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Cephalopod Complex Cognition

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ABSTRACT

Cephalopods, especially octopuses, offer a different model for the development of complex cognitive operations. They are phylogenetically distant from the mammals and birds that we normally think of as 'intelligent' and without the pervasive social interactions and long lives that we associate with this capacity. Additionally, they have a distributed nervous system — central brain, peripheral coordination of arm actions and a completely separate skin appearance system based on muscle-controlled chromatophores. Recent research has begun to show how these apparently separate systems are coordinated. Learning and cognition are used toward prey, in antipredator actions and in courtship. These examples show how they attain complex cognition in Emery & Clayton's (2004) categories of flexibility, causal reasoning, imagination and prospection.

Cognition is 'the mechanisms [or operations] by which animals acquire, process, store, and act on information from the environment' [1]. Intelligence (the capacity to do such operations) evolved in animals with a highly centralized nervous system to solve specific social and ecological problems, leading to complex cognitive operations in some birds and mammals [2]. These processes were not expected in Mollusks, although we have learned much about the neural basis of simple learning from studies in Aplysia [3]. Cognition and Intelligence could be seen in four categories of operations: flexibility, causal reasoning, prospection and imagination [2]. Why might coleoid cephalopods, who are solitary and have a much more distributed system of control, need these abilities? They face variability and hostility in the shallow ocean environment [4], with many predators and diverse prey choices [5]. Competition with the bony fishes [6] may have triggered the evolution of their cognitive abilities, and RNA rather than DNA changes might have enhanced this individual flexibility [7]. Cephalopod behavior is controlled in three somewhat separate domains — brain decision making, arms manipulation, and chromatophore skin appearance. Until recently, these systems were seen as separate and command from the brain as open loop (not using feedback during their execution) in many cases [8].

How might coleoid cephalopods show intelligence? First, they have a relatively large brain, as their brain–body ratio is higher than that of many vertebrates [6], though see [9] for the operations that can be carried out with small insect brains. They may have consciousness [10],

although the extent to which octopuses monitor their output systems is debated. The control system of the arms, with up to 3/5 of the neurons, is somewhat separate from the brain, but new information shows that feedback from the arms is also available to it [11], and the brain can also use feedback from the skin appearance system [12] (Figure 1). All of these systems are united in actions such as the sequential decisions responding to the presence of predators [5], discussed later.

Brain and cognition

Can different brain structures support comparable cognitive capacity? Avian and mammalian systems are relatively similar in their neural substrate of consciousness [13] and parallel cognitive abilities [2]. Cephalopods might have the cognitive decisions associated with pain perception [14*], but the specific brain areas controlling such evaluation are not known. They have lens eyes, a bilateral brain organization, and half a billion neurons [6]. The cephalopod brain has an optic lobe for visual analysis and around 40 interconnected lobes [15]. It is not somatotopically organized like the mammalian brain [15]; it may use embodied organization [16], with interaction of sensory and mechanical systems with the neural controller. Both the dorsal chain of ganglia in each arm and the extensive brachial plexus linking the arms may partly substitute for hierarchical descending control [17] of the arm muscles in the complex muscular hydrostat movement system, as an autotomized (discarded) arm moves and behaves normally.

Figure 1. Actions of and evaluations by the distributed nervous system (in brain, arms and skin) of cephalopods. Structures are presented as bolded, results as capitals, outflow and inflow as arrows.

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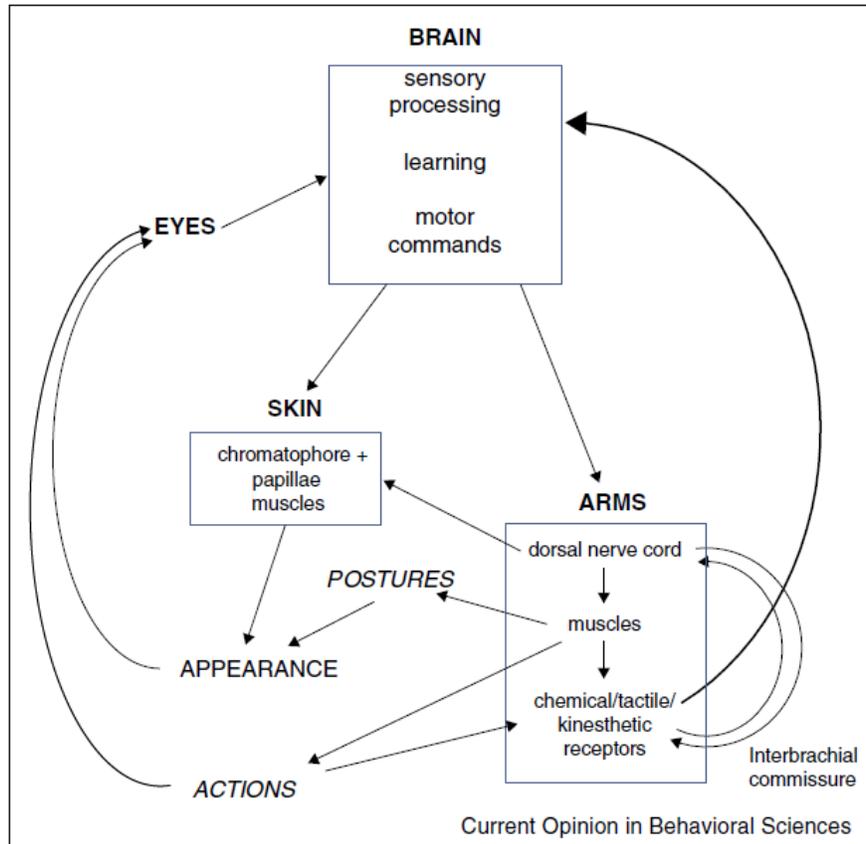
There is a quantitative representation of learned material in brain areas, tested in Octopus by optic lobe ablation [8]. The monocular octopus remembers a comparison better if it is tested on the same side as it is presented, but memory storage could transfer to the other half of the brain by the next day. Like split-brained humans, octopuses cannot do so if the brain was bisected before the comparison is learned [8]. Ablations studies of the octopus vertical lobe show it is involved with both short term and storage of long-term memory [8]; such studies are reinforced by modern stimulation studies [18]. In cuttlefish, post hatching growth of the vertical lobe correlates with the acquisition of learning to refrain from attacking a visual stimulus [19]. The vertical lobe may be involved in their spatial learning, as lesion in the dorsal half blocks memory retention, and in the ventral half limits its acquisition [20]. Thus the cephalopod brain is responsible for integration of information and planning of actions.

Cephalopods use problem solving extensively. Octopuses can learn to open a jar for a food reward using visual and chemical cues sequentially [21], and can conditionally discriminate [22]. They can learn to pull an L-shaped container through a hole in a barrier [23*], and subsequently to use various strategies, not stereotyped motor learning, when it is placed in different orientations. Sepia cuttlefish can learn 'what, when, where' in a food retrieval task [24] and Sepioteuthis squid can react to possible fish predators using species-specific cues about size, speed of approach and distance [25].

Relationships between brain and arm use

Benthic octopuses use their eight flexible arms extensively, see the ethogram outlining their common behaviors [26], using localized coordination [17], so they may have such decentralized control that they have two 'brains'. The central brain carries out decision-making, and the arm ganglia may integrate and represent spatial information of self and control movement details [27**]. There are three sets of propulsion actions, used flexibly based somewhat on demands for speed. Octopuses use jet propulsion to move through the water [26]. The arms are used for push–pull locomotion, but with no specific gait or arm movement sequence in walking [28]. During walking, octopuses can also balance the necessity to maintain cryptic appearance with propulsion, even using only two arms for propulsion while holding others in camouflaging postures [29]. The eight arms are lined with suckers, and octopuses can move slowly across the substrate using just these suction cups [26].

Octopus arms are important for operations on the environment such as exploration and action. Such exploration is often chemotactile, out of sight of the eyes, but they can use visual, proprioceptive or tactile information to guide arms in prey search [5]. Arms are essentially vehicles to carry these suckers to action. Suckers alone can carry out tasks, such as passing a small object along an arm or tiptoeing along the substrate [26]. Octopuses usually allocate push–pull locomotion to the posterior arms [28] and exploration to the four anterior ones, but flexibly based on the direction in which they are moving. Each individual has a 'favorite' one for exploratory actions, and neighboring arms are recruited for assistance [30] in a reaching task, probably by information passing around the interbrachial commissure.

Rather than immediately following perception with action, octopuses in a novel situation seek information [31]. They make a vertical head bob [26] to gain visual information by motion parallax, perhaps using information located on a [32] Global Workspace before action. Even

when visual information is available, they combine it with chemotactile information from the suckers and mouth [21]. Given a novel object, they move from exploration with arms and mouth to habituation and sometimes to play [33], by jetting water at a floating object. They can play across domains of use, as they also use arm actions in a playful manner [34], with arm use rising in level on a 'play scale' of complexity of actions over time.

In cuttlefish and squid such tactile exploration of the physical environment is seldom observed in laboratory conditions; though see contact with the substrate before digging into sand [35]. It is thought that behaviors in nature are mainly visually guided in these groups. However, tactile inputs and arm coordination are also important in prey capture [36] and manipulation [37], in cuttlefish and also in octopuses, sometimes [21] without any visual feedback. While the optic lobes guide storage of visual information both for learning [8] and skin pattern displays [38], the frontal lobes (inferior and superior, respectively) have a central role in active learning of tasks in the completion of prey manipulation, in chemical learning such as taste avoidance of crabs [39] and in tactile cued avoidance of capture attempts of prey enclosed in a glass tube [40,41].

Body patterning and cognition

The appearance system of cephalopods is a fast-changing and sophisticated one, with pigment-containing elastic sacs pulled out by muscles in milliseconds [42]. Body patterning is used for camouflage, to frighten or manipulate prey, avoid potential predators, and for inter-individual communication (see [43] for a review). It is controlled at three levels. The first is a simple stimulus–response process, where opsins in the skin automatically control darkening [44], largely considered as innate [45]. Skin displays can be a useful tool to study cognitive processing at two other levels [46], often for interaction with predators [47,48].

The second level of skin patterning control in coleoid cephalopods is production of camouflage, which is dynamic [48] in the sense that body patterning (composed of color, postures, skin textures and movements) is neurally controlled; it can be almost instantaneously changed to allow animals to be perfectly concealed. Octopuses and cuttlefish match contrast and texture of the background, but also its color [46] even though they are color blind, since their retina contains only one photopigment (rhodopsin). However, the special shape of cuttlefish pupils allow them to get some spectral information from reflected light [49**]. This 'chromatic' information may serve cephalopods to refine their back-ground matching.

Camouflage body patterning is not rigidly fixed since the repertoire depends to some extent on age in octopuses [50] and cuttlefish [45], but also on previous experience of each individual [51]. Juvenile cuttlefish coming from enriched rearing conditions have better skills to conceal in a new environment than those coming from impoverished ones. Some capacities of self-awareness [possibly consciousness] are involved in animal concealment strategies [46]. When matching a checkerboard, cuttlefish adjust component size of their skin patterns in relation to their own size [52]. This may require a complex visual feedback loop, in which the individual integrates in some measure a perception of its own body.

Cephalopods may manipulate body appearance at a third cognitive level, often toward potential prey. Casual observation of many coleoids shows that arm or tentacle tips may be extended and paled, randomly moving in a 'wiggling' pattern, presumably to attract prey (see

[43]). Skin displays are used more specifically, in the 'passing cloud' display of cuttlefish and octopuses. Chromatophores are sequentially expanded and contracted in an area moving along the animal's dorsal body surface, mimicking the shadow of a cloud passing along a landscape below and producing apparent motion. The only quantitative study of this display [53] found that octopuses used passing clouds after a failed capture attempt of a crab, presumably in an attempt to startle it into motion. Metasepia squid display several passing clouds across different segments of the dorsal surface [54], but the function of this complex display is unknown.

In the presence of predator threat, an individual can potentially choose between different strategies, some of which are skin displays, or use several strategies together [12]. These responses are not 'all or none' in a given environment, except in hatchling cuttlefish in laboratory conditions [45,51]. Body patterning display could then be a potential result of decision-making processes. For example, subadult cuttlefish have an eye-spot deimatic pattern which may make the animal appear larger and threatening [55,56]. They are displayed toward small but not large threatening fish, a selectivity which is also true for Sepioteuthis squid [25], and to visual predators and not those who hunt using chemical cues. This selective signaling reveals capacities for threat discrimination, categorization and risk assessment. Surprisingly, these behaviors are observed in inexperienced cuttlefish, so innate and experience-dependent processes are probably intertwined in body patterning. Subadult squid respond to the threat of approaching fish due to different cue combinations for different species [25], suggesting the possibility that they have a simple 'theory of mind' [57], though see [58] for caveats.

Body patterning plasticity is even more obvious in sexual signaling during mating at the end of the lifespan. Squid [59] and cuttlefish have a rich repertoire of sexual and agonistic patterns during courtship, for example, and male–male contests are primarily carried on by display [60,61]. [62] suggested that the nuances of patterns across skin space and time were so varied that squid might make a visual language on their skin. While the gradations, especially of the agonistic Zebra patterns, are very sophisticated [60], these are only communications about the individual oneself and its motivation, and thus do not meet the criteria for a language [63].

Skin patterns can be actively manipulated, especially in these social displays. Some male octopuses use skin dis-plays to females and male rivals [64], and habituation of response to an unreceptive female can result in attenuation of the display area [63]. Small male cuttlefish can change body patterns from a Zebra display (male sexual/ agonistic signal to other males) to a marble display (female pattern) to avoid rivalry from other males [65]. Male cuttlefish and squid can also spatially manipulate sexual patterns, displaying reproductive invitation to a female on one side of the body and simultaneously making an agonistic or neutral pattern to a rival male on the other [60,66]. This directional aiming decreases disruption of courtship by a potential rival. Such plasticity is demonstrated in a laboratory setting when cuttlefish are conditioned to change body pattern in response to a reward [67*], demonstrating the involvement of learning and memory in body patterning.

This variety of skin displays implies complex integration of visual information at different cognitive levels, from simple sensory discrimination to learning, memory, executive functions, decision making and potentially self- awareness. The exceptional multipurpose ability of cephalopods to

change body patterns challenges researchers trying to understanding general rules for cognition in animals (see Figure 2).

Figure 2. Example of categories of cognitive operations in cephalopods.

EXAMPLES	SITUATION	GROUPS
Flexibility (same end, different actions modified or selected to attain it)		
Activity change to casual not common predators [71]	Facultative predation	Octopus
Skin background matching (pattern, texture) [48]	Immediate visual feedback	All groups
Arm use allocation by body movement direction [28]	Goal direction	Octopus
Home construction by modification [68]	Learned kinesthetic feedback	Octopus
Causal Reasoning (action s selected or modified by feedback about attaining a specific end)		
Deimatic skin display use [55,56]	Predator action or choices	All groups
Passing cloud skin display [53]	Previous prey startle	Octopus
Change/combination of actions to predators [48,72]	Previous attack	All groups
Learning characteristics of potential prey [39]	Previous attack success	Cuttlefish
'Theory of mind' about predator actions [57]	Previous evasions success	Squid
Prospection (selecting actions broadly for a category of desired ends)		
Head bob to get motion parallex information [26]	Ambiguous situation	Octopus
Coconut carrying to a location with no shelter [70]	Need for future shelter	Octopus
Manipulation of sexual skin displays [65,66]	Avoidance of competition	Cuttlefish, Squid
Navigation, especially after displacement [20]	Cognitive map	Octo, Cuttlefish
Imagination (actions selected from a new/modified category in a novel situation)		
Arm/tentacle tip wiggle [43]	Prey capture	All groups
'Pain' behavior [14]	Mitigate body damage	Octopus
Moving item through hole [23]	Manipulation for reward	Octopus
Play by water jet or arm [33,34]	Boredom relief	Octopus

Combination of systems and operations

Although this presentation has emphasized the separate control of the three areas of action — brain planning, arm movement and skin patterns — they are used together. Evaluations of behavior in the lab are simplistic, but the sequence of antipredator actions of cephalopods in the field demonstrates the complexity and combination of the three behavioral systems in their natural environment (see [5], Figure 6.4). Cephalopods produce the four categories of cognitive operations, as [2] suggested for complex cognition, and Figure 2 gives definitions and examples for these operations. For instance, octopus conceal themselves in 'homes', often flexibly using dis-carded trash from humans [68], modified by tool use [69] and using their brain for matching

shelter appearance to 'what they want'. They carry coconut shell halves out to soft substrate for future shelter [70], using arms and brain and showing prospection. Their cycle of activity, when to move out of shelter, is modified by the presence of a casual but not a consistent predator [71], showing situation flexibility in applying their learning.

Outside of shelter, cuttlefish, squid and octopuses use their excellent background-matching camouflage by skin chromatophores and papillae [26,45]. Octopuses [29] also modify arm appearance and posture together, as do squid [72], using skin, arms and brain together and again demonstrating flexibility. If a moderately threatening visual predator approaches, octopuses [26], squid [25] and cuttlefish [56] all present a startle skin pattern (skin system and arm postures), using causal reasoning to select this action only for particular targets. If a predator attacks, animals in all three groups will show flexibility and com-bine appearance change, inking that provides both a smoke screen and a chemical repellent [73] to a predator, and jet propulsion away from the threat. Cuttlefish and squid use deceptive skin display systems during courtship to avoid competition [65,66] using prospection. Animals from all three groups show imagination in extending and wiggling an arm or tentacle tip to attract potential prey [43]. Octopuses use causal reasoning in sending a passing cloud skin display to startle a potential prey that has evaded capture [53]. Using pushing manipulation of an item to bring it through a hole [23*], octopuses show imagination.

Conclusion

As we learn more about animal behavior, we more often see complex cognition from invertebrates, and we are beginning to discuss [74] insect cognition. But it is still unexpected in octopuses, with their decentralized control system for behavior. This paper shows that we find cognitive control of many responses in cephalopods, despite much peripheral control of lower-level functions in arms and skin and different amounts of feedback to the central brain controller. This model of behavior control, which nevertheless demonstrates many uses of cognitive operations [sensu 2] challenges our ideas of what is necessary for nervous systems to evolve complex cognitive operations controlling behavior.

Conflict of interest

The author's have no conflict of interest in this paper.

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Octopuses were trained with puzzle tasks requiring more and more complex behavior. They started with retrieving a food reward from an L-shaped tube, then pulling it through a hole, to reaching through to pull when the tube was at one or changing orientations. As duration dropped at each task level then returned, it was concluded that they were not using stereotyped motor actions but adapting to different task demands.

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