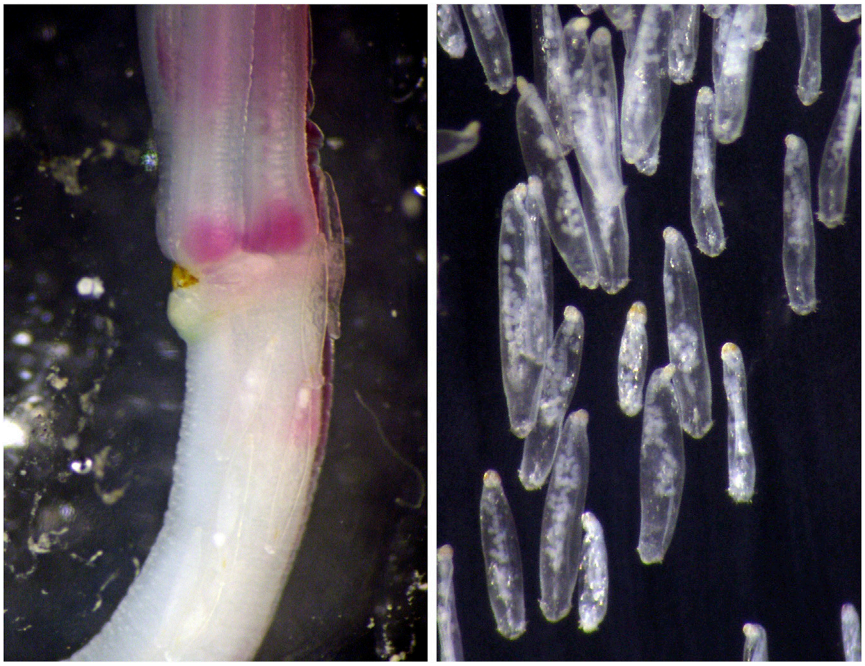

Figure 2. Extreme sexual size dimorphism.
Osedax rubiplumus. On the left, a female with a harem of males. On the right, dwarf males that normally live in a harem around the female's oviduct. The males are maximally around 1 mm in length. Images courtesy of Greg Rouse.

In the case of *O. priapus*, the reversal is a particularly spectacular case, as it concerns the overall structure of the body and ecological and reproductive strategy. Yet, a hypothetical scenario of how free-living males might evolve from dwarf forms seems even more tangible. There are indications that the dwarf-male phenotype in *Osedax* is a case of paedomorphosis — the sexually mature males keep some features of the larvae, similar to an axolotl, a sexually mature larval salamander. The genes for building a body with foot and trunk and palps, however, will not degenerate in species with dwarf males, as they are needed to build the female body. And if male dwarfism in indeed due to a switch in developmental timing, whereby sexual maturation is activated in a larval body, it is even conceivable that the inactivation of this switch could lead to fully-fledged males, much like treatment of neotenic axolotls with thyroid hormone can lead to grown-up salamanders.

Then, of course, the ultimate question is, why the dwarf male strategy, which seems to make so much sense in light of *Osedax*'s deep-sea habitat and ecology, would have been abandoned in a species that otherwise does not seem all that different from its close relatives. A clue might come from the fact that *O. priapus* females are comparatively small, so perhaps there is less competition for resources between the sexes. But again, that is just a guess. Chances are, however, that from the carcasses the bone devourers will spit out more interesting secrets before long.

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Animal Cognition: Monkeys Pass the Mirror Test

A new study finds that rhesus monkeys display self-recognition behaviors toward a mirror after multimodal sensory-motor training. This finding closes a prior gap in the evolutionary continuity of animal cognition and opens new frontiers for exploring the neurobiological basis of self-awareness.

Koji Toda and Michael L. Platt

The sense of self — a unified subjective experience of being that extends in space and time — is a core facet of human cognition. Whether animals also possess a sense of self or whether this faculty is uniquely human remains hotly debated. In this issue of *Current Biology*, Chang *et al.* [1] deploy a clever new technique to reveal that rhesus macaques are capable of recognizing themselves in a mirror, passing a hallmark test for self-awareness they had failed in previous studies.

Almost half a century ago, Gallup [2] pioneered the experimental investigation of the sense of self in non-human animals. In his seminal work, he first presented captive chimpanzees with a mirror and observed their behavior. The chimpanzees initially threatened their reflected images in the mirror, as if the images represented a second, unfamiliar chimpanzee, but after experience with the mirror used it to inspect and groom difficult-to-see parts of their bodies. Gallup then experimentally anesthetized chimpanzees and marked their faces with odorless red dye. After the chimpanzees awoke, they were presented with a mirror. The chimpanzees tended to reach out and touch the red spot, which was otherwise invisible. Gallup argued that the chimpanzees must have recognized their faces and bodies in the mirror and that this behavior implied a sense of self, based on the intuition that because humans recognize themselves in mirrors and connect this experience with self-awareness, then the same must be true for animals.

Since Gallup's pioneering work, the mark test has been applied to many animals, including chimpanzees, bonobos, orangutans, dolphins, elephants, and magpies, which all pass the test, and gibbons, several Old and New World monkeys, and crows, which typically fail the test [3,4]. Animals that pass the test, like chimpanzees and dolphins, are often those that we consider 'smart' and have large brains for their body size [5], validating the naive intuition that intelligence and the sense of self are linked [6]. Yet there are many surprises as well. Gorillas rarely pass the mark test [3], despite their phylogenetic affinity to humans, chimpanzees, and orangutans, and magpies and pigeons sometimes pass the test despite their dissimilarity to humans. Moreover, performance on the mark test within a species, even for chimpanzees, is often highly variable and inconsistent [7].

This variable pattern of findings raises the possibility that performance on the mark test may be a less reliable assay of self-awareness than previously thought [4]. Animals may fail to pass the test because the mark is not salient or meaningful to them or because their sensory systems differ strongly from our own [8]. Indeed, blind people and people with prosopagnosia — a congenital or acquired impairment in face recognition — cannot recognize themselves in a mirror but are clearly self-aware [9]. Neurological studies also suggest that self-awareness may not be a unitary phenomenon that is either present or absent, as implied by the pass/fail nature of the mark test, but may in fact be cobbled together from multiple subordinate mechanisms [9].

Until now, a major gap has been the failure of macaque monkeys to demonstrate that they recognize their faces and bodies in a mirror, even following extensive experience [10]. After all, recent studies have demonstrated that macaques show other cognitive capacities and behavioral biases that were once thought to be uniquely human or shared only with great apes, including gaze-following [11], vicarious reinforcement [12], hot-hand bias [13] and metacognition [14], amongst others. Moreover, the brains of rhesus macaques, chimpanzees, and humans are highly similar, with the same cortical areas connected in largely similar fashion, though there are some clear differences in the sheer size of association cortex, the frequencies of certain cell types like von Economo neurons [15], fiber pathways related to language, and levels of gene expression [16]. These observations invite the possibility that cognition — language aside — varies largely in degree and not kind amongst macaques, great apes, and humans. In this view, failure of macaques to pass the mark test indicates a failure of performance rather than the absence of self-awareness.

Chang *et al.* [1] demonstrate that rhesus macaques can in fact pass the mark test when the mark itself is made behaviorally meaningful. First, the authors showed that macaques fail the mark test under standard conditions, as reported previously. Next, they used a mildly irritating red laser in combination with a mirror to train monkeys to touch a spot on their faces for a food reward. Critically, the monkeys generalized their behavior to a new condition in which the laser was not irritating and there was no food reward associated with touching the spot (Figure 1). Most importantly, the monkeys further generalized to spontaneously using mirrors to inspect and explore hidden parts of their bodies using mirrors placed in their home cages, just as chimpanzees do.

Clearly, the behaviors demonstrated by the monkeys in this study required extensive training. However, the importance of experience and learning to passing the mark test has been noted previously [17]: human toddlers do not pass the mark test until 18–24 months of age [18], and not all chimpanzees pass the mark test [6]. Even pigeons can pass the mark test following extensive training [17]. These findings imply that appropriate environmental history and learning are required to pass the mark test. Whether immediate, spontaneous self-recognition by adult humans and some chimpanzees indicates a qualitative gap in cognition between humans, great apes, and monkeys remains an open question.

The new study by Chang *et al.* [1] is the first to demonstrate experimentally that macaques can pass the standard mark test. Nevertheless, it has been shown previously that macaques can learn to use a mirror to guide their hands to reach an out-of-sight object [10]. Moreover, a recent report [19] showed that monkeys with prosthetic head implants used a mirror to groom the otherwise invisible implants, although it remains possible that this grooming behavior was stimulated by somatosensory cues caused by the implants [10]. In the work of Chang *et al.* [1] somatosensory stimulation from the irritant laser pointer increased the salience of the mark, thus drawing monkeys' attention to it and initiating the process of exploration and learning. The results support the hypothesis that multi-modal integration is critical for the expression of behaviors linked to self-recognition and self-awareness.

These are remarkable findings. They show at a minimum that macaques possess a latent capacity to recognize the spatial

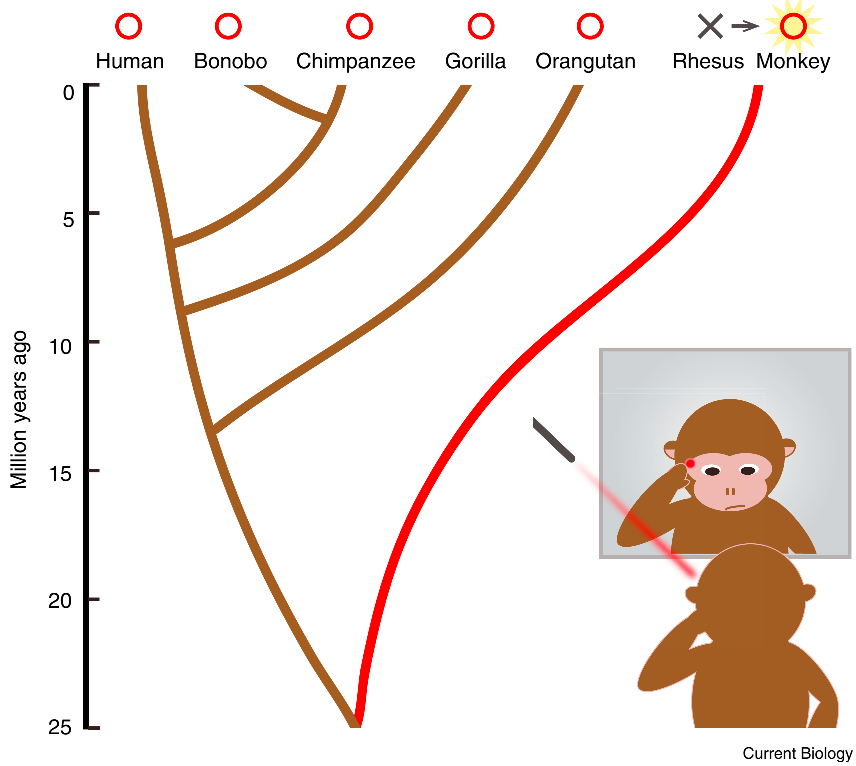

Figure 1. Rhesus monkeys pass the mark test.

Chang *et al*. [1]. used a mildly irritating red laser in combination with a mirror to train monkeys to touch a spot on their faces for a food reward (the inset illustrates the training method). After that, the monkeys generalized dot inspection behavior to a new condition in which the laser was not irritating and there was no food reward associated with touching the spot. The monkeys further generalized to spontaneous use of mirrors in their home cages to inspect and explore hidden parts of their bodies. Phylogenetic tree of primates indicates species showing a capacity for mirror self-recognition. Prior studies showed that humans and great apes pass the mark test, but macaques did not. The new study shows that rhesus monkeys also possess the capacity for mirror self-recognition.

and temporal correspondence between the movements of their hands and faces and visual information reflected in a mirror, and can use this information to guide adaptive behavior. At the maximum, these findings suggest macaques actually possess a sense of self that is no different from that of chimpanzees, but is only manifested in the standard mark test when the mark is made behaviorally relevant. Between these two extremes lie some intriguing possibilities with important implications for understanding how brains detect visuo-motor correspondence — that is, self-agency — and how this process contributes to self-awareness. If self-agency and by extension self-awareness can be developed or even enhanced through training, then similar techniques could be used to remediate disorders in which self-agency and self-awareness are compromised, such as schizophrenia.

Despite the medical and philosophical importance of self-agency and self-awareness, the neural mechanisms mediating these processes remain poorly understood, in part because neurobiological studies have been limited to analysis of lesions and noninvasive neuroimaging studies in humans. Current understanding links self-agency and self-awareness to brain regions implicated in multi-modal integration of somatosensory information, interoception, and forward models of motor planning and control [20]. The technique developed by Chang *et al.* [1] opens new avenues for neurobiological exploration of the biological mechanisms mediating the sense of self in non-human animals. In so doing, we may come to know ourselves better as well.

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