4-2004

Reflections on Animal Selves

Marc Bekoff
University of Colorado

Paul W. Sherman
Cornell University

Recommended Citation

Reflections on Animal Selves

Marc Bekoff[1] and Paul W. Sherman[2]

[1] University of Colorado
[2] Cornell University

ABSTRACT

Is self-cognizance a uniquely human attribute, or do other animals also have a sense of self? Although there is considerable interest in this question, answers remain elusive. Progress has been stymied by misunderstandings in terminology, a focus on a narrow range of species, and controversies over key concepts, experimental paradigms and interpretations of data. Here, we propose a new conceptual and terminological framework, emphasizing that degrees of self-cognizance differ among animals because of the cognitive demands that their species-specific social structures and life-history characteristics have placed upon them over evolutionary time. We suggest that the self-cognizance of an organism falls at a point on a continuum of social complexity and conscious involvement.

Although laypersons and researchers from many disciplines have long been interested in animal self-knowledge (or self-cognizance) [1–3], and a large amount of information has accumulated, few unambiguous conclusions are available. This is mainly because of the difficulty of objectively assessing self-knowledge and quantifying its neurobiological substrates among organisms whose patterns of communication we only partially understand. Progress has also been limited by inconsistencies in terminology, and by experimental paradigms that concentrate on visual rather than on chemical or auditory cues. Moreover, relatively few species have been examined in detail, and all were vertebrates, mostly primates.

Here, we suggest that it is appropriate and useful to consider knowledge of self, or 'self-cognizance', as a continuum ranging from self-referencing to self-awareness to self-consciousness (Box 1).We argue that degrees of self-cognizance are better predicted by the behavioral ecology of a species rather than by its relative brain size or phylogenetic closeness to humans. In social animals, cognitive demands imposed by selection for cooperation, maintenance of pair bonds, nepotism, and reciprocity on the one hand, and avoidance of being cheated and effectiveness in competition on the other hand, have resulted in the evolution of increased mental complexity [1–3]. Studies of self-cognizance will benefit from capitalizing on this diversity, and also from considering self-cognizance in invertebrates and vertebrates. We argue that the degree of self-cognizance of individuals in any species can be represented as a point on a continuum of complexity and conscious involvement.

However, documenting degrees of self-cognizance is difficult. Ideally, individuals should be studied in their natural environments when they are making decisions about how to modify their behavior toward other individuals of their social group in light of the previous responses of those group members to them. Thus, it will be useful to combine field observations of dynamic changes in the behavior of an individual in social situations requiring self-cognizance, such as deciding how long or hard to fight over a resource [4] or responding to being cheated in a social contract [5,6], with noninvasive neural techniques to determine

whether the target behaviors are linked to electrophysiological responses of the types, and in the specific brain regions, that are active in self-cognizant humans.

Currently, technical difficulties preclude applying certain neural techniques to field situations. However, relevant techniques are being developed and, in the meantime, cleverly designed laboratory experiments [5,7,8] might enable us to infer what is happening within the brains of animals as they make decisions requiring self-cognizance.

Animal selves: what is the problem?

Although there is considerable interdisciplinary interest in animal self-cognizance [1–3,7–11], few unequivocal answers are available. Individuals of most species behave as if they 'know' that they are similar to, but distinct from, others of the same species [12]. For example, they seldom mate with the wrong species; they position their body parts in space so that they do not collide with nearby conspecifics as they move, or travel as a coordinated hunting unit or flock; and, they discriminate members of their social group from foreign group members, relatives from nonrelatives, and close from distant kin [13–16]. However, there is presently no agreed-upon objective way to assess the degree of self-cognizance of an individual.

Here, we address five specific questions, namely: (i) what does it mean to say that an animal is self-cognizant?; (ii) is self-cognizance a dichotomous phenomenon or a continuum?; (iii) does the occurrence of self-referent phenotype matching [17] imply that an animal is self-cognizant?; (iv) is knowledge of the neural mechanisms underlying self-cognizance in humans useful for inferring self-cognizance in other animals?; and (v) what are the promising directions for future research?

Is self-cognizance a continuum?

In 1871, Darwin [18] asserted that 'the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind'. By contrast, Hauser [7] recently suggested that 'our own species may be on its own in having the capacity to understand what it's like to have a sense of self, to have unique and personal mental states and experiences'. So, is self-cognizance best characterized as a dichotomous variable (either an animal has it or it doesn't) or as a continuum?

We argue for characterizing self-cognizance as a continuum. First, too few species have been studied in sufficient detail to support empirically the claim that a general cognitive discontinuity exists between humans and all other animals [1,2,7,11]. Second, even if there were discontinuities between humans and other animals in some cognitive capacities (e.g. language abilities [19]), we are not forced to accept that discontinuities therefore exist in all cognitive capacities [1,20–22]. We hypothesize that species exhibit different degrees of self-cognizance (Box 1), which reflect variations in their social environments and life histories. The position of an individual on the self-cognizance continuum is determined, ultimately, by natural selection, based on the degree to which members of its species or group (e.g. males or females) repeat competitive or cooperative interactions with the same conspecifics over their lifetimes and benefit from changing their responses in light of outcomes of those previous interactions (see also [1,7,23]).

We suggest that self-cognizance is favored to the degree that individuals benefit from reflecting on their own behaviors in light of the previous responses of conspecifics, and dynamically and adaptively adjusting their future behaviors accordingly. These are differences in degree, rather than in kind, among species and individuals, and they should be reflected in a continuum of self-cognizance.

Box 1. Categories (degrees) of self-cognizance

In our scheme, 'self-cognizance' is used as an umbrella term to cover the continuum from self-referencing to self-consciousness. We hypothesize that species exhibit different degrees of self-cognizance, which reflect variations in their social environments and life histories. The position of an individual on the self-cognizance continuum is based on the degree to which members of its species or group engage in repetitive competitive or cooperative interactions with the same conspecifics over their lifetimes and benefit from changing their responses in light of outcomes of those previous interactions (see also [1,7,23]).

Self-referencing
(also referred to as self-referent phenotype matching and the 'armpit effect': [17,31,42–45]). Self-referencing is a perceptual process involving matching phenotypic characteristics of a target individual against the phenotype of the discriminator. Discriminators compare labels of the target (such as of odor or appearance) against labels learned from their own phenotype, and accept or reject that target based on the degree of similarity [42,46]. Self-referencing can be reflexive and noncognitive, even occurring in the immune system and in creatures without brains, such as tunicates and plants [13,14,17]. If a brain is present, it might be used in deciding, consciously or nonconsciously, what behavioral action to take once recognition occurs [47].

Self-awareness
(also referred to as 'perceptual consciousness' [1] and 'body-ness' or 'mine-ness' [9,10]). Self-awareness is the cognitive process that enables an individual to discriminate between its own body and those of others, or to discriminate possessions such as 'my bone' or 'my territory' from the similar possessions of others. A sense of 'body-ness' is necessary for most animals to function in their social and ecological milieus (i.e. to find mates, to evade predators, or to avoid bumping into each other). A brain is required for this level of self-cognizance, although the actual discrimination can be conscious or unconscious. Being self-aware does not imply that individuals use self-referent phenotype matching or vice versa.

Self-consciousness
(analogous to 'reflective consciousness' [1], 'sense of self' [7], 'self-reflection' [35], 'I-ness' [9] and 'I-self' [34]; having 'sympathy, empathy and a theory of mind' [27] also are included). Self-consciousness involves having a sense of one's own body as a named self, knowing that 'this body is me' and thinking about one's self and one's own behavior in relation to the actions of others. A brain is required and the underlying processes are conscious. Being self-conscious implies that an individual is self-aware, and that it can use self-referent phenotype matching. We hypothesize that self-consciousness evolves when individuals benefit from analyzing and revising their own behavior in light of how specific members of their social group, including actual or potential mates, responded to their behavior in the past. Self-consciousness leads to dynamic and finely graded behavioral outputs, ranging from cooperation to selfishness, depending on the costs and benefits of previous responses of conspecifics to the focal individual.

Methodological issues

It is obvious to most pet owners that their companion animals are self-cognizant to some degree [certainly self-aware, and perhaps even self-conscious (Box 1)]. Initially, it also seemed reasonable to suppose that our closest primate relatives, such as chimpanzees, gorillas and orangutans, share a human-like capacity for self-consciousness (i.e. the highest degree of self-cognizance). However, none of these conjectures can be proven, because there is no agreed upon objective way to quantify self-cognizance.

Research on this topic has been conducted on a few captive individuals, some of which received extensive training [1,7,12,22,24–26]. We actually know very little about degrees of self-cognizance among companion animals, less still about free-living nondomesticated species and essentially nothing about interindividual variation in degrees of self-cognizance in nature, for example between males and females, juveniles and adults, or dominants and subordinates. Most importantly, we do not know how variations in expression of self-cognizant behaviors affect the survival and reproductive success of their bearers [10].

Thirty years ago, Gallup [25,27] proposed using the mirror test to infer self-consciousness. This test was based on the observation that some captive chimpanzees would gaze into a mirror and then touch a colored spot that had been placed on their forehead whilst they were sedated. This response became the gold standard for inferring animal self-consciousness.

Recently, however, many authors [7,22,26,28,29] have highlighted problems with interpreting the results of the mirror test. Most importantly, it can yield false negatives: if an individual fails the test, it does not necessarily mean that the animal is not self-conscious. For example, an individual might fail the test because vision is not the primary sensory modality of recognition in that species; chemical cues often are more important [30–32]. Even in animals that primarily use vision in recognition, the mirror test can yield false negatives; for example, if an individual recognized itself but did not give a detectable behavioral response [13,14]. This might account for some of the well known variability in mirror-test results [7]. Finally, some species or individuals (e.g. male canids and primates) tend to avoid eye contact with same-sex conspecifics, because it is a threatening gesture. These individuals are hesitant about gazing directly into a mirror.

If failing the mirror test does not prove that an individual lacks self-consciousness, what does passing the test mean? Some researchers [3,7,9,10] believe that it indicates only that chimpanzees are self-aware (Box 1). Others offer a richer interpretation. Thus, Gallup [27] concluded that 'not only are some animals aware of themselves but such self-awareness enables these animals to infer the mental states of others. In other words, species that pass the mirror test are also able to sympathize, empathize and attribute intent and emotions in others – abilities that some might consider the exclusive domain of humans'. Gallup believes that passing the mirror test implies self-consciousness and having a 'theory of mind'.

However, too little is known about the behavioral ecology of animal self-awareness to support either the rich or the impoverished interpretation of passing (or failing) the mirror test. Moreover, results from a few captive individuals might not reflect the capacities for self-cognizance of an entire species in nature. By itself, the mirror test is therefore neither necessary nor sufficient to infer where species or individuals lie along the continuum of self-cognizance.

Bringing together ethology, behavioral ecology and neurobiology

The foregoing discussion about degrees of self-cognizance poses more questions than it answers. For example, do the great apes have a special, refined sense of self-cognizance that is similar to self-consciousness in humans but which is lacking in the other creatures? To what degree are other social animals, including insects, spiders, rodents, herpestids (mongooses), canids, birds or fish self-cognizant? How would we find out? Addressing these issues requires objective criteria for recognizing degrees of self-cognizance, criteria that take into account the sensory capabilities and behavioral ecology of each species. Given the diversity of animal social and sensory systems, no single technique is likely to provide an acid-test for determining degrees of self-cognizance across all taxa.

However, a relatively new and potentially promising general approach to designing tests of self involves the use of noninvasive techniques to detect neural activity, as measured by firing rates and cell metabolism. These methods include the measurement of evoked response potentials (ERPs) and the use of positron emission tomography (PET scans) or functional magnetic resonance imaging (fMRI). These techniques can be coupled with others, such as transcranial magnetic stimulation (TMS), that create mini-disruptions of neural activities in specific brain regions.

Neural imaging has recently been used on humans to identify brain areas involved in certain perceptual and emotional processes [33,34], including what Johnson et al. [35] termed 'self-reflection' (our self-

consciousness: Box 1). Based on results of neuroimaging studies, Keenan et al. [36] suggested that "there may be a bias for the processing of 'self ' within the right prefrontal cortex in humans and other primates".

We eagerly anticipate the broader application of neuroimaging and other neurobiological techniques, perhaps eventually to free-living animals in their native ecological and social environments. However, there are major technical hurdles that must first be overcome, because current methods require the confinement of subjects, and even then artifacts resulting from their movements can lead to confusion in the interpretation of data.

Nonetheless, we are optimistic. Technical solutions are emerging, such as being able to capture brain activities during socially relevant situations in a highly restrictive scanner. Until appropriate technology is available, it might be possible to design relevant laboratory experiments [5,7,8] that, when coupled with existing technology, enable us to infer where and when activity is occurring in the brains of animals that are only loosely restricted.

If so, the next step would be to visualize the neural processes that occur in humans when we engage in tasks requiring mobilization of self-consciousness, such as thinking about our own thoughts and actions [1] or considering how to respond to being cheated in a social contract. If neural imaging studies yield a baseline profile of what brain activities are associated with behaviors requiring self-consciousness in humans, it would be a place to begin the search for objective evidence of self-consciousness in non-humans. For example, to investigate the degrees of self-cognizance enlisted in the mirror test, it would be valuable to map the brain regions and neural activity profiles that occur in chimpanzees that are passing the test, as well as in those that are failing it. Results could be compared with neural imaging data from humans who were taking the mirror test or otherwise were behaving self-consciously [35,36]. If active brain regions and neural profiles of chimpanzees that pass the mirror test were similar to those of humans engaged in tasks known to involve self-consciousness, but different from chimpanzees that do not pass, then, by analogy, the mirror test has revealed probable self-consciousness in chimpanzees. However, if brain regions and neural profiles of chimpanzees that pass the test are very different from those of self-conscious humans, then either chimpanzees are self-aware but not self-conscious (Box 1) or else chimpanzee brains and neural processes are quite different from those of humans.

Thus, neurobiological studies of other social species that are engaged in relevant behavioral tasks, although currently technically impossible, are likely to be rewarding in the future. Neural correlates that are associated with various degrees of human self-cognizance might differ from those in other species because of variations in neuroanatomy (e.g. the presence or absence of a prefrontal cortex) or because of the use of different sensory modalities. However, this is more of a caution than a deterrent to such investigations.

We predict that species will exhibit various degrees of self-cognizance, reflecting differences in their social environments and life-history characteristics [1,2,7,9,10]. In particular, greater degrees of self-cognizance (Box 1) are expected in species in which individuals benefit most from reflecting upon and revising their own behavior in light of how particular conspecifics have responded to them previously. Self-cognizance should thus be most developed in long-lived, group-living animals, in which individuals have repeated interactions, both cooperative and competitive, with the same suite of conspecifics [23]. The putative self-consciousness of chimpanzees and gorillas [7,25,26] supports this hypothesis, but that of orangutans [7,37] might not, because they are relatively nonsocial on Borneo. However, orangutans are more social elsewhere in their range (e.g. on Sumatra). It would be interesting to compare the self-cognizance of individual orangutans living in these different areas.

It also will be illuminating to investigate degrees of self-cognizance in social vertebrates and invertebrates, such as honey bees *Apis mellifera*, paper wasps *Polistes fuscatus*, damp-wood termites *Zootermopsis nevadensis*, gray wolves *Canis lupus*, naked mole-rats *Heterocephalus glaber*, lions *Panthera leo*, meerkats *Suricata suricata*, gray parrots *Psittacus erithacus*, Florida scrub jays *Aphelocoma coerulescens* and acorn woodpeckers *Melanerpes formicivorus* [6,37–40]. In each species, mated pairs and other group members interact repeatedly over their lifespans, groups comprise close and distant kin, and intra-group dynamics can involve nepotism, reciprocity, competition and selfishness [40]. The abilities of individuals to reflect upon and modify their own behaviors in response to previous responses of members of their social group would presumably enhance cooperation and group coordination in finding food (honey bees, wolves and lions), maintenance of food stores (woodpeckers and naked mole-rats) and pair bonds (damp-wood termites and parrots), and avoidance of predators (paper wasps, meerkats and jays).

We hypothesize that degrees of self-cognizance evolved along with cooperative breeding and sociality. Moreover, we expect highly social species to be self-conscious because if individuals only were self-aware (Box 1), they would be unable to respond adaptively to the previous responses of group-mates to them. Lack of self-consciousness could thus restrict the ability of individuals to cooperate and to compete effectively, which, in turn, could compromise group cohesion and stability, and limit the reproductive opportunities of the individuals concerned.

Where to from here?

Studies of self-cognizance as a continuum will undoubtedly lead to bold programs of interdisciplinary research and forge new links among animal behaviorists, evolutionary biologists, cognitive ethologists and neuroscientists. Future studies must pay attention to the behavioral ecology of each species as well as to basic and well accepted biological ideas, such as evolutionary continuity and the comparative method.

It is useful to return to basics. We must revise our definitions and refocus our questions, and an agreed-upon terminology is a good place to begin. Defining what self-cognizance means, what behavioral abilities accompany different degrees of it, and what neural activities are diagnostic of each degree, are essential (e.g. Box 1). In particular, if we can agree on objective criteria that characterize human self-consciousness [36], for example based on behavioral and neural responses to perceived cheating on social contracts [41], we might then be able to apply those same criteria to infer self-consciousness in other animals.

Although there are major methodological hurdles, we are optimistic that researchers and technological innovations can meet these challenges. Our goal should be to quantify and compare degrees of self-cognizance among animals in natural or semi-natural ecological and social settings, and also to investigate how different sensory modalities contribute to enabling different degrees of self-cognizance.

Finally, and in light of Darwin's principle of evolutionary continuity [18], we urge abandonment of the anthropocentric view that only big-brained creatures, such as great apes, elephants and cetaceans have sufficient mental capacities for the most complex degree of self-cognizance: self-consciousness. We hope the current conventional wisdom that only a few species are self-conscious will become a historical curiosity and that, in its place, will arise an empirical understanding of where the minds of various social vertebrates and invertebrates lie on a continuum of self-cognizance.

References

1. Griffin, D.R. (2001) Animal Minds, University of Chicago Press
2. Dawkins, M.S. (1998) Through Our Eyes Only?, Oxford University Press
3. Bekoff, M., et al. eds (2002) The Cognitive Animal MIT Press
4. Taylor, P.W. and Elwood, R.W. (2003) The mismeasure of animal contests. Anim. Behav. 65, 1195–1202
5. Hauser, M.D. (1992) Costs of deception: cheaters are punished in rhesus monkeys (Macaca mulatta). Proc. Natl. Acad. Sci. U. S. A. 89, 12137–12139
6. Reeve, H.K. and Nonacs, P. (1992) Social contracts in wasp societies. Nature 359, 823–825
7. Hauser, M.D. (2000) Wild Minds: What Animals Really Think, Henry Holt
8. Brosnan, S. and De Waal, F.B.M. (2003) Monkeys reject unequal pay. Nature 425, 297–299
9. Bekoff, M. (2002) Animal reflections. Nature 419, 255
10. Bekoff, M. (2003) Consciousness and self in animals: some reflections. Zygon 38, 229–245
11. Keenan, J.P. (2003) The Face in the Mirror: The Search for the Origins of Consciousness, HarperCollins
12. Allen, C. (2003) Animal Consciousness. In The Stanford Encyclopedia of Philosophy (Zalta, E.N., ed.), (http://plato.stanford.edu/archives/sum2003/entries/consciousness-animal/).
13. Sherman, P.W. et al. (1997) Recognition systems. In Behavioural Ecology, 4th edn, (Krebs, J.R. and Davies, N.B., eds), pp. 69–96, Oxford University Press
14. Holmes, W.G. (2001) The development and function of nepotism. In Handbook of Behavioral Neurobiology (Vol. 13) (Blass, E., ed.), pp. 281–316, Plenum Press
15. Griffin, A.S. and West, S.A. (2003) Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science 302, 634–636
16. Buchan, J.C. et al. (2003) True paternal care in a multi-male primate society. Nature 425, 179–181
17. Hauber, M.E. and Sherman, P.W. (2001) Self-referent phenotype matching: theoretical considerations and empirical evidence. Trends Neurosci. 24, 609–616
18. Darwin, C. (1871/1936) The Descent of Man and Selection in Relation to Sex, Random House
19. Hauser, M.D. et al. (2002) The faculty of language: what is it, who has it, and how did it evolve? Science 298, 1569–1579
20. Allen, C. and Bekoff, M. (1997) Species of Mind, MIT Press
21. Shettleworth, S.J. (1998) Cognition, Evolution, and Behavior, Oxford University Press
22. Bekoff, M. (2002) Minding Animals: Awareness, Emotions, and Heart, Oxford University Press
23. Gallup, G.G. Jr (1998) Self-awareness and the evolution of social intelligence. Behav. Proc. 42, 239–247
24. Pepperberg, I.M. (1999) The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots, Harvard University Press
25. Gallup, G.G. Jr et al. (2002) The mirror test. In The Cognitive Animal (Bekoff, M. et al., eds), pp. 325–333, MIT Press
26. Shumaker, R.W. and Swartz, K.B. (2002) When traditional methodologies fail: cognitive studies of great apes. In The Cognitive Animal (Bekoff, M. et al., eds), pp. 335–343, MIT Press

27. Gallup, G.G. Jr (1998) Can animals empathize? Yes. Sci. Am. 9, 66–71
28. Heyes, C.M. (1994) Reflections on self-recognition in primates. Anim. Behav. 47, 909–919
29. de Veer, M.W. and van den Bos, R. (1999) A critical review of methodology and interpretation of mirror self-recognition research in nonhuman primates. Anim. Behav. 58, 459–468
30. Mateo, J.M. (2002) Kin recognition abilities and nepotism as a function of sociality. Proc. R. Soc. Lond. Ser. B 269, 721–727
31. Todrank, J. and Heth, G. (2003) Odor-genes covariance and genetic relatedness assessments: rethinking odor-based 'recognition' mechanisms in rodents. Adv. Stud. Behav. 32, 77–130
32. Wyatt, T.D. (2003) Pheromones and Animal Behavior: Communicating by Smell and Taste, Cambridge University Press
33. Keenan, J.P. et al. (2001) Self-recognition and the right hemisphere. Nature 409, 305
34. Damasio, A. (2001) Fundamental feelings. Nature 413, 781
35. Johnson, S.C. et al. (2002) Neural correlates of self-reflection. Brain 125, 1808–1814
36. Keenan, J.P. et al. (2000) Self-recognition and the right prefrontal cortex. Trends Cogn. Sci. 4, 338–344
37. Miles, H.L.W. (1994) Me Chantek: the development of self-awareness in a signing orangutan. In Self-awareness in Animals and Humans: Developmental Perspectives (Parker, S.T. et al., eds), pp. 254–272, Cambridge University Press
38. Sherman, P.W. et al. (1995) The eusociality continuum. Behav. Ecol. 6, 102–108
39. Shellman-Reeve, J.S. (1997) The spectrum of eusociality in termites. In The Evolution of Social Behavior in Insects and Arachnids (Choe, J.C. and Crespi, B.J., eds), pp. 52–93, Cambridge University Press
40. Pusey, A.E. and Packer, C. (1997) The ecology of relationships. In Behavioural Ecology, 4th edn, (Krebs, J.R. and Davies, N.B., eds), pp. 254–283, Oxford University Press
41. Sugiyama, L.S. et al. (2002) Cross-cultural evidence of cognitive adaptations for social exchange among the Shiwiar of Ecuadorian Amazonia. Proc. Natl. Acad. Sci. U. S. A. 99, 11537–11542
42. Sherman, P.W. (1991) Multiple mating and kin recognition by self-inspection. Ethol. Sociobiol. 12, 377–386
43. Petrie, M. et al. (1999) Peacocks lek with relatives even in the absence of social and environmental cues. Nature 401, 155–157
44. Hauber, M.E. and Sherman, P.W. (2003) Designing and interpreting tests of self-referent phenotype matching. Anim. Cogn. 6, 69–71
45. Mateo, J.M. and Johnston, R.E. (2000) Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching. Proc. R. Soc. Lond. Ser. B 267, 695–700
46. Reeve, H.K. (1989) The evolution of conspecific acceptance thresholds. Am. Nat. 133, 407–435
47. Neff, B.D. and Sherman, P.W. (2002) Decision making and recognition mechanisms. Proc. R. Soc. Lond. Ser. B 269, 1435–1441