Body ownership: A Cephalopod has a sense of self

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Abstract: Octopuses show advanced intelligence which has evolved independently from our own. New research shows that these animals show multisensory body illusions strikingly similar to those found in humans and other mammals.

William James noted more than a century ago that the body is "the innermost part of the material self"[1] (pg. 292). The experience of the body is commonly linked to our sense of self and personal identity. Neurological studies have reported cases in which patients deny that body parts are their own[2], claim to have additional supernumerary limbs[3], or believe that parts of their body have become evil[4]. Such extraordinary distortions of ordinary experience underline the key role that the feeling of body ownership – the feeling that my body is my own – plays in human mental life.

In healthy humans, experimental research has used multisensory illusions to investigate body ownership and the sensorimotor signals which produce it. For example, in the rubber hand illusion[5], a prosthetic hand is placed in front of the participant and touched in synchrony with touches applied to the participant's unseen hand. Most people report feeling like the rubber hand is part of their body. Moreover, when the rubber hand is then threatened, autonomic and neural responses indicate that the rubber hand has become incorporated in the brain's networks for defence of the body[6].

Over the past decade, evidence has begun to emerge that the mechanisms producing body ownership are not unique to humans. Studies have shown effects comparable to the rubber hand illusion in both old world macaque monkeys[7] and mice[8]. Such results suggest that body ownership in humans reflects mechanisms common to all mammals. In a new study reported in this issue of *Current Biology*, Kawashima and Ikeda[9] dramatically extend this comparative work, showing a rubber arm illusion in octopuses.

Kawashima and Ikeda tested plain-body octopuses (*Callistoctopus aspilosomatis*) by placing a realistic-looking fake arm above the octopus's real arm while the animals sat at the bottom of a tank. In the critical illusion condition, the fake and real arms were touched at corresponding locations in temporal synchrony with each other. Three control conditions were also tested, in which (1) the touches on the real and face arms were temporally asynchronous, (2) no tactile stimuli were presented, or (3) the posture of the real arm (curved) mismatched the posture of the fake arm (straight). These conditions are all highly similar to those used in studies of the rubber hand illusion in humans. Following each of these conditions, the fake arm was pinched with a pair of tweezers and the octopus's behaviour was recorded.

Kawashima and Ikeda measured behavioural responses to the illusion in four ways, by looking at changes in colour, which octopuses use defensively to camouflage themselves, changes in body posture, retraction of the actual arm, and escape. The results were clear. All four of these behaviours were substantially more common following synchronous visuo-tactile stimulation than in any of the control conditions. The most common response was retraction of the arm, which was observed in 79% of trials in the illusion condition, but in no more than 10% of trials in any of the control conditions. Other posture changes were seen in 56% of trials, colour changes in 47% of trials, and 25% of the time the octopus escaped from the scene entirely. Each of these behaviours was almost entirely absent in the control conditions, showing that they are specific responses to the visuo-tactile stimulation in the illusion condition.

These results put the evolution of body ownership in a new light. It is plausible that the last common ancestor of humans and mice, a small insectivorous mammal who lived around 75 million years ago[10], may have had bodily experiences broadly similar to modern rodents. Thus, the rubber tail illusion in mice[8] may very well be *homologous* to the rubber hand illusion in humans[5] in that both arose from mechanisms shared in our last common ancestor. In striking contrast, the last common ancestor of humans and octopuses was likely a worm-like creature living around 600 million years ago[11]. The rubber arm illusion in octopuses is therefore almost certainly not homologous – but merely *analogous* – to body ownership in humans, as they likely evolved completely independently. As the ethologist Konrad Lorenz noted in his Nobel Prize Lecture[12], the identification of analogies in distantly related animals can provide insight that homologies cannot. Whereas homologies may simply be accidents of common descent, analogies suggest convergent evolution in response to similar selection pressures.

The existence of body illusions in octopuses is also striking given the dramatic differences in how sensorimotor control of the limbs is organised in these animals compared to humans. Beyond the obvious difference that octopuses have eight limbs, rather than four, the control of each arm is decentralised, with each arm capable of organising coordinated movements independent of the central nervous system[13]. Their arms move with virtually unlimited flexibility and operate largely without visual input, relying instead on a chemotactile "taste-by-touch" sense, that responds to prey-derived chemicals and movement as they explore the seafloor [14]. The octopus central nervous system also lacks the somatotopic maps of the body that are so conspicuous a feature of the mammalian sensorimotor cortex[15]. Despite these profound differences in the structure of both the body and the nervous system, octopuses appear to integrate external objects into mental representations of their body in a manner strikingly similar to that in mammals such as mice[8], monkeys[7], and humans[5,6].

In humans, the most striking evidence concerning body ownership comes from subjective reports of the experience of both neurological patients[2,4] and healthy participants experiencing illusions[5]. Such evidence is, however, completely absent in animals like octopuses. We have no way of knowing what it is like to be an octopus experiencing the rubber arm illusion[16]. A deflationary interpretation of Kawashima and Ikeda's results might therefore suggest that while these animals' nervous systems have sophisticated mechanisms for organising defensive responses to potential threats, they lack the rich subjective experiences of embodiment found in humans. Indeed, there are reasons to think that responses to threats are evolutionarily much more ancient than consciousness, in which case the presence of defensive responses should not be taken as evidence of bodily awareness[17]. At the same time, the responses of octopuses in the present study do not appear to be reflexive responses to any single sensory cue. In contrast, they require a precise integration of visual, tactile, and proprioceptive cues and manifest in a range of linked behaviours involving physiologically distinct systems. These features provide stronger reason for thinking that the behaviours correspond to conscious awareness[18]. In this sense, the present study has interesting links to recent research investigating pain in octopuses[19]. Injection of acetic acid into one arm produced a range of behaviours consistent with experiences of pain, including avoidance of the location where the injection had occurred and grooming and concealment of the affected arm. Thus, both in the case of acute pain[19] and multisensory body illusions[9] octopuses' behaviours show a range of coherently linked responses suggesting that the responses are not reflective and reflect higher-level cognitive processes, suggestive of conscious awareness.

Octopuses offer a rare opportunity to investigate whether body representation is fundamentally centralised, or if it can emerge locally through low-level sensorimotor integration. Future work could adapt somatic illusion paradigms to exclude vision, testing whether chemotactile signals alone can induce embodiment. Such research may clarify how peripheral and central systems contribute to constructing body representations, and whether they can arise without a centralised brain. While tetrapods are developmentally constrained to have four limbs and up to five digits, cephalopods show a very different pattern: octopuses have eight arms, squids have ten appendages, and nautiluses have dozens of tentacles. Future research could investigate whether octopuses can experience supernumerary body parts, like humans can[20], or whether they have a constraint to their body plan.

That octopuses can be tricked into adopting a fake limb shows that the sense of body ownership can emerge from somatosensory signals, a strategy shared by both humans and octopuses, despite their distant evolutionary paths. This provides compelling evidence for an analogous mechanism of embodiment shaped by convergent evolution. Octopuses have bodies very different from our own, and have an intelligence which has evolved independent from ours. Despite these profound differences, the most intimate aspects of our embodied experience may be something that we share with these animals.

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