had some structural brain asymmetries at 30 days of life [13]. One, a larger right peduncle lobe and more monoamines in the left optic lobe, was not associated with turning bias. However, another, differences in individuals in the size of the right optic and right side of the vertical lobe, correlated with turn biases, although the investigation was not extended past such relationships. Schnell et al. [14] carried the laterality research in a different direction. They established that there was true laterality [14] in that cuttlefish preferentially used the right eye to scan from the shelter into a circular open arena, and that they chose a rightward-placed prey item over a left side one when given a simultaneous choice. When placed on a substrate divided laterally into areas of different brightness, cuttlefish chose to more closely match a brighter right side [15]. Tapping into the idea of an evolutionary advantage for lateralization, they [16] found that giant Australian cuttlefish males preferred to use the right eye in agonistic interactions, but that males who used the left side presentation were more likely to win the interactions. Nevertheless, males preferentially approached females from the left side, and they had more success in attaining mating if they moved towards a female from the left.

A summary of the information about lateral allocation of different functions in the cephalopods would suggest that we can make no conclusion thus far. There is too much contradictory information, several different tasks, and a significant proportion of the subjects who are not lateralized. Even when there are consistent differences, it is not obvious that these are the choice of eye use, and the results from several different tests, including gaze as well as turns in a maze, may not correlate well. Surprisingly, there was an experimental situation carried on in the 1950s and 1960s by a research group in Naples and funded by the US Office of Naval Research that attempted to understand octopus brain function, including lateralization. The strength of this research lies in the fact that they tested lateralization of control in not just the visual but also the tactile modality.

1.2. Location of the Storage of Learned Visual and Tactile Discrimination in Octopuses

Researchers at Naples performed a unified investigation to find brain behavioural links in the octopus (see Wells [17] for a review). This began with an attempt to find out how the octopus encoded visual shapes [18] but extended to the function of the brain in cognition and memory as well. The basic paradigm was a simple one. Octopuses are vulnerable, so they normally shelter in a protective 'home', from which they emerge to search for prey [19]. In the laboratory, such a shelter was built with a few bricks at one end of a tank, and stimuli were presented at the other end. Visual stimuli (figures) were presented sequentially, with touches by the arms (attacks) within 20 s on the positive stimulus being rewarded with a small piece of fish and those on the negative stimulus being given a small 10 V electric shock. Animals learned quickly and had a high rate of performance (80% correct responses), particularly with the contrast between a white rectangle oriented vertically and one oriented horizontally (note that octopuses are win-switch foragers [20], and as such will never have a very high response rate; see [21] for a comment about their response variability in a learning task). The paradigm is not particularly ecologically appropriate, as octopuses normally use chemotactile search to find prey [22], but they use vision for navigation, so have extensive use of this sensory modality, nevertheless.

The idea of splitting the brain centrally to find out about the unity of consciousness came about as a result of operations in humans to confine epileptic seizures by cutting the corpus callosum in patients [2]. Subsequent detailed testing revealed that visual information could be acted on by only one hemisphere at a time [4]. The individuals so

affected appeared able to perceive stimuli in the left visual field, delivered to the right brain, yet were not able to linguistically report their presence. This suggested that consciousness could reside in more than one area of the brain, though it is noticeable that while perception seemed split, subsequent actions appeared unified. No definite conclusions can be made about where consciousness 'is' in people, but this eventually led to studies on non-human animals, particularly birds, who have little information transfer across the middle of the brain [4]. One of the variations in the learning paradigm of the Naples group was to see whether octopuses' brains could be similarly cut and whether that would isolate the two halves when processing visual information [23–25].

Because octopuses have lateral eyes and monocular vision, it was fairly easy to set up a variation in the normal situation, where visual stimuli were presented 90 degrees from the midline and thus only visible in one eye (called the trained eye) and the discrimination was learned, presumably with only one half of the brain [23]. The authors speculated that cross-brain transfer would normally be complete but storage or retrieval would not be as good in the contralateral as in the ipsilateral area of the brain. They found this to be true, with performance on remembering through different 'distortions' of the figure. Additionally, transfer of the task to 'difficult' stimulus shapes, such as a diamond that had similar vertical and horizontal extents as the initial rectangle but more complex shapes, was lower in the untrained eye. In order to test for retention and transfer, there were two manipulations: removal of the vertical lobe (the processing centre for visual memory) and splitting the brain by cutting the superior frontal vertical tract. Removal of the vertical lobe produced inferior performance, depending on what percentage of the lobe was removed, impairing memory transfer. However, when the animal's brain was bisected before the training, there was no transfer to remembering stimuli introduced to the untrained eye [24]. To check this conclusion, he did a subsequent contrast of the performance with bisection before and after training [25]. When the brain was split before training, there was no transfer, and when it was split after training, the untrained eye could use the learned information. Thus, he concluded that the 'engram' or acquired information trace was normally bilaterally stored.

In a different paradigm, Wells [26] taught octopuses to perform a detour test. They viewed a crab through a window and then were forced to take a detour down a corridor where the crab could not be seen and turn to find and capture it. Previous studies had led him to believe that the octopus could not monitor the position of its body and only completed the task by following the corridor wall with its arms. However, even though glass is an unusual situation not understood by many animals, some of his subjects completed the maze, and others were taught the detour by the researchers pulling the crab down the corridor on the end of a string. To check whether the octopus needed to monitor the body position, the statocysts (balance organs) were removed, and the octopus could still complete the detour. However, the author noted that the orientation to the crab stimulus was lateral, and the octopus was performing the task monocularly, with the guidance of the eye that had first viewed the crab. When octopuses were trained to perform a detour and then had the vertical lobe removed, those that completed the detour in under one minute were successful, but those that were slower or had a delay imposed could not finish the 'run'. Wells [27] interpreted this as showing that the vertical lobe was the site of memory processing for the procedure, so the octopuses that moved quickly did not need memory, but those that were slower needed but could not use interocular transfer. In a final study [28], he cut the octopuses' commissure. This made no difference on detour performance, the expected result if visual guidance was monocular (despite bilateral storage of information). However, then, the optic commissure was cut so that each side was visually separated from the other, where he reported that octopuses moved out, returned, delayed, and chose again. He interpreted this as showing that there was 'conflict' between the guidance by the two sides of the brain. Subsequent to this, a few animals were blinded in one eye by cutting the optic nerve and he reported that the vacillation stopped, and detours were performed fairly correctly again. This series of damage and brain disruptions

means that this interpretation is compatible with an explanation of bilateral storage and monocular use of visual information, but it is far from the only possible explanation.

Although other non-visual sensory systems are highly lateralized, de Haan et al. [22] pointed out that splitting the brain to see how their functioning is allocated has not been done in vertebrates. Possibly because it was apparent that chemotactile information was important to octopuses, the Naples group carried out a series of experiments to study lateralization of touch information. Working in an era before consideration of their subjects was seen as important (it is only several years since cephalopods were protected by animal welfare legislation in the EU, anyway), they simply blinded their subjects before conducting tactile testing. Then, they delivered incised Perspex cylinders to an arm of the blinded octopuses, who tended to sit with arms outstretched [29], and rewarded them with a piece of fish or shocked them with a small electrical shock when the item was tucked under the web between the arms. Within a few trials, octopuses easily distinguished a smooth cylinder from a grooved one but could not discriminate the orientation of the grooves. When a cylinder was given to the second left arm and the octopus trained in the discrimination (three to four trials), and then it was immediately presented to the second right arm, there was no sign of right-side access to learning. If the researchers waited half an hour, the information storage had passed to the other side [30]. An octopus could also distinguish a cube from a sphere, apparently by the distortion of the suckers grasping its surface, as smoothing the corners eliminated this ability [29]. However, the octopuses could not discriminate on the basis of weight of the cylinder [31], apparently not being able to include arm proprioception information in this sensory evaluation. This is not surprising given that the arm is controlled as a muscular hydrostat [32] and the huge amount of information necessary to monitor all these muscle positions would likely overwhelm the brain. The situation of brain control and storage of tactile information was more complex than that of the visual system. Removal of the vertical lobe essentially abolished new learning, but the ability to store such information was lost when the subfrontal, median inferior frontal, and superior frontal areas of the brain were removed. It was possible to split the brain, but not just at the subfrontal, but also the cerebrobrachial tract. With this split, again the arms on one side could perform the discrimination of tactile stimuli to a high level of over 80% while the arms on the other side performed at a chance level [30]. If the animal was trained and then the commissures split, performance on the trained arm fell to 64%, suggesting that some information had been stored bilaterally. The performance of this arm was raised to 82% with more training, so it was a deficit in access to some of the stored information and not of learning *per se*. As it was for vision, bilateral storage was revealed through unilateral access and a split brain.

Physical splitting of the brain to reveal the unity of the location of consciousness in any animal is only a partial answer to whether consciousness is unitary. De Haan et al. [22] described the controversy about what happened in humans after splitting of the corpus callosum, and after nearly 2500 subsequent papers, the answer to where consciousness 'resides' is not clear. Both visual and tactile information appear to be stored bilaterally in the octopus, but does this mean that consciousness is bilateral? Looking at the data on people with split brains, de Haan et al. [22] pointed out that perception appears to be lateralized while actions are bilateral. Discussing what these studies tell us, Godfrey-Smith [33] pointed out that a person or animal is a coherent unified agent, presumably with consciousness. As an agent, it has a point of view (also see [34]). He suggested that the mind, rather than being a 'thing' located in a part of the brain, should be seen as a pattern of brain activity, and this description would make it easier to see that separate vs. unified allocation is a flexible expression of such patterns.

2. Central-Peripheral Allocation of Control: The Arms

To understand the possibility of centralised vs. distributed control of the body, especially of the arms, of octopuses, some basic physiology is necessary. There are two ways in which cephalopod control of action is 'special' in the animal kingdom. One is that the

structural motor system consists of muscular hydrostats, as there are no fixed skeletal structures. The second is probably a consequence of the first, in that extensive and perhaps redundant neural structures control arm movement. This is most obvious in the octopus, where 3/5 of its neurons are in the arms, including tactile and chemical receptors, and the nerve cord is realized as a chain of linked ganglia down the length of the arm, each of which controls a sucker ganglion and also connects to the next-door ganglia (see [35] Figure 5.2). Yet, there is not a large set of either afferents from the brain or efferents back from the arms to the central nervous system [36], as if indeed the brain leaves details of movement and sensation to the periphery. Rowell [37] found a complicated response to an arm prick even in an excised arm: first, a skin flinch, then arm withdrawal, followed by sucker extension as if to explore the source of the stimuli, even when no brain control could be involved. Subsequently [38], he showed the ganglion had a wide repertoire of phasic responses to simulation in the area around it, as well as a delayed response to shaking of the table, which likely came from central statocyst responses. Zullo et al. [39] found a dual system in the axial nerve cord with a throughput cerebrobrachial tract linked not to muscles but to medullary cord circuits, i.e., the ganglia, more evidence against direct brain control. Gutfreund et al. [40] showed that the accessory peripheral motor system might generate proprioceptive feedback to these circuits. This neural allocation to the arms has led to speculation that control of behaviour is split between central brain and a 'brain' composed of the arms' neural plexus [35,41] and that consciousness might not be unitary. To evaluate the assumptions, we must first understand how this specific motor system functions.

A muscular hydrostat movement system has one disadvantage and one advantage. Without a fixed skeleton against which to articulate, the system must have a very complex set of musculature so that some can stiffen and act as a skeleton while others articulate from and move against them. Kier and Stella [32] describe three sets of muscles—transverse, longitudinal, and helical—as well as an aboral circular muscle wrapping around the arm. These are linked by extensive sheets of connective tissue, both inward and lateral. The longitudinal muscle especially can contract at a single part of its length. Around the base of the arms is the circumbrachial commissure, which connects the brachial nerve cords at the base of the arm. Much processing of lower-level assessment and movement control is carried out by all these connections, giving the arm movement system a very large number of degrees of freedom [42]. An octopus arm can extend and retract; bend any place along its length and in oral, aboral, lateral, and medial directions; it can twist; and the arms can splay from one another away from the midline.

Of course, all the degrees of freedom cannot be realized, and there must be some constraints on actions. Kennedy et al. [43] observed a very large set of arm actions and found some probabilities. By far the most common action was bend, less common in the proximal 1/3 and more likely in the oral-aboral directions. The first and second pairs of arms were more likely to produce bend actions, which is logical as they are more likely to be the exploratory pairs, since the octopus crawls forward more often using pairs 3 and 4 [43]. Elongation-shortening and torsion were more commonly carried out all along the arm. At first, arm-sucker action control was dismissed as reflexive [37], but it is far from that. Grasso's [44] observational study revealed that suckers 'explore around' the site of future actions, and that they are coordinated both locally and with suckers far from them on the arm. He reported that a group of suckers could perform 'arm walk' in coordination, and also do 'arm lift' and 'octopus lift'. Still, Levy et al. [45] could find no pattern of coordination of arm combinations (gait) in walking. Octopuses could move in any direction, propelled mostly by the trailing four arms, though they tended to move forward and thus 'walk' on the posterior arms of pairs 3 and 4; see Huffard [46] for the posterior fourth pair being used most often for this task. Hochner's group (see Gutfreund et al. [47]) reported that a reaching action into midwater for a food reward was solely the result of a stereotyped bend propagation along the arm from the distal tip and discussed the idea of a 'pseudo joint' being formed and moving along the arm in bending. However,

Hannassy et al. [48] subsequently discovered that in this ‘stereotyped’ action, the bend was variably accompanied by an elongation, particularly in the proximal region. When Richter et al. [49] constrained octopuses’ action by requiring that they reach through a hole in a plexiglass container, only some of their subjects used an arm bend at the hole during extension. Others simply waved the arm in the water, and transport of the food item to the mouth involved a simple pull by arm retraction. The octopuses used whatever actions were suitable to the task, so stereotypy of action in the Hochner studies was mostly the result of the simplicity of the task demands; the arm system has much more flexibility in action as well as decisions.

As a result of these studies, the assumption grew that octopuses could not monitor the state of their arms, and that arm control was generated by a subsystem, and that the octopus had ‘two brains’. Grasso [35] produced an elegant model of how the plexus of many ganglia could unite to form a functional control system and thus another but different type of brain, although he did point out that there were no ganglia specialized for different functions in the arm and thus not a brain as we know them. There must instead be a set of subroutines controlling sensory-motor coordination and different amounts and types of descending control, depending on the action. The allocation of actions to arms can be similar but separately allocated, as when octopuses are performing chemotactile search in several different hidden areas of the landscape. However, there can also be coordination of similar postures, where octopuses have spread arms that move along an anterior-posterior axis, from the defensive arm-retroflexed to the prey-capture web-over with skin between the arms pulled down in a balloon-like structure to capture hidden prey [50]. Different arms can coordinate with different actions, as in the octopus extending an arm to block the ‘exit hole’ from under a rock before crawling under to capture hidden prey or aiming ‘slap’ actions at an attacking fish with anterior arms and holding on to the substrate with the posterior ones (personal observations). Octopuses and cuttlefish can monitor their arms visually to some extent. The recruitment of ‘neighbouring’ arms in a reaching task [51] suggests spreading activation through the intrabrachial commissure. Byrne et al. [51] found that octopus eyes use a guided arm choice in a reaching task, and cuttlefish camouflaging against a striped surface aligned their arms with parallel stripes, in masquerade. Both squid [50] and octopuses [49] moving in dangerous open spaces placed their arms in positions that mimicked algae clumps, sometimes described as a ‘moving rock’. The studies of Gutnick et al. [52,53], demonstrating that octopuses learn to use a single arm to reach into a Y-shaped maze, showed this more graphically. Animals could learn to reach into a maze guided by the sight of a rewarded stimulus at the end of one arm [52], but they could also use kinaesthetic cues, learning to choose the right or left side, and could be guided by tactile cues, stripes incised into the lower surface of the maze [53]. The visual guidance was particularly interesting, as the octopus was capable of making a choice with one arm that it had learned by using another. In other words, the site of the learning was the brain, as it was not arm specific. This allows the reader to think back to the studies of Muntz [25]. Information about tactile cues in a reaching task was learned with the action of one arm, controlled by the vertical lobe, but it was stored bilaterally in the brain, although not transferred to the use of the arms of the other side of the body if the brain halves were split.

Contrary to the assumptions that have grown up, the octopus’s nervous system has a fair degree of unity, especially in tasks that are learned. Carls-Diamante’s [41] assumption that octopuses have “much functional separation and little intercommunication” between control areas is contradicted by recent and the much older Naples work. Of course, cephalopod arm control is not as centralised as that of mammals, as actions are guided by a ‘distributed control network’ [35] but only as movement and body sensory subroutines. The brain-arm neural control areas are somewhat separate but not equal in decision-making capacity. It is the brain that learns, and Shigeno et al. [54] drew a parallel between the vertical lobe and the mammalian limbic system in a comparison of the brain function of octopuses and mammals. They suggested the arm plexus is comparable to the spinal cord

of mammals, and a quick glance at the function of the human spinal cord shows that we have underestimated its capacity. Besides its control of automatic reflexive behaviour, Roh et al. [55] pointed out that the human brain stem and spinal cord construct ‘modules’ of motor output. Thus, these areas in both humans and octopuses are more like junior partners with the brain in the control of behaviour, rather than separate equal entities.

3. Integration of Sensory Information

Researchers have given us a lot of information about the use of vision in octopuses, less in terms of mechanoreceptive and chemical cues [56], but few studies about the combination of cues from more than one modality even though people and animals live in a multimodal world. Because the octopus moves out from its sheltering ‘home’ and conducts saltatory (stop-and-go) search in the nearby areas [57], it must be using a combination of visual information from the eyes [58] and chemotactile cues to the arms [59] to find prey. Researchers have presented items soaked in various chemicals [31,60] to octopuses. Many that were components of proteinaceous prey were accepted and some, like melanin-containing octopus ink, were rejected. Allen et al. [61] drew from the paradigm used by the Naples research group to look at the combination and interference in learning visual and tactile information about potential prey items. Rough and smooth plexiglass balls were presented to octopuses, and their visual appearance was varied. The contrast in appearance was not a very appropriate one, as subjects learned on opaque balls and their appearance was then altered by painting them white or black. By necessity, the visual comparison was delivered first, as the octopus saw the ball approaching and the chemotactile stimulation only happened when it touched the arm. There was some cross-modality interference with learning, particularly by the visual (first noted) to the tactile, but the study had a poor design and very small N (in one condition, a single octopus), so it is impossible to draw conclusions except to say that the octopus can attend to two different cues simultaneously.

The situation is different and clearer in the case of prey enclosed in a glass jar, a favourite of demonstrators everywhere. The first researchers to examine octopus behaviour when confronted with the crab-in-a-jar situation were Fiorito et al. [62,63]. They simply dropped a jar with a crab inside it 40 cm in front of the octopus and measured the time to attack and time to open over six trials, given only a visual stimulus. Though the octopuses grabbed the jar and pulled it under the arm web, there was a great deal of variability and no clear reduction of the time to capture that one would expect from learning [62]. Reasoning that it might be the effect of the novelty of the situation, they gave octopuses pre-exposure to the jar [63] but that did not change the situation. An accidental variation in the cues presented during a public demonstration gave Anderson and Mather [64] a clue to stimulus variation. Anderson had previously offered octopuses a jar with a piece of herring inside, with smears of mucus left behind on the jar by his dirty hands, as a demonstration to aquarium visitors, and noted a significant decrease in the time to open. Formalising the comparison, they offered trials with sight of an enclosed crayfish alone compared to crayfish with smeared herring mucus on the jar, and a jar painted black so that the crayfish was unseen, even though the chemical herring cues remained. Both cues were needed for the octopus to significantly decrease the time to capture, and after 10 trials, there was significant transfer to the visual-only trial, so octopuses had learned from the cue combination. Subsequently, Maselli et al. [65] decided to look for cue combination and interference in a similar prey-in-a-jar situation. Octopuses were given jars with chemical, visual, a combination, or chemical and deceptive visual cues in different jars. Octopuses explored all the jars before choosing which one to open. They were successful in 50% of the visually cued jars and all of the chemical ones. Adding visual information about the prey identity did not affect the speed with which the octopuses opened a jar using the chemical cue, and interference meant that the octopuses chose the jar with the chemical cue and ignored the one with the visual cue (note that humans in a similar intersensory conflict choose the sight of an item in ‘visual capture’). Giving a visual cue on the same jar with the chemical one did not significantly improve performance compared with the chemical only

cue. There may have been a confound here, as the prey items chosen were bivalves, and the researchers did not use the visually active and much more preferred crabs [66]. Clearly, the most effective timing and combination of cues has yet to be identified, but octopuses can use more than one type of sensory information at one time, for enhancement and possibly interference in a unitary combination.

4. Conclusions

Unity in a complex nervous system with many distinct components is always going to be difficult to prove. Even though the common model of a bilateral brain has some allocation of specialization, it still appears to normally store information as a single unit. Despite a large neural allocation to managing the sensory-motor coordination of the arms, the octopus appears to centre learning and cognition in the brain and though the study of intersensory integration has just begun, it is promising in unravelling the integration of incoming information. Nevertheless, we are not going to find out where in a sophisticated and multifaceted brain the seat of cognition and consciousness is ‘parked’, and we should move away from the idea, as Godfrey-Smith [33] suggests, that “experience is always housed neatly” and look for a sophisticated organization of ‘self’ that lives up to the complexity of the nervous system that fosters it.

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