would be unable to inhibit the automatic provoked responses. This hand would therefore show 'anarchic' behaviour. The 'frontal' account of anarchic hand makes sense if one considers the basic role of the frontal lobes in the human brain: to allow humans to interact with the environment.

If damage to one SMA results in AH, damage to both SMAs elicits utilization behaviour (Boccardi et al. 2002). In both cases the affected patients will perform inappropriate actions. The environment triggers the actions performed by patients showing utilization behaviour, exactly as it does those of people with AH syndrome. However, the patients with utilization behaviour are not aware that their behaviour is inappropriate, and do not show any conflict between wanted and unwanted actions. It may well be that the lack of awareness observed in these patients comes from the complete impairment of the medial system.

Think about a possible scenario that could apply to us all. One Saturday morning while driving to the country for the weekend you cross the usual road to your office. Absent-mindedly, you may turn and find yourself driving to the office for a while before recognizing your error. The environment provided a trigger strong enough for you to initiate an *automatic behaviour, which you had to inhibit to go back to your intended plan. You would have performed an action that you did not mean to do. This is what often happens to people affected by utilization behaviour who lack the capacity to inhibit behaviour triggered by environment.

AH is a clear example of uncontrolled behaviour triggered by the environment caused by a lesion to a sub-region of the frontal lobes. Are the anarchic actions still intentional? Whose will are they responding to? It would be possible to maintain that this epistemological problem springs from the conflict between stated will and performed action.

AH epitomizes the inability to inhibit actions triggered by the environment. The syndrome suggests that conscious will could only veto some undesired actions. From this perspective it looks as if our brain may have laid away a free 'won't' rather than a free will. The only control we would have over our actions is a negative control; the possibility of inhibiting them. To achieve the (desired?) aim, the motor system makes non-stop refinements, of which we are usually not aware. These include inhibition of actions triggered by environmental affordances. AH is the result of the lack of such inhibition, due to a lesion of the mainly inner driven medial–frontal motor system.

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animal consciousness Consciousness has periodically been a pressing issue in the scientific study of non-human animals, and we are currently in one of these periods. As with humans, discussions of consciousness in other species are often inconclusive; however, recent conceptual clarifications and empirical observations are facilitating new perspectives. Here we focus primarily, but not exclusively, on the importance of ethological studies for gaining essential insights into animal mentality and its evolution. Knowledge about what animals do in various situations (e.g. interacting socially, foraging, and avoiding predation) is of critical importance in learning about animal minds and how they operate (Allen and Bekoff 1997).

There are five primary issues in the study of animal consciousness (see Allen and Bekoff 2007): (1) What is consciousness, and how many kinds or levels are there? (2) How can we determine if other species are conscious? (3) Which species have which type(s) of consciousness (the distribution question)? (4) What can we know about the nature of the private or subjective experiences of other species (the *qualia question)? and (5) How and why has consciousness *evolved? We will consider all five with varying degrees of brevity.

For ethologists, who study the natural behaviour of animals from an evolutionary perspective in both the field and the laboratory, the issue of consciousness is valuable insofar as it helps us understand how and why animals behave the way they do. Ethologists assume that all features of animals have some continuity with some ancestral population or process. Thus, we must ask why various levels of consciousness have evolved in species showing different life-history strategies. Philosophical analysis and neuroscience data thus inform, but do not drive, comparative behavioural studies. Baars (2005) reviews the history of animal consciousness and concludes that consciousness is a 'fundamental biological adaptation'. The scientific literature on animal consciousness is now voluminous (e.g. Baars 2005, Merker 2007). Typically, however, most treatments discuss only some of the most widely reported cognitive accomplishments of select species (e.g. dolphins, birds, and non-human primates, especially the great apes—see the following entries).

More specifically, the aims of ethology are typically viewed as: to understand (1) the proximate sensory, learning, and physiological mechanisms underlying behavioural performance; (2) the development (ontogeny) of behaviour; (3) the adaptiveness of behaviour (especially in a species' natural habitat); and (4) the evolution and phylogenetic history of behaviour (Tinbergen 1963). Conspicuously absent from 'classical' ethology were issues involving consciousness. Thus, in ethology as well as in behaviouristic experimental and comparative psychology, questions of animal consciousness and related ones involving emotion and subjective experiences in general became largely taboo. To recognize a broadened view of ethology that encompassed cognitive, emotional, and conscious processes, Burghardt (1997) added a fifth aim, the study of private experience.

The eminent scientist Donald Griffin (1976, 1992) tirelessly promoted the field of cognitive ethology for the study of such topics as animal thinking, awareness, mentality, and consciousness. Although frequently criticized for advancing some questionable claims (Bekoff and Allen 1997), Griffin had considerable impact in reviving the search for mental abilities in non-human animals. Increased interest outside ethology, psychology, and philosophy in issues of animal conservation and animal rights and welfare (including the treatment of laboratory and agricultural animals) also helped foster interest in cognitive ethology (e.g. Dawkins 1992). It turns out that the subjective lives of non-human, as well as human, animals might not be as private as used to be thought, and that the privacy-of-mind argument (no one has access to another individual's mental states) is invoked too rapidly when studying such phenomena as consciousness (Burghardt 1997, Bekoff 2007).

Careful observation of animals in naturalistic contexts is an essential feature of ethology and a benchmark for evaluating claims for animal mentality. Rare, often serendipitous, observations by informed observers can allow glimpses into the inner life of animals and inspire formal studies as well as help us to evaluate and extend laboratory-based phenomena.

1. Current stances on animal consciousness
2. The study of animal consciousness
3. The origins of consciousness
4. The need for broad interdisciplinary research

1. Current stances on animal consciousness

As a result of renewed interest in animal awareness and consciousness, many popular and scientific books and articles are making strong and sometimes questionable claims about animal mentality, raising again the problem of anthropomorphic interpretations of behaviour. On the other hand, many biomedical and behavioural scientists refuse to acknowledge any essential similarity in the mental lives and experiences of human and non-human animals. Yet many creative scientists, when developing research questions, essentially put themselves in the animal's 'shoes'. To provide some guidelines for doing this, Burghardt (1985) suggested the employment of a 'critical anthropomorphism' that utilizes both our own stance as sentient problem-solving creatures and the careful incorporation of scientific knowledge about a species (e.g. ecology, neuroscience, perceptual abilities) in developing testable hypotheses about the private experiences of other species. An explicit critical anthropomorphism needs to be adopted because humans have a natural propensity to attribute human psychological attributes to both living and non-living entities, including the weather (a 'violent' storm). We seem to be programmed to see human-type mentality in events where it cannot possibly be involved.

An associated issue is that some of the severest critics of the study of animal mentality are sociobiologists, behavioural ecologists, and selfish-gene theorists who view the detailed study of animal mental abilities as irrelevant, yet often use anthropomorphic terms in discussing the wants, desires, and needs of genes, animals, and groups. Although these researchers typically assert that such terminology is just useful shorthand, the use of this double standard (Bekoff 2007) has the effect of making the endeavour to determine the actual status of animal mentality more problematic, and lessens interest by evolutionary biologists.

Additionally, in ethology and comparative psychology it is common to discuss 'mind' in animals while omitting any discussion of consciousness, as was true of much early cognitive psychology (Burghardt 1985). While acknowledging that animals have minds, and that we can study aspects of them and how they may work, it basically ignores the issue of what having a mind means, experientially, to the animals themselves. It is basically the study of the problems animals can solve, and relies on behavioural means alone. This is fine, but we can also try to test more experientially inferential questions about consciousness as well as those inferring cognitive processes from behaviour. As we will see, neuroscience is becoming relevant as well.

2. The study of animal consciousness

Clearly, the conception one has of consciousness influences whether one accepts that it is nearly universal in all living things, or at least vertebrates; present in at least some other species; possibly present in some but not yet firmly established; or impossible to ever determine in other species (or, in an extreme mode, people other than oneself). That almost all scholars accept the existence of various kinds or levels of consciousness compounds the problem, in that all are covered by the same word. Views of consciousness may range from being awake, alert, or responsive to being able to reflect on one's own experiences and 'intentionally' communicate them to other beings. For some writers, behavioural expressions of emotional states such as pain, rage, or pleasure are important markers of consciousness.

How can we effectively characterize and study the mentality and private experiences of other species, and especially their evolution? We can begin by parsimoniously accepting that if consciousness occurs in people it has adaptive counterparts and homologues in other species, a view perfectly in line with evolutionary continuity of morphology, brain, and behaviour expressed by Charles Darwin. The focus should be on the specific mechanisms, evolution, and development of continuity, not whether or not it exists. Baars (2005) argues that grounded inference from both behavioural and brain studies strongly suggests that non-human animals, especially mammals with 'human-like brains and behavior', have subjective experiences. Here Baars invokes two venerable methods, *subjective analogical inference* and *neural analogical inference* (Burghardt 1985).

Typologies of consciousness that go beyond mere wakefulness and responsiveness to stimuli in the environment vary, but all require these first two most basic types of consciousness. *Phenomenal consciousness* is often used to refer to subjective, qualitative, or experiential aspects of consciousness and incorporates emotions, feelings, qualia, and sentience in general (Allen and Bekoff 2007). Here the focus is both on attempting to determine which animals have such consciousness (the distribution question) and also on trying to gain some knowledge of what such conscious experiences are like for other species (Burghardt 1997). How do other species perceive and experience the external world and their own bodies? Basically, the best we can do is comparable to how we answer this question about other people, except that we need to use behavioural and neural methods and inference grounded in a critical anthropomorphism. For example, our anthropocentric inclinations harbour the danger of minimizing attributions of pain in species that do not show distress in ways we are programmed to view empathically, such as screams or whines. This almost guarantees a confounding of biological relatedness or similarity with our concept of consciousness.

The Cartesian view, that human-style language is necessary for consciousness to occur, and thus is absent from all animals, is still encountered. In this approach, studying animal consciousness besides the obvious awake/alert sense can only follow discovering of human types of communication in other species. This is a high bar, and was basically used to deny the need to explore consciousness in other species. More useful is the acceptance that there are a group of types of conscious experiences in which animals may use their experiences to make more or less rational (adaptive?) decisions. This has been called *access consciousness* by Block (1995). While access consciousness does not require language to exist, it does make animals more like intentional actors than mere passive responders.

Much current interest centres on **self-consciousness*, also referred to as self-awareness, self-cognizance, or reflective consciousness (thinking about one's thoughts). *Mirror self-recognition, developed by Gordon Gallup, was one of the first methods to test a sense of self in other species, but there have been criticisms of how this approach has been employed (Bekoff 2007). While definitive answers on the general issue of self-awareness remain elusive, progress can be made by clarifying the terms listed above, perhaps by arranging a continuum of levels such as self-cognizance, self-referencing, self-awareness, self-consciousness, and reflective consciousness, each with differing behavioural markers based on long-term observations of social interactions (Bekoff and Sherman 2004). In any event, researchers need to produce and largely agree upon a standardized vocabulary and consider modalities other than our anthropocentric emphasis on vision.

Those who focus on reflective consciousness often invoke the **theory of mind*, the idea that being able to posit mental states in others (e.g. anger, knowledge of where food is hidden), including 'intentional' deception, is the key issue. Brüne and Brüne-Cohrs (2006) argue that theory of mind originated in non-human primates and evolved from the need for 'social intelligence' based on living in large groups. They even identify putative neural locations involved in these mechanisms.

Finally, another type of advanced consciousness is *episodic memory*, the ability to construct or represent a simple narrative (Terrace and Metcalfe 2005). If animals can show recall of the sequential order of past events (mental time travel), then perhaps this involves consciousness as well. Monkeys have shown this ability repeatedly in experimental research, and rats may show it too (Babb and Crystal 2006). Field observations of animals have often suggested such abilities, and evidence is accumulating in birds and other vertebrates as well.

3. The origins of consciousness

Although we know that human abilities differ in many ways from those of other species, we still want to uncover the origins of cognitive abilities and subjectivity, both those accentuated in human beings as well as those less developed in us, such as many perceptual, sensory, and memory abilities. We should not keep raising the bar for what we accept as evidence of consciousness or 'private' experiences as animals continue to show unexpected abilities that are very difficult or impossible to explain without invoking the presence of subjective experiences using existing criteria. Indeed, cognitive arguments appealing to consciousness, intentions, expectations, and beliefs might be more useful, even more parsimonious, than complex reductionist behaviourist explanations. Those who favour such behaviourist explanations often cannot offer evidence that their views are better for understanding and predicting behaviour than the views they eschew (Bekoff 2007).

As noted above, the type of conscious experience (or mental capacity) invoked will impact views of its existence in other species. There is a tendency to arrange these varying types of consciousness in a hierarchy, with some animals reaching one level and others that level and more advanced ('higher') ones (e.g. Merker 2007). Usually this is tied to a linear hierarchy of mental abilities, with 'higher' animals such as chimpanzees having more complex abilities than monkeys, who have more complex abilities than dogs, who have more complex abilities than rats, and so on. This 'ladder' approach, still widely accepted (see Merker 2007 and comments thereon), is incompatible with a more modular view of brain and behavioural organization, and with modern evolutionary theory. The continued popularity of such simplistic views suggests that they may be as endemic to human nature as naive anthropomorphism. Other recent approaches focus on relative brain size, but this trait can be independently evolved as well (e.g. in whales, bears, ravens, parrots, and squirrels). Rarefied abilities on arbitrary tasks, cognitive modules, or relative brain size and neural development should not be the sole markers confirming consciousness.

If the continuity position is most reasonable from an evolutionary perspective, plausible phylogenetically testable scenarios for its origin are necessary. Baars (2005) accepts that consciousness evolved in early mammals and is probably found in birds, but he is more reserved about reptiles and cephalopods. Merker, beginning with an analysis of peripheral sensory feedback in earthworm locomotion, identifies the origins of consciousness in the evolution of central representations that allow a 'distinction between self and something else *within one representational space*, short of which it cannot embody even a minimal criterial definition of consciousness' (Merker 2005:107–108). This is a property that arose from the demands for mobility and integrating diverse sensory information. More recently he has developed a theory that places consciousness in brainstem mechanisms and basal ganglia, with brain cortex involved primarily in influencing and refining the more advanced types of consciousness (Merker 2007).

A rather different approach to the evolution of consciousness is taken by Cabanac (1999) who, on the basis of several behavioural and physiological measures of emotion and preference, argues that consciousness arose somewhere between the evolution of amphibians and reptiles. His data show that reptiles, but not amphibians, experience emotional fever (e.g. ectotherms increase their preferred temperature by choosing warmer locations), illness-induced food aversions, and other traits showing response to internal states accompanied by emotion in other species, and thus he concludes that emotional private experiences do not exist in amphibians, fish, and invertebrates. Although this is intriguing, more species in these groups need be studied before accepting this major evolutionary leap in animal consciousness. Note also that in this scheme consciousness does, however, have adaptive consequences.

4. The need for broad interdisciplinary research

From various perspectives, then, there is much agreement that animals other than humans are conscious and have subjective experiences that rely on some degree of consciousness (Bekoff 2007). Nonetheless, questions about the taxonomic distribution of different kinds of consciousness remain unanswered. We must broaden our taxonomic interests beyond non-human primates as it becomes increasingly clear that we and our relatives are not the only species in which consciousness (not necessarily 'human'-type consciousness) has evolved. Primatocentric speciesism ignores many of the interesting questions about the evolution of consciousness and animal minds and its relationship to various life-history strategies. We also need to incorporate diverse perceptual and neural systems underlying these strategies. To learn more about animal consciousness we need interdisciplinary integrative research on diverse species living in conditions in which individuals are free to express a full (or natural) behavioural repertoire, especially in social conditions that reflect those in which they evolved or currently live. Comparative and developmental behavioural data from ethological studies are crucial to our learning more about animal consciousness and how and why it evolved.

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animal consciousness: dolphins Researchers interested in animal consciousness face the daunting task of designing experiments that can address this elusive concept. For the researcher, *consciousness* may be approached experimentally by defining tasks that can reveal the animal's *awareness of self.* An early task of this type was the **mirror self-recognition task* (MSR). This task, originally created by Gallup (1970), asked whether chimpanzees recognize themselves in a mirror. Animals characteristically fail to recognize that the reflection in the mirror is itself. To test whether MSR might develop with experience, Gallup placed a mirror in a chimpanzee's cage and noted that after a long period of exposure the chimp began to attend to its mirror image in ways that suggested it understood that it was viewing its own image and not that of another chimpanzee. Gallup's definitive test was to place a coloured mark on the forehead of a chimp while it was under anaesthesia. When the chimp recovered and once again approached the mirror, it attempted to wipe the mark off of its forehead, thereby demonstrating MSR. Until recently, the only animals that passed the mark test were the great apes. Lesser primates failed this test, as did all other species examined. Marten and Psarakos (1994) were among the first to attempt a mark test with dolphins. These researchers placed zinc oxide or some other bright substance on parts of the dolphin's body not visible without a mirror. The results were suggestive of MSR but, unfortunately, the study had two major weaknesses. First, the dolphins did not have prolonged exposure to mirrors prior to the test, so that initial reactions suggesting they perceived the image to be another dolphin were not extinguished. Second, there was no control condition where the tactile components of marking occurred, but no mark was actually applied (*sham marking*). Similar limitations occurred in a dolphin mark study by Marino et al. (1994). Reiss and Marino (2001) published the first definitive study showing that dolphins (bottlenosed dolphins *Tursiops truncatus*) could in fact pass the mark test. Two dolphins, with long exposure to mirrors in their pool, were either marked with temporary black ink on body parts not visible without a mirror, or were sham-marked with a water-filled marker. Thus, the tactile sensations were the same for real marking and for sham marking. Both dolphins spent significantly more time at a mirror, or other reflective surface, examining themselves when real-marked than when sham-marked. Importantly, the dolphins turned in ways that enabled them to view the parts of their body that had been marked. Reiss and Marino concluded that the dolphins perceived the mirror image as themselves and that mirror-self recognition by great apes and by dolphins may be attributable to the high degree of 'surplus' brain tissue (*encephalization*) and general cognitive ability shared in common by these otherwise very evolutionarily divergent species.

Consciousness, operationalized as 'self-awareness' (see SELF-CONSCIOUSNESS), is best viewed as a multidimensional phenomenon, with self-recognition but one facet. Researchers at the University of Hawaii examined two other facets. The first was a test for the dolphin's awareness of its own behaviours, and the second a test for its awareness of its own body parts. To test for behavioural awareness, defined as conscious awareness of its own recent behaviours, the investigators created and trained two distinct symbolic gestural commands. One gesture required the dolphin to do again the behaviour it just did, i.e. to repeat it. The second gesture required the dolphin to do a different behaviour than that just performed, i.e. to not repeat it. A set of five different behaviours were selected, each controlled by a unique gestural command and each behaviour to be carried out on an object floating in the dolphin's pool. The gestural behavioural commands were: *go over*, *go under*, *touch with the tail*, *touch with the pectoral fin*, and *bite* the object. The dolphin was first given one of these commands and after carrying it out was either given the 'repeat' command or the 'don't repeat' command. In the latter case, the dolphin was to choose one of the four remaining behaviours. For example, if the dolphin was initially instructed to jump over the object, did so, and then was given the don't-repeat command, it could choose either to go under the object, bite it, or touch it with the tail or the pectoral fin. The dolphin was not only successful at repeating or not repeating the initial behaviour, but could also respond successfully to a string of successive commands. For example, a four-item sequence might be *go under*, *repeat*, *don't repeat*, *repeat*, in which case the dolphin, after swimming under the object, is expected to swim under it again, then choose a different behaviour, and finally repeat that latter self-selected behaviour. The dolphin was highly successful at carrying out various four-item sequences of this type in all possible three-way permutations of 'repeat' and 'don't repeat'. In order to perform at this level, the dolphin must retain a representation in memory of the behaviour it just did, process and carry out the subsequent instruction to repeat it or not, and update its memory of what it just did for each successive behaviour performed. The findings of high levels of performance in this task reveal conscious awareness by the dolphin of its own recent behaviours (see Mercado et al. 1998 and summaries in Herman 2006).

Conscious awareness of one's own body parts is easily measured in young children by their ability to identify and point to their own body parts, when asked, by their caregiver, e.g. 'where is your nose, your eye, your foot', and so forth. Children as young as 2 years can identify as many as 20 different body parts, and can also respond appropriately to action requests, such as 'push the ball with your foot'. The young child's ability to do this follows a developmental progression and reveals the emergence of a **body image* that allows for conscious awareness and conscious control of his or her own body parts. As adults, we take this capability for granted, but there are certain types of brain lesions that destroy this capability. In *autotopagnosia*, for example, the patient is unable to point to a body part on request. The patient has thus lost conscious awareness of these body parts. Herman et al. (2001) demonstrated that a bottlenosed dolphin could understand symbolic gestural references to its own body parts, by either showing the referenced body part, shaking it, or using it to either touch or toss a referenced object in her pool. Further, the dolphin was able to use a referenced body part in unique, novel ways, on request by the experimenter. For example, when given for the first time the three-item gestural sequence glossed as '*frisbee* + *dorsal fin* + *touch*', the dolphin swam to the frisbee floating in her pool (there were five different objects floating in the pool), turned on her side, and laid her dorsal fin precisely on top of the frisbee. This was a behaviour that this dolphin or other dolphins would not likely do spontaneously. Results like this showed that the dolphin had a body image that allowed for conscious awareness and conscious control of its own body parts as well as an understanding of symbolic references to those body parts.

The dolphin's awareness of its own body image and own body parts also manifests itself in its remarkable ability to imitate the motor behaviours of human demonstrators. The dolphin is arguably the best behavioural imitator among non-humans. In the wild, dolphins are naturally synchronous, e.g. as shown in their leaps through the air in close synchrony with one or more companions. In the laboratory, as shown by further studies of Herman and colleagues, bottlenosed dolphins can mimic the behaviour of a human demonstrator who may, for example, be performing a pirouette, leaning over backwards, or raising a leg in the air (Herman 2002). For the latter behaviour, the dolphin raises its tail in the air, in effect analogizing a relation between its tail and our leg. Thus, the dolphin is relating directly or by analogy its body image to the human body plan, even though the two body plans are so different. Further, the dolphin is able not only to imitate human behaviours demonstrated live, but also behaviours appearing on a television screen displayed behind an underwater window, revealing that it recognizes abstract or degraded images of the human form (Herman et al. 1990).

Finally, self-awareness in dolphins is also suggested by a study of meta-cognition—awareness of one's own state of knowledge. Smith et al. (1995) tested a bottlenosed dolphin in a psychophysical task requiring it to discriminate between a high and a low tone, but the low tone was of variable frequency that at times closely approached the frequency of the high tone. The dolphin had available separate levers for judging 'high' or 'low', as well as a third lever that it could use as an 'escape' when uncertain. Five human subjects were tested in an equivalent task. The humans and the dolphins each evidenced small thresholds, a narrow interval of uncertainty, and used the escape response similarly. Smith et al. concluded that the 'uncertain' task taps cognitive self-awareness while tasks like MSR may tap body self-awareness.

There are many other questions about consciousness that await further study, including, for example, the dolphin's awareness of 'self' in others. There is no doubt, however, that dolphins, especially the well-studied bottlenosed dolphin, are highly intelligent, rivalling their 'cognitive cousin', the chimpanzee, in that capacity, particularly when intelligence is measured by the species' flexibility in developing new behaviours or in adapting effectively to new challenges in its natural world or in the very different world of the aquarium or laboratory.

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animal consciousness: great apes Great apes (chimpanzees, gorillas, orangutans, and bonobos) are evolutionarily the closest relatives to humans. They engage in a variety of intelligent behaviours, such as tool use and tool manufacture; they present cultural variations in such behaviours (e.g. under similar ecological conditions, some communities use stones as hammers to break open hard nuts, whereas other communities use sticks to exploit ant and termite resources), and in captive conditions they learn to use manual gestures or artificial symbols in what, according to some, might amount to a rudimentary language (Gómez 2004).

Because of this cognitive complexity and their closeness to humans, great apes are specially interesting candidates for showing consciousness in the animal kingdom. A number of behaviours have been highlighted as indicators of consciousness in apes.

1. Mirror self-recognition
2. Tests of metacognition
3. Metacognition of others' mental states

1. Mirror self-recognition

A manifestation of self-awareness is the ability to recognize that the image reflected by a mirror corresponds to oneself. When great apes are confronted with mirrors, initially they show social responses, treating their mirror image as a conspecific. However, as they have experience with the mirror, in a matter of days, social reactions disappear and, instead, they show self-inspecting behaviours, especially directed at parts of their bodies that are not directly visible to them, such as their faces or the inner parts of their mouths. In contrast, the vast majority of other animals, including all non-ape primates, such as macaque monkeys, continue to give social responses to the mirror image; or end up ignoring it, but never make the transition to use the mirror for self-inspection or self-contemplation (Parker et al. 1994). This suggests that apes, but not monkeys and other animals, have the ability to self-recognize.

To formally test this suggestion, Gordon Gallup developed the mirror test (Gallup et al. 2002; see MIRROR TEST). At its most stringent, this test requires the subject to be anaesthetized and, while sleeping, marking an invisible (for the subject) part of its body, for example, the eyebrow, with odourless dye. When the subject wakes up, its behaviour without a mirror is quantitatively compared with its behaviour when a mirror is available. If the painted mark is inspected only or preferentially in front of the mirror, using the reflection as a guide, then the conclusion is that the subjects indeed recognize the image in the mirror as a reflection of themselves, and therefore show the ability for self-awareness.

Chimpanzees, orangutans, and bonobos typically pass the mirror test, provided they have had at least a few days' experience with mirrors prior to the test, and provided they have not been reared in isolation. Another variable affecting their performance is age: younger and older chimpanzees are less likely to pass the test, and some may lose the ability as they age (Gallup et al. 2002). In contrast, the first gorillas tested failed the mirror test. Only a few gorilla individuals are reported to pass some version of this test (the first and most proficient being Koko, a 'linguistically' trained gorilla), or engage in mirror self-inspection suggestive of self-recognition (Patterson and Cohn 1994, Posada and Colell 2007). The relatively poor performance of gorillas as a species in mirror self-recognition remains a puzzle. It is still contentious if this is due to performance problems (e.g. shyness, aversion to mirrors) or competence factors (e.g. they may have lost or lessened the ability for self-awareness during their own evolution diverging from the other great apes). One possibility is that mirror self-recognition does not directly reflect *one* ability, but is an emergent result of the combination of several skills, which in gorillas are more rarely combined, maybe only under unique rearing conditions such as those enjoyed by Koko, the linguistically trained gorilla. For example, in language training experiments, great apes have been taught to use artificial symbols (manual gestures or geometric shapes) to refer to objects and events in the world. Among the 'words' they have been trained to use are symbols to refer to themselves, such as their own names or pointing gestures directed to themselves. In one case (the orangutan Chantek), a relationship has been reported between the progressive learning of such symbols and the emergence of mirror self-recognition (Parker et al. 1994).

In contrast to the generally good performance of apes, a robust result is that no other non-human primates pass the mirror test even after intensive exposure and training with mirrors. Monkeys initially react to their mirror image as if it were a conspecific, and although eventually they learn that it is not a real monkey, they show no sign of recognizing themselves: neither passing the mark test nor engaging in self-inspecting behaviours. Surprisingly, however, they show good evidence that they understand the mechanism of the mirror in relation to other objects; thus, they can accurately use mirrors to find hidden objects or objects behind themselves. They can find anything with the help of a mirror, except themselves (Anderson 2001). An interpretation is that this inability reflects the absence of a notion of themselves as individuals—an inability to be aware of themselves as objects of their own attention.

Methodological objections to the mirror test have proved unfounded. For example, the suggestion that monkey species fail because eye-contact with their own image is so arousing that they cannot process correctly the information or perform the necessary behaviours has been disproved by using mirrors placed in an oblique position, such that eye contact with the reflected image is impossible. No improvement in monkey performance has been detected with this procedure (Anderson 2001).

This sharp and robust phylogenetic divide within primates between monkeys and apes in mirror self-recognition (with the possible exception of gorillas) has prompted speculation that the mirror test captures some key cognitive difference closely related to the human ability for *self-consciousness. The fact that only our closest relatives pass this test would suggest that it is diagnostic of some key cognitive step towards humanness (Parker et al. 1994). Gallup's original suggestion was that it implied a complex form of metacognition, or awareness of mental states. However, critics suggest that it might rather measure an ability to represent body schemas, rather than cognitive schemas; i.e., awareness of oneself as a physical entity rather than awareness of oneself as a psychological entity (Gallup et al. 2002).

A recent, partial challenge to the phylogenetic divide singling out apes and humans comes from studies with dolphins and elephants claiming that some individuals of these species are capable of passing the mirror test (see ANIMAL CONSCIOUSNESS: DOLPHINS). The argument is that the type of self-awareness measured with mirrors could be linked to some ability for *empathy that would have evolved independently in different species where empathetic skills were selected for (Plotnik et al. 2006). Among primates this would have happened only in some apes and humans.

2. Tests of metacognition

Other approaches to primate self-awareness have tried to address directly the issue of awareness of one's own mental states, avoiding the confusion with awareness of one's own body. Two main paradigms dominate the field.

In the so-called *optional test paradigm* (Hampton 2005, Smith 2005), participants can choose whether or not to take a test on the basis of whether they know or do not know the correct response. It is therefore supposed to require the ability to evaluate one's own state of knowledge. In a typical optional test, a monkey learns that he will receive a reward when among two or more images on a computer screen he chooses the one that is identical to a sample shown a few moments before. This is a test of recognition memory for the sample image. Monkeys typically respond correctly in 80–90% of trials when the delay between sample and choice is under 30 s. With longer delays, their performance progressively deteriorates, getting close to chance level with more than 2 min delay, when they seem to forget the sample.

In a *metacognitive test*, after seeing the sample, the monkey is allowed to decide whether or not he wants to proceed to the final phase (where he will get a preferred reward if correct, or nothing plus a time-out period if incorrect). If he wants to proceed, he touches a pattern on the computer screen, and then the test images appear; if he declines the test, he touches a different pattern, and gets a low-quality reward (a small piece of his usual monkey food). With delays slightly over 30 s (where performance in forced tests is about 70%), monkeys frequently decline to take the test and go for the low-quality reward. But their performance when they do choose to take the test is about 85% correct, significantly higher than in forced tests. This has been taken to indicate that rhesus monkeys are aware of whether or not they remember the sample, and decide to take or decline the test on the basis of this meta-knowledge.

Support for this notion comes from two additional results. First, when monkeys are given no sample (and therefore have no information to guide their choice), they are much more likely to use the decline option, in some cases in 100% of the trials. Second, as the delay between sample presentation and option increases, so the probability of choosing not to take the test increases. This suggests that declining the test is indeed related to the probability of having forgotten the sample. Rhesus monkeys pass this test, whereas pigeons fail. To date, this test has not been given to great apes, but the prediction is that they would pass.

Great apes (chimpanzees and orangutans) have received a second metacognitive test—the *looking to know* test (Call 2005). In this test, a piece of food is inserted into one of a number of hollow tubes that are then presented in horizontal position to the ape, in such a way that, if the ape wishes, she can bend down and look inside the tubes before choosing one. When apes see the baiting process and therefore know which tube the food is in, they typically (75% of times) reach directly for the tube without bothering to first look inside. However, if a 5 s delay is introduced before they are allowed to make a choice, their looking behaviour (during the delay) may increase to 50%. When the apes are not allowed to see which tube the food is placed in during baiting, looking behaviour significantly increases to 60% with immediate choice and up to 85% with the 5 s delay. This suggests that the apes are aware of whether or not they know the location of the food, and take appropriate action in the latter case. All four species of apes—chimpanzees, orangutans, bonobos, and gorillas—perform similarly in this test. Moreover, in a proportion of occasions, the apes chose the baited tube after having looked only into the other, empty tube: i.e. they inferred the presence of the food in the other tube from its absence in the one they had checked. This reveals that the looking strategy is not an automatic or reflex-like reaction (grab the food that you see), but part of a flexible problem-solving strategy (mentally establishing the location of the food). The suggestion is that in order to act like that, apes need to be metacognitively aware of their lack of knowledge

Rhesus monkeys and 2-year-old human children behave like the apes in this test (although the monkeys require preliminary training to learn to look through the tubes). However, domestic dogs fail an adapted version of this test: they do not take the opportunity of visually or olfactorily inspecting boxes before making a decision, thereby revealing an apparent lack of awareness of their lack of knowledge (Call 2005).

As in the optional test paradigm, the issue here is to what extent an explicit metacognitive representation of 'knowing' vs 'not knowing' is necessary to perform well, or it suffices some implicit computation of whether a target for action is or is not present. Primates are used to visually guided reaching and tracking of targets. If the slot for the target in their mental scheme is empty or underdetermined, this may inhibit action until the slot is filled, prompting the primates to try and find the whereabouts of the target. Rather than consciously categorizing their state in terms of knowing or not knowing, primates may simply aim at finding the missing element of their well-practised reaching schemas. But it could be argued that even this lower-level explanation may reflect a primitive, implicit type of metacognitive self-awareness—an ability to act in response to the state of internal representations rather than directly in response to external stimuli.

3. Metacognition of others' mental states

Consciousness has been related to the ability to attribute mental states to others. Indeed some models of *theory of mind propose that mental state attribution is achieved through a process of simulation or mental perspective-taking in which one uses awareness of one's own mental states to imagine others' mental states. After a period of scepticism about great apes' abilities to attribute even such simple mental states as 'attention' or 'seeing' to others, recent evidence suggests that chimpanzees and other apes may understand what others can or cannot see and even what others have or have not seen in the past (amounting to attributing knowledge and ignorance to others), especially when they are tested with conspecifics in competitive contexts. For example, subordinate chimpanzees prefer to retrieve pieces of food that are not visible to other, dominant chimpanzees, or that were hidden when the dominants were not present. Skills like these might amount to having some components of theory of mind (Tomasello et al. 2003). However, it is unclear that the attribution of visual access and knowledge in these experiments requires a conscious simulation of mental states. A simpler interpretation is that primates may be coding intentional relations between agents and targets, without explicit representations of subjective mental states (Gómez 2004). Recent experiments with rhesus monkeys suggest that they perform similarly to chimpanzees in competitive tests that require attribution of vision and knowledge to others (Santos et al. 2007). However, neither chimpanzees nor rhesus have been able to pass tests of false-belief attribution (predicting the behaviour of agents that do not just ignore, but *misrepresent* the whereabouts of a target). These might require more complex metacognition (e.g. a so-called 'meta-representational theory of mind') that might be more closely related to consciousness. The performance of chimpanzee and rhesus monkeys in theory of mind tests therefore roughly mirrors their performance in self-metacognitive tests.

When comparing the mirror test with both individual and social metacognitive tests, we are left with a paradoxical situation: the experimental test that best discriminates phylogenetic proximity to humans (mirror self-recognition) is theoretically argued to be less demanding in cognitive terms (it may reflect bodily awareness rather than metacognitive awareness), whereas the tests that theoretically seem to require more complex cognition (awareness of mental states) do not discriminate within primates (but they may do between primates and other animals). There remains the possibility, therefore, that metacognitive tests tap basic cognitive skills that may be necessary but not sufficient for human forms of consciousness, whereas the mirror test is diagnostic of something, as yet unidentified, that is closer to human consciousness.

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animal consciousness: raven The common raven, *Corvus corax*, has the widest geographical and ecological range of any native bird in the world and is prominent in the mythology of many different cultures within that range. It has been variously described as a trickster, a creator, and an omen of death. The raven has for centuries given the impression that it possesses uncommon intelligence. In recent decades its often-enigmatic behaviour has finally come under scientific scrutiny. Recent research on ravens provides reasonable inferences that meet the criteria of 'knowing'. Ravens accomplish not only physical but also social tasks that indicate at least rudimentary mental sophistication resembling that demonstrated for humans, great apes, and some other corvid birds.

1. Insight
2. Social behaviour

1. Insight

Any specific behaviour is likely the result of an ever-changing mix of the relative roles of pre-programmed behaviour, maturation, learning, and conscious insight. Modifications of the ravens' responses occur through learning as well as maturation. Consciousness may be common, but demonstrating what is 'in the head' of another who cannot use words may be next to impossible under most circumstances. Proof requires that the major distinguishing characteristic of the behaviour is neither innate nor learned. As a consequence, the test for consciousness involves exhibition of a behaviour that the animal does not normally perform yet does so proficiently at first try. The following sets of experiments, involving strings and a piece of hard salami, come fairly close to those requirements.

In one set of experiments, adult captive ravens with no experience of strings approached a metre-long string tied to a branch, from which dangled a piece of meat. They reached down, grasped the string with their bill, pulled up, placed the string on the branch, stepped on to the string and held it down on the branch, then let go of the string, reached down again and pulled up another length of string, and then repeated the precise sequence 6–10 times until reaching the food. Furthermore, while naive birds unhesitatingly attempted to fly off with food while it was still tied to a string, those who had pulled up food did not attempt to leave with it when they were startled. Significantly, this behaviour of letting go of the meat occurred following the first pull-up. When two strings were crossed with only one holding meat and the other a rock, some birds nevertheless (on their first trial) first contacted the string with food, while others initially gave a brief yank on the wrong string, which was directly below them (as on previous straight pull-ups). Apparently then noticing that the rock and not the meat moved, they then quickly switched their attention to the other string and pulled up the meat. Repeated trials did little to change the individuals' initial mistake of contacting the wrong string, as though trial-and-error learning had no or little effect. Apparently some individual birds did not know that the strings were crossed and so they persisted in what 'made sense' according to what they thought they knew. On the other hand, these same birds almost instantly corrected their mistake when they saw it. To test further whether concepts do play a role in the string-pulling behaviour, in another test other similarly aged ravens in the same aviary set-up were confronted with the illogical situation of a looped string that had to be pulled down to make the meat come up. These birds were unable to reach the meat and soon lost interest in trying.

Other potential means of reaching the meat on string include flying at it, trying to rip off the string, twisting it off, pecking it, using a twig as a tool to pull, etc. The effects of any and all of these potential responses could be either learned or acquired through maturation. Once gained, they could be tried sequentially by mental pictures, and eliminated in favour of the best option. Juvenile ravens applied most of these options overtly, presumably because they lacked accurate metal images. In 6 minutes (on average) they 'learned' that most options did not work, and they then narrowed in on the 'right' solution. Some adults, in contrast, hit on the right solution in as little as 30 seconds after contacting string and without overtly going through the repertoire of possible choices.

Ravens almost routinely exhibit behaviour that suggests they 'look ahead' or fill in beyond what is proximally available to their vision. Adult birds who have experience with a metre-long horizontal tube, and are then for the first time confronted with the tube placed at an angle, search for food they see dropped in to slide down, not where they last see it (at the entrance) but at ground level where it has slid down but is not visible. They routinely stash surplus food next to them, to then pick it up all in one packet, but only when competitors (who would pick up loose food) are absent. They effectively slice hard suet by pecking it in directed lines, to then haul off chunks suitable for carrying (Comstock 2006).

2. Social behaviour

Ravens' social dependency lasts throughout their lives. The reliance of the offspring on their parents extends for 1–3 months after the young fledge. The non-breeders and young then become gregarious and often gather into non-kin groups. These groups commonly feed on temporary food bonanzas such as large animal carcasses, and to gain access to this meat they must contend both with dominant resident pairs that try to monopolize the resource and also with dangerous carnivores. By the age of about 3 years they form stable, lifelong partnerships. Pairs stay together year-round.

Numerous tactics have been identified that relate to social manipulation. First, as a counter-strategy to the dominant adults, the juveniles recruit conspecifics from communal nocturnal roosts and thereby gain access to clumped and defended food by swamping the dominant's defences. However, after the crowd has gained access, the individuals within it engage in a competition to haul off meat and hide it out of sight of their competitors. Thus, the same behaviours that give them access to the food also create competitors that take it away. Numerous complex cognitive problems and opportunities arise from the conflicts at locally abundant but ephemeral food.

The meat that the birds haul off for later use is tucked into crevices or is buried and camouflaged with debris, so that it is invisible. Ravens remember the locations not only of their own food caches, but also of those they see others make (Heinrich 1995). As a counter-tactic, birds attempt to cache in private and may use visual obstructions to screen the sight of their cache. As a counter-counter-strategy, potential cache-raiders remain hidden and approach another's cache when the owner is absent. If (under experimental conditions) the cache-makers have the potential audience of a viewer while another nearby bird is hidden behind an obstruction, they attempt to repel the viewer when it later comes near the cache but ignore non-viewers (Bugnyar and Heinrich 2005). These results suggest that the birds can attribute knowledge to others. An alternative explanation, that the 'knower' may have divulged its knowledge of the cache, via subtle behavioural cues when near it, is not supported by empirical evidence. When experiments were repeated with a human as a cacher, and observing and non-observing birds were pitted against each other by simultaneously allowing both into the caching area, observing birds pilfered the cache ten times faster when they were in the presence of another bird (who also had had a view of the cache-making) than in the presence of a non-observer (Bugnyar and Heinrich 2006). In the latter case, when paired with a non-observer they did not hurry in cache-recovery, nor did they attempt to repel non-observers that wandered near the cache. This provides evidence that observing birds have an internal representation of other birds' mental states regarding the existence and location of the cache.

Ravens not only appear to know about others' knowledge, they also gauge others' behaviour and ascertain unknowns that could be relevant to them. Cueing begins with the young following their parents. The young fearlessly approach objects (such as carcasses) near their parents. After leaving their parents they learn about new objects (such as carcasses to feed from, or sleeping predators) by behaviour that functions to elicit responses from these objects. Supine bodies are approached from the rear and the birds then make conspicuous 'jumping jacks', and/or they keep visiting the 'carcass' at intervals of minutes or hours before venturing near it.

The intentions and capabilities of moving predators are tested by gradually approaching and tweaking the tails of these animals. Within minutes the birds then learn the animal's reaction speeds, pursuit tendencies, and capabilities. Such knowledge becomes useful when they are required to feed alongside tested animals, such as wolves, bears, cats, and eagles. The ravens' pronounced *neophobia* of large objects, combined with apparent playful curiosity associated with dangerous predators attending food bonanzas, allow them to exploit a great diversity of food. Similarly, the young ravens' *neophilia* permits them to discover a great diversity of small food items, such as berries, eggs, insects and other invertebrates, human refuse, etc.

An individual raven's responses are greatly modulated by social considerations. If one raven in a crowd is alarmed it flies up quickly and leaves without vocalizing. Almost in the same instant all the rest then fly up and leave as well, even though the alarm object is totally out of view from them. Apparently the raven's flight behaviour is a sufficient cue to the others. Similarly, captive ravens use the gaze direction of their keeper (who feeds them) as a behavioural cue that guides their attention. They co-orient with the human's look-ups and may even reposition themselves to follow the experimenter's gaze around a visual barrier (Bugnyar et al. 2004).

Ravens live in the context of a social unit of other individuals for at least part of their lives. Perhaps they have uniquely sophisticated abilities relative to other birds because they must contend not only with conspecific associates and competitors, but also with dangerous predators whose reactions they need to anticipate in order to feed in their near proximity without being killed.

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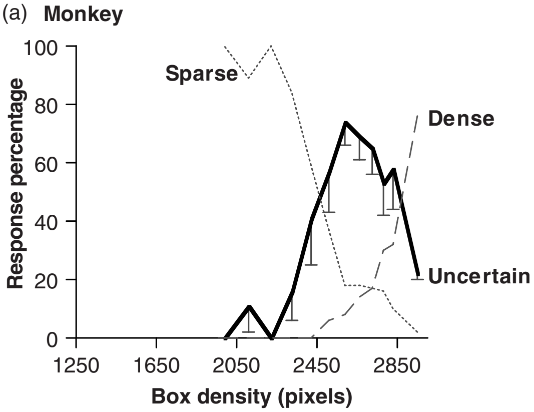
animal metacognition and consciousness Humans monitor their states of knowing and remembering, of certainty and doubt, and respond appropriately to these states by rethinking and seeking help or information when necessary. These responses ground the literatures on uncertainty monitoring and metacognition (i.e. thinking about thinking—Nelson 1992). Researchers take humans' metacognitive behaviours to show hierarchical levels of *cognitive control, cognitive *self-consciousness, and declarative consciousness (i.e. conscious mental states that are reportable to others). Because metacognition is one of humans' most sophisticated cognitive capacities, it is an important question whether animals (i.e. non-human animals) have this capacity as well. Indeed, the sophistication of the metacognitive capacity could let it rival tool use and language in revealing continuities or discontinuities between the mind and consciousness of animals and humans.

Accordingly, since 1995 researchers have investigated a new area of comparative inquiry considering whether animals have a capacity for cognitive monitoring (Cowey and Stoerig 1995, Smith et al. 1995). Researchers have used tasks in which a mix of easy and difficult trials are presented, and in which animals are allowed—in addition to the primary discrimination responses—to decline to complete any trials they choose. If animals can monitor cognition accurately, they should identify difficult trials as error-risking and decline those trials selectively. Indeed, this is what some animals do; producing data patterns in cognitive-monitoring tasks that are like those produced by humans (Smith et al. 2003). The logic of these comparative experiments—which evaluate metacognition using a non-verbal, behavioural task—has natural extensions to the ongoing study of metacognition in young human children.

In one of the original comparative studies, monkeys performed a visual discrimination task in which they were asked to make a 'Dense' response if a cued area on a computer monitor contained exactly 2950 illuminated pixels, and alternatively a 'Sparse' response if any fewer pixels were presented. A third, uncertainty response was allowed that enabled monkeys to decline difficult trials. The results are shown in Fig. A9a. When the discrimination involved easier Sparse and Dense trials, monkeys primarily used the perceptual Sparse and Dense responses, and generally did so correctly. Interestingly, the uncertainty response was used most in the region of maximum uncertainty, at the point where these two response curves cross, and where it would be maximally beneficial to respond 'Uncertain'. Thus, monkeys correctly assessed when they were at risk for error and declined those trials selectively and adaptively. Humans did so, too (Fig. A9b). Humans attributed their uncertainty responses to their mental state (e.g. 'when I wasn't sure'; 'when I couldn't tell'). Although monkeys can make no explicit attribution of their internal state, there is a clear isomorphism between the uncertainty responses of the two species. In related work using an auditory discrimination task, Smith et al.



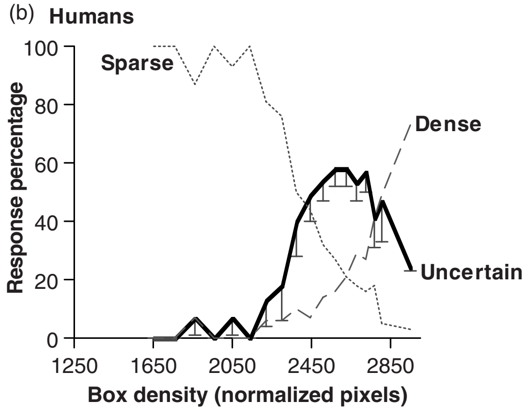


Fig. A9. Visual discrimination performance by a monkey (a) and humans (b). The horizontal axis in each graph gives the pixel density of the box, and the vertical axis indicates the percentage of trials ending with each possible response. The 'dense' response (dashed lines) was correct for boxes with 2950 lit pixels; all other densities deserved the 'sparse' response (dotted lines). Participants could also choose the uncertainty response (solid lines). The error bars show the lower 95% confidence limits. To clarify the human results by equating discrimination performance across human participants, their perceptual thresholds were aligned through a normalization procedure so that each crossover of the two primary responses lay at about 2700 pixels. The graph in (a) is from Smith et al. (1997). Copyright 1997 by Elsevier. Reprinted with permission. The graph in (b) is from Smith et al. (2003). Copyright 2003 by Cambridge University Press. Reprinted with permission.

(1995) showed that humans and dolphins make use of uncertainty responses equivalently to decline those trials that are likely to lead to error. The dolphin in this study produced various auxiliary behaviours that would be interpreted as outward signs of uncertainty in human participants (e.g. hesitation and wavering), and the strength of these behaviours predicted whether the dolphin would respond 'Uncertain' on any particular trial.

Subsequent research has made it clear that low-level explanations grounded in conditioning or stimulus control cannot explain what animals do in these tasks. Various issues have been resolved concerning the uncertainty response and the positive contingencies accidentally granted it in some studies (e.g. some researchers directly rewarded the Uncertain response, which compromised its uncertainty interpretation). Monkeys have now been shown to respond Uncertain in a number of different experimental paradigms: when facing difficult same–different judgements that are abstract and removed from the stimuli that might exert behavioural control (Shields et al. 1997); when facing difficult numerosity judgements (Beran et al. 2006); when asked in a memory task whether an item has previously been presented (Smith et al. 1998), or whether, even in the absence of any choice stimuli, they remember a previously presented sample (Hampton 2001). An example of this can be seen in Fig. A10a, which shows the performance of a monkey asked to judge whether a probe picture had previously appeared in a list of pictures. The crucial result was that the animal correctly assessed when his memory about a probe was problematic or ambiguous and he declined those trials. His uncertainty responding was the mirror image of his performance when he tried to answer the memory question on other occasions, and it was the mirror image of the predictable strength of memory traces at different positions in the list. Human observers perform this task similarly (Fig. A10b). Finally, monkeys are even able to respond Uncertain when in new tasks they are denied trial-by-trial feedback so that they have to self-construe the task and self-instruct their performance within it. This makes it impossible for conditioning processes to operate, and so in this case one knows that uncertainty responses are cognitive, decisional, and high level, not conditioned and low level (Smith et al. 2006).

Interestingly, research has failed to demonstrate equivalent high-level uncertainty responding by either rats or pigeons (Foote and Crystal 2007, Inman and Shettleworth 1999, Sutton and Shettleworth 2008). Of course caution attends null results like these—positive results might await different methods or more dogged training. Nonetheless, it is an exciting possibility that these cross-species studies are gradually drawing the map of the phylogenetic spread and distribution of metacognition and cognitive self-awareness.

Comparative metacognition researchers have naturally approached cautiously the issue of declarative consciousness in animals. There is agreement that animals in these tasks are showing a capacity—for knowing when they know or remember—that is associated with conscious cognition in humans. Thus, animals are showing functional parallels to human conscious metacognition, though they may not experience everything that accompanies conscious metacognitive experience in humans. For that matter, human metacognitive experience may not always be perfectly conscious, either. There is also an active consideration of whether animal metacognition has implications regarding animals' self-consciousness. It remains open to debate and experiment whether and how an organism must feel like a self in order to monitor the content of the self's mental states.

Nonetheless, the comparative findings on uncertainty monitoring and metacognition bring a constructive new perspective to considerations of animal consciousness. Previously, interest had focused on the intriguing idea that animal consciousness and awareness had a social origin, by which animals evolved self-awareness of mood, state, and motivation so as to model and predict the mood, state, and motivation of the conspecific (Humphrey 1978). Consciousness, in the view of Humphrey and others, was an adaptation to social living that increased social intelligence.

However, comparative metacognition research demonstrates why consciousness might have an independent adaptive role and an independent evolutionary origin. Animals frequently encounter ambiguity, impoverished inputs, threshold detection conditions, novel contexts, complex situations, and so forth. They likely have the need for a higher-level cognitive-regulatory system wherein cognitive close calls can be refereed and adjudicated. A working consciousness would be an ideal information-processing locus for the decisional assemblage that conducts such adjudication.

In fact, it has been a recurrent idea in cognitive science that cognitive difficulty and indeterminacy elicit higher-level and more conscious modes of cognitive processing. James (1890/1952:93) noted that consciousness provides extraneous help to cognition when nerve processes grow hesitant—'Where indecision is great, as before a dangerous leap, consciousness is agonizingly intense.' Tolman agreed that conscious awareness and ideation arise mainly at times of conflicting signals and predictions. In fact, in a claim remarkable for its time, Tolman (1927) suggested that animals' uncertainty behaviours—for example, the hesitation and wavering the dolphin showed in Smith et al. (1995)—could operationalize consciousness for the behaviourist. The claim—that uncertainty and difficulty are uniquely associated with higher and more conscious forms of cognitive self-regulation—is potentially an inclusive claim that has no necessary reason or way to include only human minds and exclude animal minds. Certainly, animals' success in uncertainty-monitoring paradigms encourages the extension of the claim to them.

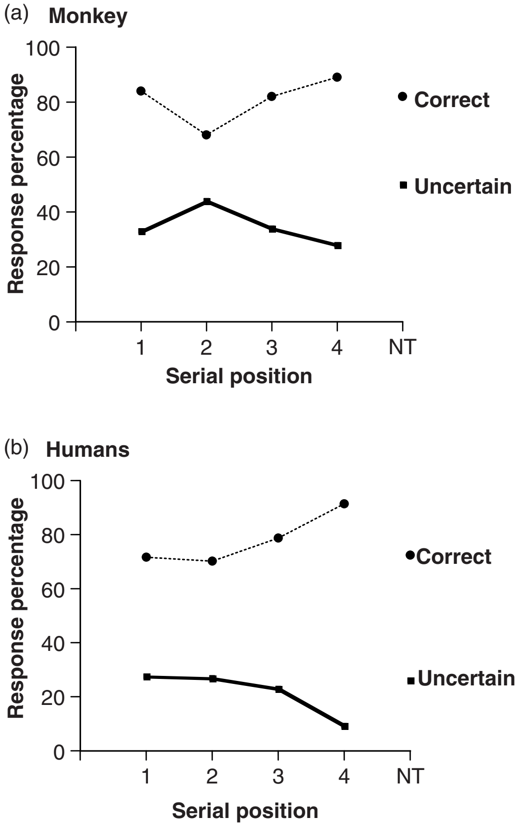


Fig. A10. Memory performance by a monkey (a) and humans (b). The horizontal axis in each graph indicates the serial position of the probed picture; 'NT' ('Not There') denotes trials on which the probe picture had not been in the preceding list of pictures. Each graph shows the percentage of total trials that received the uncertainty response (solid lines), along with the percentage correct when participants chose on other occasions to accept the memory test (dotted lines). From Smith et al. (1998). Copyright 1998 by the American Psychological Association. Reprinted with permission.

Comparative metacognition research joins related research on animals' bodily self-awareness as explored using the *mirror test (Gallup 1982) in which some animals inspect dye marks on their bodies after discovering the marks when looking in a mirror. This intriguing paradigm rightly remains a component of the discussion about animal awareness. However, the paradigm has been beset by methodological concerns (e.g. confounds with the recovery cycle from anaesthesia during which the mark is applied). Moreover, the theory behind the paradigm has been partially disconfirmed (i.e. the theory holds that only apes and humans should show mirror awareness, but dolphins and elephants have recently shown that awareness). Finally, it remains unclear just what aspect of consciousness and self-awareness is necessarily confirmed when an animal inspects a body mark in a mirror. Given these concerns, the advent of the metacognition approach is welcome for providing complementary methods and perspectives in this area, and in particular for providing paradigms that test directly animals' capacity for cognitive self-awareness and their ability to make behavioural reports of that awareness. The metacognition approach has also been valuable for moving the comparative scientific study of consciousness beyond the idea that only a common ancestor of apes and humans experienced the evolutionary flashpoint of aware mind, and toward the idea that consciousness may be broadly adaptive, and so evolved and maintained within the evolutionary history of many species.

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anosognosia The term 'anosognosia' indicates the denial of one's own disease or deficit. It can be observed in association with many different kinds of pathological conditions, ranging from *schizophrenia (Pia and Tamietto 2006) to neurological and cognitive disorders. In these latter cases, patients may be unaware of their reading, language, or memory problems (Prigatano and Schacter 1991) or may even resolutely deny the contralesional sensorimotor impairments resulting from localized *brain damage. Patients may deny being blind or paralysed, and their false beliefs are strong and often intractable.

1. Historical development
2. Denial behaviour in anosognosia for hemiplegia
3. Theories of anosognosia
4. Anosognosia for hemiplegia as a disturbance of motor self-awareness

1. Historical development

Historically, the first 'description' of anosognosia can be found in Seneca (Liber V, Epistula IX in Bisiach and Geminiani 1991). In a letter to his friend Lucilius, Seneca reported the puzzling case of a woman who suddenly became blind, most probably after a stroke affecting the posterior parts of the brain (where the areas devoted to the processing of visual information are located):

> You know that Harpestes, my wife's fatuous companion, has remained in my home as an inherited burden.... This foolish woman has suddenly lost her sight. Incredible as it might appear, what I am going to tell you is true: *she does not know she is blind*. Therefore, again and again she asks her guardian to take her elsewhere because *she claims that my home is dark.... It is difficult to recover from a disease if you do not know yourself to be ill.*

Seneca's description was very insightful because it identified the three main characteristics of ansognosia. First, the denial of the primary illness (in Seneca's case the denial of blindness) and the consequent false believe of being 'normal'; second, the confabulation that patients may produce in order to justify their problems (for instance the claim that the house was dark); and third, the negative impact that denial has on recovery (now experimentally demonstrated, e.g. Gialannella and Mattioli 1992).