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'Mind' is an ill-defined concept: Considerations for future cephalopod research

Commentary on **Mather** on *Octopus Mind*

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Abstract: Scientific discussions about the 'mind' of an octopus are empirically vacuous and should be confined to folk psychology. This form of labelling is unhelpful for science and should be replaced by specific mechanistic accounts of behavior and associated neural structures, which are amenable to rigorous scientific investigation. Mather provides a detailed review of octopus behavior, but rather than making unquantifiable assumptions about what orchestrates octopus behavior, efforts should focus on investigating cognitive mechanisms that can be measured. In this commentary, we outline two lines of research that include quantifiable methods to facilitate a more robust understanding of cephalopod behaviors and their cognitive underpinnings.

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Octopuses have highly developed perceptual, memory, and learning abilities and have been observed performing intriguing feats of behavior. Mather's (2019) target article offers a perceptive review of these behaviors but lacks a systematic approach to evaluating the cognitive mechanisms that might orchestrate these behaviors. Specifically, she argues that behavioral traits such as exploration, play, and flexibility demonstrate the presence of a '*controlling mind*'. However, this form of labelling is unhelpful for the science of behavior because the 'mind' is an immeasurable concept that is not amenable to rigorous scientific testing. Consequently, such terminology limits our ability to develop falsifiable hypotheses that can be verified or disproven to advance our understanding of octopus behavior.

That being said, we embrace the idea that octopuses and their cephalopod cousins, cuttlefishes and squids, exhibit intriguing behaviors and are endowed with sophisticated nervous systems, making them suitable candidates for investigating cognitive evolution (Amodio et al. 2018). However, unless we adopt systematic approaches to assist us with this endeavor, our knowledge of cephalopod cognition will remain rudimentary. Thanks to pioneering researchers in the field of neuro-ethology and comparative cognition, it is possible to systematically study how animals acquire, process, retain, and respond to information, without making any assumptions about the nature of their subjective experiences and awareness (see Emery & Clayton 2001; Bugnyar & Kotrschal 2002; Clayton et al. 2002; Dally et al. 2005; Rogers et al. 2013).

Rather than contemplating whether the octopus has a mind, the more compelling and quantifiable questions that should be posed are: (1) which cognitive mechanisms are present or absent in octopuses? And (2) how comparable are these mechanisms to those found in vertebrates? Here, we outline two promising fields of cognitive psychology that may help answer these questions. The first line of research centers on behavioral biases and associated cognitive biases, the second on determining whether cognitive mechanisms that underpin a specific behavior are complex or simple. Focusing on these two areas has the potential to highlight cognitive similarities *and* differences between cephalopods and other species and might also help explain the limits of cognitive convergence in the animal kingdom.

Behavioral & Cognitive Biases. As noted by Mather, some cephalopod species exhibit behavioral biases that might be driven by cognitive biases: lateralized brain function, when specific cognitive functions are processed by either the left or the right side of the brain (Vallortigara 2000; Rogers et al. 2013; Versace & Vallortigara 2015; Ocklenburg & Güntürkün 2017; Vallortigara & Versace 2017). For example, cuttlefish (Brown et al. 2012) and squid (Mather 2016) can produce bilateral body patterns whereby individuals display two different patterns on either side of their body simultaneously. We recently demonstrated that such biases might be linked to specialized brain function. Specifically, when it comes to camouflage, cuttlefish use predominantly their right eye and associated neural structures to adjust the overall brightness of their camouflage pattern (Schnell et al. 2018). Other research on cuttlefish has demonstrated that one side of the brain is specialized to process information used for predation, and the other side is used for monitoring and scrutinizing potential predators (Schnell et al. 2016). Biases in turning behavior have also been reported in cuttlefish (T-maze experiments; Jozet-Alves et al. 2012a); this bias is correlated with the size of the right optic lobe (Jozet-Alves et al. 2012b). Behavioral biases in cuttlefish occur at the population level; individuals who are biased in one direction outnumber individuals biased in the opposite direction by approximately 60% (Schnell et al. 2016; 2019).

Behavioral biases and population-level expression, however, are not ubiquitous among cephalopods. Unlike cuttlefish, octopuses lack a turning bias when tested in a T-maze (Frasnelli et al. submitted). In other contexts (e.g., when viewing prey), octopuses display lateral biases for either the left or right eye, but eye preference is present only at the individual level; there is no systematic left- or rightward bias at the population level (Byrne et al. 2002; 2004). Behavioral biases in arm use have also been observed in octopuses (Byrne et al. 2006) but again at the individual and not at the population level.

In deep-sea squid, *Histioteuthis*, anatomical biases (possibly associated with behavior) have been observed at the population level (Wentworth & Muntz 1989). In this species, individuals have a large left eye and associated optic lobe, used to look upwards in the water column – perhaps to detect predators. The right eye and associated optic lobe are considerably smaller and orient downward – perhaps to search for prey.

It should be noted that biases can be expressed at the individual and the population levels in the same species. The level of expression depends on the type of behavior. Population-level biases might be selected for when coordination is required between individuals, but in other contexts, it might be more advantageous to exhibit biases at the individual level (Frasnelli & Vallortigara 2018). It has been proposed that population-level biases may have evolved in response to social constraints that produce fitness advantages for individuals that have their biases aligned with those of other individuals (Vallortigara & Rogers 2005; Ghirlanda & Vallortigara 2004).

An extension of this hypothesis explains that biases expressed at the population level can be evolutionarily stable on the basis of fitness consequences that occur during intraspecific competition and coordination (Ghirlanda et al. 2009). This hypothesis predicts that minority-type individuals are maintained because they are more likely to adopt unpredictable behavior during competitive interactions, whereas majority-type individuals are maintained because there is a fitness advantage in having their biases synchronized with other conspecifics during interactions that require coordination. Research on giant Australian cuttlefish has recently provided empirical support for these predictions (Schnell et al. 2019). Specifically, during competitive interactions, minority-type male cuttlefish, with a right-eye bias, achieved higher fighting success. By contrast, during interactions that required coordination (i.e., mating), majority-type males, with a left-eye bias, achieved higher mating success. These findings demonstrate that population-level biases in giant Australian cuttlefish are an evolutionary consequence of the fitness advantages in intraspecific interactions. Further investigation is needed, however, to determine whether this pattern is linked to social constraints, such as the need to align biases with the majority of the population when coordination is vital.

Cephalopods are particularly suitable for this line of research because the need to coordinate during specific behaviors varies greatly between the species. For example, mating in the Larger Pacific Striped Octopus appears to require coordination because it occurs beak-to-beak; thus one might expect to observe behavioral biases during mating at the population level in this species. By contrast, in other species, such as pelagic octopuses (i.e., blanket octopus, *Tremoctopus*), there is little need for coordination during mating as the male detaches his specialized mating arm (i.e., hectocotylus) and leaves it with the female; thus in a mating context, these octopuses may lack behavioral biases or may express biases at the individual level only.

Cognitive Complexity. Cephalopod behaviors have captured the attention of diverse scientists and philosophers. Like many members of the scientific community, Mather makes the implicit assumption that these behaviors are underpinned by complex cognitive abilities. However, much of our current understanding of cephalopod complex cognition is based on anecdotal observations, with many claims yet to be validated by empirical data (Schnell & Clayton 2019).

Conducting empirical tests to determine the cognitive mechanisms that drive behavior is important because while a particular behavior might appear to be complex at the superficial level, an animal might be using simple cognitive shortcuts that do not involve complex cognition. For example, some sophisticated behaviors can be driven by simpler mechanisms such as learning of habits (i.e., conditioning) or goal-directed learning (i.e., associative learning) (Schnell & Clayton 2019). Consequently, researchers should be cautious when it comes to labelling behaviors as intelligent without conducting rigorous empirical tests.

Given the extent of sophisticated behaviors performed by cephalopods (Hanlon & Messenger 2018; Schnell & Clayton 2019), we contend that these animals are suitable for rigorous investigation into whether such behaviors are underpinned by complex mechanisms. The prospect of complex cognition emerging in cephalopods is indeed intriguing because it challenges a fundamental aspect of our understanding of the emergence of intelligence (Amodio et al. 2018). In vertebrates such as apes, cetaceans and corvids, the leading hypotheses suggest that complex cognition evolved under two key pressures: ecological and social (Byrne & Whiten 1988; Dunbar 1998; Rosati 2017). Cephalopods present a challenge to this because they evolved in relatively simple social environments and thus lacked the need to overcome many social pressures (Boal 2006; Schnell & Clayton 2019). Consequently, investigating the capacity for complex cognition in cephalopods will provide a unique perspective for understanding the origins of intelligence by highlighting whether complex cognition can emerge through different evolutionary pathways in response to partially different pressures (Amodio et al. 2018).

Cognitive research can benefit from future research on cephalopods in three ways. First, as cephalopods are widely distributed, they are exposed to highly variable ecological pressures. Thus, they can be used to investigate specific ecological factors that select for the evolution of specific cognitive abilities. Second, cephalopods exhibit varying levels of '*simplified*' sociality (i.e., sociality that does not require cooperation) ranging from solitary octopuses to schooling squids. An extensive set of phylogenetically controlled comparisons might highlight the effects of low and high levels of social pressure on the evolution of complex cognition. Finally, cephalopods have neural architecture dramatically different from that of the more commonly studied vertebrate species. Identifying shared cognitive abilities between cephalopods and vertebrates will reveal whether dramatically different brains can support comparable cognitive sophistication.

In summary, Mather has delivered an insightful catalogue of octopus behaviors, which might stimulate further research into the cognitive mechanisms that drive these behaviors. However, at present, without rigorous testing, many of her claims about octopus cognition must be considered speculative. By exploring two lines of inquiry within neuro-ethology and comparative cognition, researchers can begin to establish quantifiable explanations for cephalopod cognition and help us move toward a more comprehensive understanding of cephalopod behaviors and their cognitive foundations.

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