Octopus: Multiple minds or just a slow thinker?

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

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Abstract: An octopus has more neurons in their peripheral nervous system (PNS) than in their brain. PNS neurons could participate in forming cognitive networks with the central brain in the same way that the cerebellum is now thought to contribute to mammalian cognition. However, cephalopods lack myelinated fibres, which might decrease the ability of the PNS to participate in cognitive networks. The lack of myelinated fibres may also select for a less integrated brain, with an increased emphasis on local information processing. Alternatively, integration may still occur across distant neural centers, but proceed more slowly in cephalopods than in mammals.

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Mather (2019) tackles the difficult task of trying to understand how distributed brains work together to produce coordinated behaviour. Although octopuses and other cephalopods inherited the distributed nervous system of their molluscan ancestors, they have evolved toward a more integrated brain organization (Katz, 2016). How far has that evolution progressed? Does the degree of brain integration influence the type of 'mind' an octopus may have? Mather discusses the semi-autonomous nature of the control of the arms by the peripheral nervous system (PNS) in the octopus. How does this multi-locus centre of control challenge our understanding of neural networks in the octopus?

All invertebrates have a distributed nervous system, with brains of various sizes in different locations (Bullock et al., 1977). Molluscs have, in addition, a robust peripheral nervous system. The molluscan PNS is capable of learning even when separated from the central nervous system (CNS). Although the PNS, and sub-brains of the CNS, can function autonomously in some invertebrates, disassembling their nervous systems decreases function (see Chase, 2002, for discussion). This suggests that distributed nervous systems still form nervous-system-wide networks. Sub-brains are connected to the central brain in invertebrates via stout connectives containing thousands of axons. For example, there are approximately 6,000 axons in the connectives between the segmental ganglia in the leech *Hirudo medicinalis* (Wilkinson and Coggeshall, 1975).

Octopus arms are primarily controlled by the brachial ganglion system. This system is physically separate from the central (i.e., cerebral) brain. The brachial ganglia integrate sensory information and produce the complex motor commands needed to control an arm with many degrees of freedom (as discussed in Mather's target article). The brachial ganglia are well-connected to the cerebral ganglia of the central brain (Grasso, 2014; Shigeno et al., 2018).

Vertebrates have a compact and deeply integrated CNS. Neural networks spanning the entire brain are thought to mediate complex cognitive functions (Filley and Fields, 2016). For example, the perception of pain in humans is thought to be produced by a neural network that results in the co-activation of a large number of brain areas (Bastuji et al., 2018; Garcia-Larrea et al., 2018). Such networks are possible because of massive, myelinated connections across the brain, producing a deeply connected CNS. Although much of the microcircuitry in the human brain is unmyelinated (Kandel et al., 1991), the connections needed to produce the networks that appear to create 'mindful' events such as perceptionuse myelinated fibres to integrate the various brain areas needed to form the network (e.g., Garcia-Larrea et al., 2018). Even rodents (Gefen et al., 2018) with brains not much bigger than that of an octopus (e.g., Jung et al., 2018) use myelinated nerve fibres to connect across different brain areas (Kandel et al., 1991). How the brain produces a sense of self (i.e., the neural correlates of consciousness) remains a topic under intense study, but is thought to involve these types of complex, brain-spanning, neural networks (Pajevic et al., 2014; Garcia-Larrea et al., 2018). In theory, any group of neurons could participate in creating a complex neural network, as long as it is connected to other brain areas. For example, the human cerebellum contains more than 50% of all neurons in the brain (Azevedo et al., 2009). Although part of the CNS, it inhabits a distinct region, somewhat separate from the rest of the brain (Kandel et al., 1991). It organizes complex motor commands and, until recently, was not thought to participate in complex cognitive processing. However, its contribution to complex cognitive function has now been recognized. The cerebellum is connected via large myelinated tracts to a number of different brain regions, allowing it to participate in brain-wide information processing (Schmahmann, 2019).

The octopus brain contains about 150 million neurons, while the octopus PNS has 350 million neurons (Budelmann, 1994). Like the cerebellum, a large part of the octopus PNS (the brachial ganglia) is thought to subserve motor control (see discussion in Mather's target article). However, that does not preclude the participation of the 350 million neurons of the PNS in complex cognitive processing.

One notable difference between mammalian brains and octopus brains, however, is the presence of myelin. Myelin greatly increases the conduction velocity of action potentials down the axon. Myelinated axons in humans have a conduction velocity of 5 to 120 m/s; our unmyelinated neurons send impulses about 100 times more slowly (approximately 0.5–2 m/s; Kandel et al., 1991). Given the small axonal diameters of the fibres within the octopus brain (Budelmann, 1994), they probably have a conduction velocity of less than 1 m/s, while signals in the tracts connecting the brachial ganglia to the cerebral ganglia probably travel at about 4 m/s (Burrows et al., 1965). At this speed, the time needed for signals to travel between the cerebral and brachial ganglia would probably be a minimum of tens to hundreds of milliseconds, depending on the location of the brachial ganglia.

How does the lack of myelin influence the ability of the PNS to play a role in complex cognitive networks in the octopus? How does it alter the ability of the octopus to form complex cognitive networks within its central brain? Unfortunately, our understanding of how complex neural networks function is rudimentary; hence it is difficult to predict how slower conduction velocities will affect them. Octopuses have complex neuropil with recurrent connectivity that implies complex processing. The PNS and CNS of the octopus both devote a large number of fibres to connections across neuropils (Grasso, 2014), suggesting that they too use brain-spanning neural networks. In humans, fast neural conduction is necessary for the coordination of the large ensembles of neurons that mediate complex cognitive processes such as language and executive functioning. Lowering conduction velocity impairs cognition and function even in small mammals such as mice (Filley and Fields, 2016). However, mammalian brains have evolved under conditions of rapid information transfer. Any change in the normal function of a brain is likely to reduce brain function. The impairment of cognition with reduced conduction speeds in mammals does not necessarily mean that octopuses are condemned to reduced cognitive capacity without myelin. However, it does mean that certain theories about how advanced cognition occurs in mammals (e.g., see Pajevic et al., 2014) cannot be applied to octopuses.

It may be that the brachial ganglia require considerable autonomy because of the lack of rapid communication within the octopus nervous system. The lack of myelin may also limit the ability of the brachial ganglia to participate in brain-spanning, information-processing networks, unlike our cerebellum. What does this mean for the 'mind' of the octopus? Has the lower conduction velocity of its axons favoured the evolution of multiple 'minds'? Or do they just 'think' more slowly? Or have the cephalopods evolved a different method of producing coordinated, brain-spanning, neural networks? The brain and behaviour of the octopus still have many lessons for us.

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