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New evidence of animal consciousness

Abstract This paper reviews evidence that increases the probability that many animals experience at least simple levels of consciousness. First, the search for neural correlates of consciousness has not found any consciousness-producing structure or process that is limited to human brains. Second, appropriate responses to novel challenges for which the animal has not been prepared by genetic programming or previous experience provide suggestive evidence of animal consciousness because such versatility is most effectively organized by conscious thinking. For example, certain types of classical conditioning require awareness of the learned contingency in human subjects, suggesting comparable awareness in similarly conditioned animals. Other significant examples of versatile behavior suggestive of conscious thinking are scrub jays that exhibit all the objective attributes of episodic memory, evidence that monkeys sometimes know what they know, creative tool-making by crows, and recent interpretation of goal-directed behavior of rats as requiring simple non-reflexive consciousness. Third, animal communication often reports subjective experiences. Apes have demonstrated increased ability to use gestures or keyboard symbols to make requests and answer questions; and parrots have refined their ability to use the imitation of human words to ask for things they want and answer moderately complex questions. New data have demonstrated increased flexibility in the gestural communication of swarming honey bees that leads to vitally important group decisions as to which cavity a swarm should select as its new home. Although no single piece of evidence provides absolute proof of consciousness, this accumulation of strongly suggestive evidence increases significantly the likelihood that some animals experience at least simple conscious thoughts and feelings. The next challenge for cognitive ethologists is to investigate for particular animals the content of their awareness and what life is actually like, for them.

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Introduction

Experimental and observational data about the complexity and versatility of animal cognition have been reported and discussed extensively since the subject was reviewed in the first issue of this journal (Griffin 1998). The term cognition is ordinarily taken to mean information processing in human and nonhuman central nervous systems that often leads to choices and decisions. But the possibility that nonhuman cognition is accompanied or influenced by consciousness has received relatively little attention, largely because many behavioral scientists have been extremely reluctant to consider nonhuman consciousness on the grounds that it is impossible to obtain objective evidence about subjective experiences. Yet much of the new evidence strengthens that case as well, and it is time to reconsider the longstanding aversion to scientific investigation of animal consciousness. In view of the confusions surrounding terms describing mental states, and despite the fact that some scientists feel that consciousness is a higher and more complex state than awareness, we will follow the common usage of aware and conscious as synonyms that describe subjective experiences. We will assume that these states or processes are produced by the functioning of living nervous systems and not something ethereal and different in kind from anything in the physical universe, as emphasized by Searle (2000, 2002) and Donald (2001).

In addition to papers describing specific experiments and observations, the most relevant recent publications include: (1) ten books by single authors: Shettleworth (1998), Damasio (1999), Heinrich (1999), Pepperberg (1999), Seager (1999), Hauser (2000), Povinelli (2000), Donald (2001), Griffin (2001) and deWaal (2001); (2) more than 200 chapters in books edited by: Balda et al. (1998), Hauser and Konishi (1999), Heyes and Huber (2000), Metzinger (2000), Matsuzawa (2001), Roth and Wullimann (2001), Bekoff et al. (2002) and deWaal and Tyack (2003); and (3) 12 substantial review papers by Boysen and Hines (1999), Capaldi et al. (1999), Cartmill and Lofstrom (2000), Nelson and Rey (2000), Searle (2000), Thompson and Derr (2000), Dehaene and Naccache (2001), Baars (2002), Byrne (2002), Lovibond and Shanks (2002), Mitchell (2002) and Tulving (2002). Finally Piggins and Phillips (1998) have assembled, in a special issue of *Applied Animal Behaviour Science*, ten papers by scientists and philosophers concerned with animal welfare.

Consciousness is the subjective state of feeling or thinking about objects and events. The word is often interpreted to mean full-blown human thinking, although of course no animal attains more than a trivial fraction of the scope and versatility of human conscious thinking. But many animals give evidence of what Natsoulas (1983, p. 29) defined as consciousness 3, "the state or facility of being mentally conscious or aware of anything." This has been called perceptual, primary or basic consciousness. However limited its content may be, such awareness is importantly different from unconscious cognition. Consciousness is often considered a complex and "higher" form of cognition; but as Dawkins (2000) has emphasized, the content of human consciousness ranges from very simple to enormously subtle and complex. Insofar as animals are conscious, the content of their awareness probably varies along a continuum from the simplest and crudest feelings to thinking about the challenges they face and alternative actions they might choose.

Computers process information, and robots can even simulate animal behavior; but they can only do what human designers have programmed them to do. It is very unlikely that they have subjective experiences without a living central nervous system. Although no single piece of evidence that an animal is conscious is totally conclusive, and alternate explanations not involving consciousness are always conceivable, suggestive evidence can serve as an entering wedge that stimulates further investigation leading to improved and more conclusive data. Following up on these possibilities provides opportunities and challenges for scientific investigation to evaluate the following hypothesis: Animals are sometimes aware of objects and events, including social relationships, memories, and simple short-term anticipation of likely happenings in the near future, and they make choices of actions they believe are likely to get what they want or avoid what they dislike or fear. Such basic consciousness may but need not include self-awareness or metacognition – thinking about one's thoughts or those of others – (Natsoulas' consciousness 4). We will give only passing consideration to self-awareness

and metacognition in this paper. Complex cognition can occur in our brains without consciousness; but when unexpected challenges arise, considering alternative actions and choosing the one believed to be most helpful in solving the problem at hand is often more effective than reliance on routine responses. It seems increasingly probable that conscious thinking sometimes provides animals with the same advantage.

Some scientists hold that consciousness cannot be defined with the precision needed for scientific investigation. But Searle (1998) and Churchland (2002) point out that when approaching a difficult and confusing problem with very limited data available, our first need is a commonsense definition simply to make clear what we are talking about. As the subject is better understood the definition can be improved. We all know that we are sometimes aware of objects, events and emotional feelings, that we sometimes use these experiences in our planning and decision-making, and that the difference between being aware or unaware is important to us. The central question about the consciousness of animals is whether they experience anything of the same general kind, and if so what is the content of their awareness. Whatever they feel and think must be important both to the animals concerned and to our understanding of them and their ways of life.

It is helpful to consider questions about the content of an animal's awareness in terms of the probability of awareness, pA. If we have complete certainty that a given animal has a particular conscious experience, then pA=1.0, and pA=0 means that we know with certainty that it does not. If we take literally the claim that it is impossible to learn anything about the so-called private experiences of other species, we are obliged to assume that pA is always 0.5. In practice, however, there has been a tendency to conclude from the impossibility of setting pA at 1.0 that it must be zero. Crist (1999) has explored in depth the degree to which scientists' choices of terms applied to animal behavior have been influenced by a "mechanomorphic" viewpoint about animals that avoids implications of consciousness. There are obviously cases where pA must be far below or above 0.5, even though we cannot always rigorously prove that it is zero or 1.0, because many important questions about animal consciousness cannot yet be answered with any certainty for lack of relevant evidence. Of course a low value of pA for a particular experience does not mean that the animal is never conscious at all.

There are three general categories of evidence that show animals' pA is sometimes well above 0.5: (1) close similarity of basic central nervous system structure and function in a wide variety of animals, indicating that whatever processes lead to conscious experiences are not limited to human brains, (2) versatile adjustment of behavior in response to unpredictable challenges, and (3) animal communication, which often seems to inform receivers about the conscious experiences of the sender; and which can also provide information about them to eavesdropping cognitive ethologists. We rely heavily on both verbal and nonverbal communication to infer what our human companions are thinking and feeling, and the same basic ap-

proach can be applied to many other species. We will review these three areas in this paper.

Neural correlates of consciousness

As Crick and Koch (1998, p. 105) put it "The explanation of consciousness is one of the major unsolved problems of modern science. After several thousand years of speculation, it would be very gratifying to find an answer to it." It is theoretically conceivable that only the human nervous system has the capability of producing consciousness. If so, it is an important challenge for the neurosciences to discover the nature of this unique consciousness-producing ability. Some point to the size or the complexity of the human brain, or to specific areas, or else to language ability. But there is no clear evidence that any of these factors is necessary for consciousness. Another theoretical possibility is that simple conscious thinking is an important core function of living central nervous systems, and that in small brains it may therefore constitute a larger proportion of brain activity than in animals with very large brains.

Recognition of the importance of these questions has been part of the motivation for an extremely active and talented series of investigations that have recently attempted to identify the neural correlates of consciousness (NCC), as discussed by Crick and Koch (1998, 2000, 2003), Taylor (1999), Metzinger (2000), Searle (2000, 2002), and Baars (2002). Kanwisher (2001) has summarized significant recent investigations of NCC, emphasizing that "A variety of striking correlations...between specific neural signals and perceptual experiences" (Kanwisher 2001, p. 89) show that these signals appear to be necessary but are probably not sufficient for consciousness. Like many other neuroscientists, she is inclined to infer that widely distributed but functionally coordinated activity in the brain is also required. These considerations lead to the speculation in regard to visual consciousness that "in order for a focal neural representation to reach awareness it may have to be accessible to other parts of the brain...(and)...a conscious percept is not simply a disorganized soup of activated visual attributes, but rather a spatiotemporally structured representation in which visual attributes are associated with particular objects and events" (Kanwisher 2001, p. 109).

Baars (2002) has lucidly reviewed how modern methods of imaging brain function have provided objective evidence of neural activities correlated with consciousness. In many of these recent investigations of NCC, animals are used for better control of experiments or for invasive procedures, and it is simply taken for granted that they are conscious. Logothetis (1999, p. 70), in his investigations of binocular rivalry, notes that "monkey brains are organized like those of humans, and they respond to stimuli much as humans do. Consequently, we think the animals are conscious in somewhat the same way as humans are." Kanwisher (2001) concurs, stating "It seems reasonable to assume that when a monkey reports the presence of a particular stimulus, he is aware of the stimulus in something

like the way that a human would be. Nevertheless it would be reassuring to find similar results in the human brain." She and her colleagues (Tong et al. 1998) do find similar results in a human experiment that was modeled after the monkey experiments of Logothetis. Engel and Singer (2001), after reviewing numerous studies, some of which involved monkeys and cats, implicitly assume that these animals were conscious. Seward and Seward (2000, p. 86) conclude that "in rodents and lower vertebrates, normal visual awareness is partly due to synchronized oscillatory activities in the optic tectum and partly due to similar activities in the visual cortex."

Hesslow (2002), following in the footsteps of Alexander Bain, proposes a "simulation theory of cognitive function... (by which)...behaviour can be simulated by activating motor structures, as during an overt action, but suppressing its execution" (Hesslow 2002, p. 242). This, he suggests, may help to establish "the inner world that we associate with consciousness...(and that)...it is a strength of the simulation hypothesis that it can account for cognitive functions in terms of mechanisms shared by all mammals" (Hesslow 2002, p. 246). And Dehaene and Naccache (2001, p. 31) add "The biological substrates of consciousness in human adults are probably also present, but probably in partial form in other species."

Blindsight is an intriguing phenomenon that has provided an opportunity to test whether a monkey is or is not conscious of particular visual stimuli. It was given this name by Weiskrantz et al. (1974) from studies of certain human patients who had lesions in the visual cortex that produced large blind areas in the visual field but who could nevertheless respond in limited ways to visual stimuli in their blind fields. If stimuli are presented in these blind areas and the patient is required to guess about them, he is as surprised as anyone that his guesses are far more accurate than expected from chance. One such patient could even distinguish horizontal bars in his blind field from identical bars tilted by as little as ten degrees (Weiskrantz 1997). Other parts of the visual system, probably including the superior colliculus, are able to produce these correct responses without any awareness on the patient's part (Sahraie et al. 1997; Kentridge and Heywood, 1999).

Cowey and Stoerig (1995, 1997) and Stoerig et al. (2002) showed similar results in monkeys with large cortical lesions. The monkeys had been trained to touch a small bright square on a touch-sensitive computer screen to obtain food. With sufficient training they were able to do this even when the square fell in their blind field. These monkeys were then trained to touch a different visual pattern when no bright square was presented, and surprisingly they then touched this "no stimulus" pattern when the bright square was presented in their blind field – even though in other experiments they would touch the square to obtain food. It was thus possible to distinguish, under these experimental conditions, whether the monkey was or was not aware of particular stimuli.

Roth (2000) emphasizes brain size: "Among all features of vertebrate brains, the size of cortex or structures ho-

mologous to the mammalian cortex, as well as the number of neurons and synapses contained in these structures, correlate most clearly with the complexity of cognitive functions, including states of consciousness" (Roth 2000, p. 94). There is as yet no way to determine the minimum brain size necessary for the most basic level of consciousness, although several thousand neurons would seem adequate for the kinds of NCC that appear most plausible to contemporary neuroscientists. Roth is critical of the idea that language is required for consciousness. If we accepted that suggestion, he points out, "we would be forced to assume that animals are capable of unconsciously mastering cognitive tasks that in humans require highest concentration" (Roth 2000, p. 95).

Damasio (1999) emphasizes the importance of bodily emotions for consciousness. He allows that artifacts such as computers might be created that have the formal mechanisms of consciousness, but they would not be conscious in the full sense. "Feeling is, in effect, the barrier, because consciousness may require the existence of feelings. The "looks" of emotion can be simulated, but what feelings feel like cannot be duplicated in silicon" (Damasio 1999, p. 314). In Damasio (2000), he distinguishes what he calls "core consciousness," which "provides an organism with a sense of self about here and now...(but)...does not pertain to the future or the past," from "extended consciousness," which "provides the organism with an identity and a person, an elaborate sense of self, and places that self at a specific point in an individual historical time...(It)...offers awareness of the lived past and of the anticipated future, along with the objects in the here and now." Emphasizing that "consciousness depends most critically on evolutionarily old regions (of the vertebrate brain)," Damasio believes that core consciousness is not exclusively human, and that "simple levels of extended consciousness are present in some nonhumans" (Damasio 2000, pp. 112–118).

Tononi et al. (1998), Tononi and Edelman (1998) and Edelman and Tononi (2000) also distinguish between two levels of consciousness, both of which are found in some animals in addition to humans: (1) primary, which necessitates brain structures that can construct a mental scene but have limited semantic or symbolic capabilities; and (2) higher-order, which also includes a sense of self, expanded semantic capability and awareness of past and future. They advance a "dynamic core" hypothesis that neurons can be part of an NCC only if they participate in "a distributed functional cluster that, through reentrant interactions in the thalamocortical system, achieves high integration in hundreds of milliseconds...to sustain conscious experience, it is essential that this functional cluster be highly differentiated as indicated by high values of complexity" (Edelman and Tononi 2000, p. 146).

Edelman and Tononi's dynamic core hypothesis is supported by experiments on binocular rivalry in which two patterns flickering at different frequencies were shown to the two eyes, and the subject alternately reported seeing first one and then the other. Measurements of the magnetic field generated by activity in the brain showed quantitative differences in amount of distributed activity at the frequency of one of the stimuli between situations in which human subjects were or were not aware of the corresponding visual pattern. Binocular rivalry has been manipulated experimentally to provide comparable evidence as to when a monkey is aware of a particular pattern presented to one eye but not a different pattern presented simultaneously to the other eye (Logothetis and Schall 1989; Tononi et al. 1998; Logothetis 1999; reviewed in Rees et al. 2002).

In a similar vein, Crick and Koch (2003), propose a "framework" applicable to the visual system of primates, which they believe "knits all these ideas together, so that for the first time we have a coherent scheme for the NCC in philosophical, psychological and neural terms" (Crick and Koch 2003, p. 124). This framework emphasizes "competing coalitions" of neurons and two-way communication between coalitions in the back and front of the brain. They conclude that explicit representations and synchronized activity such as gamma frequency oscillations may be necessary, but not sufficient for consciousness. Reentrant pathways and back projections are widespread in central nervous systems, however, and if they constitute NCC there is no reason to rule out at least simple consciousness in many animals with central nervous systems.

Has this intensive search for NCC disclosed any structure or process necessary for consciousness that is found only in human brains? The short answer is no. But neither has this search identified any specific structure or process that we can yet be sure is both necessary and sufficient to generate human conscious experience. Thus it remains possible that if and when such an essential consciousness-generating neural mechanism is discovered, it might turn out to be something found only in human brains. On the other hand, recent scientific ideas about this question postulate processes that are present in many if not all central nervous systems. Menzel et al. (2001), reviewing the complexities of insect brains (including the honey bee brain made up of approximately 960,000 neurons), support the conclusion by Koch and Laurent (1999) that "no brain, however small, is structurally simple." We suggest that this general conclusion can reasonably be extended from structure to function, including whatever neural processes lead to consciousness.

Versatility

A type of versatility that is particularly relevant as evidence of consciousness is the departure from routine behavior patterns to cope with novel and unpredictable challenges in ways that suggest at least short-range planning of intended actions. Such versatility is helpful in allowing us to distinguish relatively inflexible preprogrammed behavior from being aware of the availability of alternative actions and choosing those the animal believes will have desired consequences. Smith et al. (2003) suggest that "Difficulty and uncertainty elicit conscious modes of self-reg-

ulation...(in)...some animal species... Working consciousness is ideal for integrating multiple streams of information, for resolving conflicting goals, for coping with the novel and unfamiliar... (It)...is the perfect referee for life's close calls...(and)...may thus have substantial phylogenetic breadth." Both natural selection and individual experience have doubtless contributed to the development of such versatile thinking and action; but the specific reactions to particular situations can scarcely have been preprogrammed if neither the animal nor its ancestors have previously encountered such situations.

Classical conditioning

Classical Pavlovian conditioning of responses such as eyeblink or changes in electrical resistance of the skin used to be viewed as a basic and primitive type of learning, a simple neural association between local circuits, which did not entail consciousness. But this view has been rejected, and detailed analysis of classical conditioning led Rescorla (1988a, 1988b) to conclude that "Pavlovian conditioning is not a stupid process by which organisms willy-nilly form associations between any two stimuli that happen to co-occur. Rather, the organism is better seen as an information seeker using logical and perceptual relations among events along with its own preconceptions, to form a sophisticated representation of the world" (Rescorla 1988a, p. 154). Therefore learning from classical conditioning how best to act in novel situations is often an example of versatility.

Even more of a departure from previous views is the accumulating evidence that certain types of classical conditioning succeed with human subjects only when they consciously recognize that the conditioned stimulus predicts the unconditioned stimulus. Lovibond and Shanks (2002) review extensive evidence from the numerous types of classical conditioning, including autonomic responses such as skin conductance changes, as well as eyeblink conditioning, conditioning with subliminal stimuli, conditioning in patients with amnesia, conditioning under anesthesia, and evaluative conditioning. They conclude (Shanks and Lovibond 2002, p. 42), "there is little convincing evidence for Pavlovian conditioning without awareness" in human subjects. Since many animals can be classically conditioned, this conclusion has obvious implications for the question of animal consciousness.

The major criticism that Lovibond and Shanks level against experiments that purport to show conditioning without awareness is that the procedures used do not provide a sensitive, valid and reliable evaluation of awareness. They offer specific recommendations: the most reliable way to determine awareness is by a concurrent continuous measure of the subject's expectation of the unconditioned stimulus, administered as the acquisition phase of the experiment progresses, along with a short recognition questionnaire, composed of directly relevant questions only, administered immediately after the acquisition phase, and with no intervening extinction phase. They believe that the methods used in many investigations of conditioning, as well as in other areas that look for "implicit" learning (reviewed in Shanks and St. John 1994; Goschke 1997), "systematically underestimate contingency knowledge" (Lovibond and Shanks 2002, p. 21).

Lovibond and Shanks single out evaluative conditioning using tastes and odors (Baeyens et al. 1990; Stevenson et al. 1998) as a possible exception to their conclusion that awareness is necessary for all types of classical conditioning. On the other hand, they are not at all persuaded by the claim of Öhman et al. (1995) that skin conductance conditioning with aversive conditioned stimuli, such as pictures of snakes or spiders, can proceed without awareness. Öhman suggests that biologically prepared aversive stimuli activate a specialized system that allows an immediate response to danger without the need for cortical involvement. Wiens and Öhman (2002) in the same journal issue, have serious questions about "the validity of Lovibond and Shanks' conception of awareness" (Lovibond and Shanks 2002, p. 30). Lovibond and Shanks do not believe that the stimuli used by Öhman have been truly subliminal. They agree with him that aversive stimuli change the usual conditioning process, but they suggest that the difference could be due to selective sensitization rather than to an unconscious associative process.

Although Öhman's approach might be useful for investigating animal awareness, we have a different concern with using aversive conditioned stimuli. It seems to us to entail a direct contradiction of the traditional and still generally accepted definition of classical conditioning: "In classical conditioning paradigms, a previously neutral stimulus (conditioned stimulus or CS) comes to elicit a behavioral response through temporal pairing with an unconditioned stimulus (US)... Hence, classical conditioning is a form of associative learning involving linkage between a neutral stimulus and a stimulus with high intrinsic behavioral significance" (Büchel et al. 1998, p. 947). The aversive stimuli used by Öhman and his colleagues are clearly not neutral.

When it comes to eyeblink conditioning (Clark and Squire 1998, 1999; Manns et al. 2000a, 2000b), Lovibond and Shanks are very critical, especially about the manner in which awareness is evaluated. Manns et al. (2002), in the same journal issue, defend their methodology and add to their evidence for differences between delay and trace conditioning. Trace conditioning is a special variation of conditioning in which an empty interval intervenes between the end of the CS and beginning of the US. Clark et al. (2002) hypothesize that maintaining a representation of the CS in working memory over the empty interval requires awareness. They do state, however, that eyeblink conditioning can probably proceed without awareness only in the simplest delay eyeblink conditioning, either with a single cue or in differential conditioning with two easily distinguishable cues.

Lovibond and Shanks as well as Clark, Squire and their colleagues concur that the findings from human conditioning are relevant for animals. Lovibond and Shanks state, "The ongoing difficulty in finding convincing evi-

dence of conditioning without awareness in humans poses a significant challenge for the field of animal conditioning... Most contemporary conditioning researchers continue to think of associative learning as a basic process that is quite divorced from higher order cognitive processes. The finding that conditioning in humans is closely tied to conscious awareness raises a fundamentally different perspective" (Lovibond and Shanks 2002, p. 23). Clark et al. (2002, p. 530) add, "The close correspondence of findings in humans and experimental animals suggests that the characteristics of eyeblink classical conditioning and its neural substrates are highly similar across vertebrate species... As it becomes possible to identify more precisely the circumstances when knowledge of the stimulus contingencies (i.e., awareness) is crucial for conditioning, it also becomes possible to specify when the same or similar cognitive processes are likely to be occurring in experimental animals."

Although the evidence that awareness is needed for certain types of conditioning is still controversial, it already seems clear that in human subjects awareness is necessary for at least differential skin conductance conditioning using an aversive US and for trace eyeblink conditioning. This means that such conditioning of animals is strong evidence that they are aware during acquisition that the CS predicts the US. Of course many animal experiments (e.g., Tully and Quinn 1985 with Drosophila) include some of the same procedural elements described above (e.g., delay, trace, shock). However they often use substantially different methodologies (e.g., conditioned avoidance) from those used in experiments with human subjects that have found that awareness is necessary for successful conditioning.

Persuasive evidence from aversive differential skin conductance conditioning of human subjects shows not only that awareness is necessary for successful conditioning but also that conditioning does not occur until the time when the subject becomes aware of the contingency (reviewed in Dawson and Schell 1987). This makes it tempting to use aversive differential skin conductance conditioning with other species. Although it has not been easily adapted to animals (Wickens et al. 1961), there are techniques that have been used effectively (e.g., Roberts and Young 1971). One strong benefit of using eyeblink conditioning is the considerable animal literature that has already accumulated. Most of the evidence comes from studies in rabbits, but data have also been obtained for cats, rats, mice and monkeys (Clark and Zola 1998; reviewed in Green and Woodruff-Pak 2000).

Because the use of neutral conditioned stimuli is central to classical conditioning, in future investigations with animals conditioned stimuli should be truly neutral, as far as can be determined from ethological evidence about what is salient for the animals concerned. It is especially important to keep the experimental methodologies as similar as possible to those providing the strongest evidence of awareness in humans, while still being sensitive to species differences, as in selecting the optimum empty interval for trace eyeblink conditioning (Green and Woodruff-Pak 2000).

Both eyeblink and skin conductance conditioning are beginning to be used in conjunction with modern imaging techniques to extend our present knowledge (e.g., Büchel et al. 1998, 1999; Williams et al. 2000). Another technique that shows promise with animals is nonverbal reporting, which has been adapted imaginatively to monkeys in vision studies (Cowey and Stoerig 1997; Sheinberg and Logothetis 1997; Stoerig et al. 2002). Even verbal reporting is possible with apes and parrots trained to use the functional equivalent of human words.

Explicit learning and episodic memory

Students of human learning and memory often distinguish explicit from implicit learning and their resulting memories. The former can be both recalled and reported verbally; the latter entails changes in behavior resulting from prior exposure to stimuli that the subject cannot report because he is currently unaware of them. The concept of explicit memory is similar to declarative memory, which was so named because such memories could be reported or "declared" by human subjects. It is usually assumed that animals cannot have declarative memories because they lack (human) language. This widespread assumption is seriously undermined, however, by twentieth century discoveries about the versatility of animal communication, which can convey information based on memories by other means than human language, as reviewed by Griffin (2001). Clark and Squire (1998, p. 80) also suggest that "Characteristics that have been helpful in extending the concept of declarative memory to nonhuman animals include its flexibility and the ability to use it inferentially in novel situations" (see also Eichenbaum 1997; Schacter 1998).

Memories of past events that include awareness of oneself perceiving the event on some remembered occasion are termed episodic; and Tulving (1972, 2002) and others have claimed that episodic memory is based on a uniquely human neural system. A strong challenge to the claim of human uniqueness comes from recent experiments by Clayton and Dickinson (1998) and Clayton et al. (2000, 2001, 2003). They first demonstrated that scrub jays (*Aphelocoma coerulescens*) can learn that a particular type of preferred food (wax-moth larvae) become unpalatable 5 days after the birds had stored them, but that peanuts, a less preferred food, remain edible. The jays were trained to cache these two types of food by burying them in sand in two different locations. When tested 4 days after caching, and after the sand had been replaced to prevent odor cues from affecting their choices, the jays were more likely to choose the location they knew contained larvae. But after 5 days they usually went where they had stored peanuts.

Clayton et al. (2001, p. 28) prefer to call this type of memory episodic-like rather that episodic because the latter term has been applied to human "autonoetic" memories, which are verbally reported to include a conscious experience of self. This they claim "has no obvious manifestation in nonlinguistic behaviour (Griffiths et al. 1999). For this reason, we regard the what-where-when memory for

caching episodes as no more than an analogue of human episodic memory." But as Clayton and Dickinson (1998, p. 274) put it, "In terms of purely behavioural criteria...the cache recovery pattern of scrub jays fulfils the three 'what', 'where' and 'when' criteria for episodic recall."

Tulving (2002, p. 2) recognizes that animals "have minds, they are conscious of their world...but they do not seem to have the same kind of ability humans do to travel back in time in their own minds, probably because they do not need to." But Emery and Clayton (2001, p. 443) discovered that scrub jays "with prior experience of pilfering another bird's caches subsequently re-cached food in new cache sites...but only when they had been observed caching. Jays without pilfering experience did not, even though they had observed other jays caching... Jays relate information about their previous experience as a pilferer to the possibility of future stealing by another bird, and modify their caching behavior accordingly." These birds appeared to have profited from traveling backwards and perhaps also forward in time. A similar example was provided by the dolphins Pryor et al. (1969) trained to perform on command a completely novel acrobatic action, since they had to remember their complete repertoires in order to create something new. Thus the claim that episodic memory in the full sense of the term is uniquely human rests largely on the assumption that nonhuman animals lack a conscious sense of self.

Knowing what one knows

Some scientists claim that although animals often know simple facts, they do not know *that* they know. This is a type of metamemory or memory about one's own recollection and would certainly be a higher level of awareness than is usually assumed for animals. With our human companions we assume they know that they know something because they can use human language to express this distinction. But how can we learn, for example, whether an animal not only knows that food is available at a certain time and place but also knows that she knows this? As with many such questions about nonhuman mentality, this one has seemed impossible to answer; but instead of recognizing our ignorance, it has been customary to leap to a negative conclusion.

After reviewing earlier experiments designed to detect metamemory in animals, Inman and Shettleworth (1999) developed an ingenious procedure, along the lines suggested by Cowey and Stoerig (1992) and Weiskrantz (1986, 1997) to test whether pigeons could indicate a memory about a memory; but they obtained inconclusive results. Hampton (2001) adapted this method so that two rhesus macaques could indicate whether they did or did not remember which one of four visual patterns they had seen a short time previously on a touch-sensitive video monitor. Touching this pattern yielded a favorite food, but touching one of the other three produced no food.

Before this test, the monkeys had learned that touching one of two different images turned on the memory test, but that touching the other yielded a less preferred food. The monkeys usually touched the "take the test" image after short delays (15–30 s) when they presumably remembered which of the four test patterns would get the preferred food. But after longer delays (2–4 min) one of the monkeys always settled for the less preferred food and never chose to take the test, while the other made many more errors when he did. In occasional probe trials, inserted to rule out the possibility that the monkeys' choices were controlled by something other than the state of their memory, the four initial images were not present, so that there was no "correct" image to remember. One monkey never chose to take the test under this condition, and the other was much more likely than in normal trials to decline the test. Hampton concludes that "Rhesus macaque monkeys can report the presence or absence of memory. Although it is probably impossible to document subjective, conscious properties of memory in nonverbal animals, this result objectively demonstrates an important functional parallel with human conscious memory" (Hampton 2001, p. 5359). Consciously considering the contents of memory, in contrast to automatically using stored information, is a kind of metacognition, which many are still hesitant to infer in animals. However, Smith et al. (2003) suggest that at least monkeys may think consciously about the uncertainties they face in nature and in appropriately designed laboratory experiments.

Goal-directed desires and actions

Dickinson and Balleine (2000, p. 202) review experiments on goal evaluation by laboratory rats, which lead them to conclude that "Goal-directed actions of the rat are mediated by intentional representations of the causal relationship between action and outcome and of the value assigned to the outcome. The capacity for goal-directed action requires not only the evolution of intentional representations, but also the co-evolution of an interface between these representations and the animal's biological responses to the goal objects, events, or states. This interface, we suggest, is simple, nonreflexive consciousness in which the biological evaluation of a potential goal is manifested as an affective or hedonic response conjointly with an internal representation of the goal." By "simple, nonreflexive consciousness" Dickinson and Balleine appear to mean what we and others have called primary or perceptual consciousness. And if we understand them correctly, they are using the terms intention and intentional to include, though perhaps not be limited to, the customary sense of consciously intending to do something, and as one example of the broader philosophical usage of intentional to mean aboutness.

This suggestion by Dickinson and Balleine typifies the degree to which the antimentalistic taboos of behaviorism have been abandoned by leading investigators of animal learning. In addition to suggesting that rats experience simple consciousness, they believe that it plays a crucial role in producing adaptive behavior. Furthermore they propose

that emotional feelings play an essential role in goal-directed intentions and the resulting goal-directed behavior. It is certainly reasonable to assume that the animals perceive their goals as desirable; and there is no reason why simple consciousness could not also accompany other forms of perception and influence other types of action.

Tools

The use and especially the making of tools require at least short-term planning and adaptation of behavior to specific and often unpredictable situations. Hart et al. (2001) describe how Asian elephants modify branches to make them useful for fly switching. Many aspects of tool use by chimpanzees are described in detail in Matsuzawa (2001). Sousa and Matsuzawa (2001) demonstrated that captive chimpanzees not only use tokens they have learned to exchange for desired food but also save the tokens for future use. Tonooka (2001) described how some chimpanzees fold leaves to hold drinking water.

New Caledonian crows (*Corvus moneduloides*) have provided perhaps the most surprising and significant new examples of tool use and manufacture, as described and analyzed in detail by Hunt (1996, 2000a, 2000b) and Hunt and Gray (2003). These crows probe for invertebrates in crevices and use different types to probe in different locations. The most complex tools are of two types: twigs stripped of leaves and often of bark and then cut so that a short projecting piece of a branch forms a hook, and long strips torn from pandanus leaves fashioned into tools by removing material from one end to form a hook. The crows then insert these hooks into cavities and drag out prey that would otherwise be difficult or impossible to dislodge. Although most hook tools are discarded after the prey has been obtained, they are sometimes carried about or later retrieved and reused. Young crows make clumsy efforts to obtain food in this way and sometimes try to probe with less effective pieces of vegetation.

Chapell and Kacelnik (2002) kept two New Caledonian crows in an aviary where they spontaneously broke off twigs and used them to probe into holes and crevices. When presented with a favorite food placed in a 30-cm length of clear plastic tubing open at only one end, the crows readily picked up one of several sticks provided in the aviary, held it in the bill and poked it into the open end of the tube to drag out the food. The food was placed at varying distances in from the open end of the tube, and sticks varied widely in length. In most cases the crows selected a stick that was just long enough, or in a few cases longer than necessary, to reach the food, and only rarely tried to use a stick that was too short.

In later experiments by Weir et al. (2002) the same two crows were presented with food in a small "bucket" with a loop-shaped handle at its top. The experimenters placed this at the bottom of a transparent vertical tube where it could not be reached by the bird's unaided bill. Two types of wire probes were provided, one straight and the other bent to form a hook at one end. It was much easier for the birds to obtain the food with the hooked wire, although the male once accomplished this with a straight wire. When only a straight wire was available, in nine out of ten trials the female bent the straight wire to form a hook and used this to obtain food. Although the problem of extracting food from a cavity was somewhat similar to natural feeding behavior, this is an especially significant case of innovative coping with a novel problem because wires are not available to these crows under natural conditions, and bending wires is a very different behavior from cutting twigs or pandanus leaves. Weir et al. (2002) explain, "The method used by our female crow is different from those previously reported and would unlikely be effective with natural materials... She had no model to imitate and, to our knowledge, no opportunity for hook making to emerge by chance shaping or reinforcement of randomly generated behavior. She had seen and used supplied wire hooks before but had not seen the process of bending" (Weir et al. 2002, p. 981).

Communication can report subjective experience

After reviewing evidence that visual imagery appears to be very similar in humans and monkeys, Frith et al. (1999, p. 107) conclude that "to discover what someone is conscious of we need them to give us some form of report about their subjective experience...however we do not need to use language to report our mental experiences. Gestures and movements can be made with a deliberate communicative intent...the same procedure can be used in studies of animals." This realization of the significance of communication as a source of evidence about conscious feelings and thoughts entails a simple transfer to animals of the basic methods by which we infer what our human companions are thinking or feeling, as discussed in detail by Griffin (1976, 1984, 1998, 2001).

There are three general kinds of animal communication that are useful as evidence of conscious experiences:

1. Systems derived from simple components of human language, such as manual gestures modified from the sign language of the deaf, as reviewed by Fouts (1997), the keyboard system used by apes at the Yerkes Laboratory, as reviewed by Savage-Rumbaugh et al. (1998) and the imitation of human words used meaningfully by African grey parrots, as reviewed by Pepperberg (1999). Fouts and Jensvold (2002) have video-recorded chimpanzees using manual gestures modeled on the sign language of the deaf to communicate with each other in the absence of any human observer. Savage-Rumbaugh et al. (1998) have added significantly to the already abundant evidence that chimpanzees and bonobos communicate a variety of conscious thoughts and emotional feelings by use of the Yerkes Laboratory keyboard system (which uses symbols for English words). These apes also understand simple levels of human speech. Pepperberg (1999) has provided a coherent account of her extensive studies of how African grey par-

rots' use their imitations of human words to express simple thoughts and answer moderately complex questions. Pepperberg and Lynn (2001) recognize that this type of communication is evidence of perceptual consciousness.

2. Experimental arrangements by which animals can communicate about their thoughts and feelings by responses to controlled stimulation designed for this purpose. For many years, animals have been used in experiments on visual perception, and their manual responses, such as pulling a lever or touching a spot on a computer screen, or making intentional eye movements, have been taken as reporting. In reference to binocular rivalry, for example, Rees et al. (2002, p. 263) remark: "Monkeys can be trained to report their percept during rivalry, and their behaviour is similar to that of humans." Herman (2002) has shown that captive dolphins can learn not only to understand gestural commands from human trainers but also that certain gestures represent body parts. Xitco et al. (2001) report that dolphins can also learn to point by orienting their bodies toward some object. They were observed to do this only when a human companion was present, and the pointing was sometimes related to the dolphin's receiving information about an object via an underwater keyboard of symbols modeled after the keyboards used with apes in the Yerkes Laboratory.

3. Natural communicative behavior of animals. Some of the most important new evidence about natural communication concerns alarm calls. Several new examples have been added to the classic experiments of Seyfarth et al. (1980) on the alarm calls of vervet monkeys (*Cercopithecus aethiops*) that designate which of three major predators has been sighted. Zuberbühler et al. (1999a, 1999b) and Zuberbühler (2000, 2001) have found that two other members of the genus *Cercopithecus*, Diana monkeys (*C. diana*) and Campbell's monkey (*C. campbelli*), use predator alarm calls that convey information about which of two major predators (leopard or crowned eagle) has been sighted. Diana monkeys also respond appropriately to predator alarm calls of Campbell's monkeys. Fichtel and Kappeler (2002) have added to earlier observations of predator alarm calls used by lemurs. They found that redfronted lemurs (*Eulemus fulvus rufus*) and white sifakas (*Propithecus v. verreauxi*) give specific alarm calls only to the calls of raptors or to lemur alarm calls elicited by raptors, while other types of alarm calls given to mammalian predators are used more generally in other frightening situations. Manser (2001) has reported that in the social mongoose (*Suricata suricatta*) different call types are given in response to different predators, and that the urgency of the danger is also indicated by the noisiness of the call. From these and earlier studies it seems that some animals can communicate both urgency and level of arousal, and to a limited extent, the type of predator. Alarm calling is not a stereotyped reaction, for vervet monkeys occasionally withhold them, as discussed by Cheney and Seyfarth (1990, pp. 107–109).

Intriguing and puzzling data about the alarm calls of prairie dogs (*Cynomys gunnisoni*) have been reported in a review by Slobodchikoff (2002). These social rodents that live in a colonial burrow system were presented with real predators, models and human intruders, and the resulting alarm calls were then recorded. Responses of the prairie dogs to playbacks led Slobodchikoff to conclude that "A call can identify the category of predator, such as coyote, domestic dog, or red-tailed hawk... Each category of predator-specific calls elicits different escape responses...hawk and human alarm calls elicit running to the burrows and diving inside... Coyote and domestic dog alarm calls elicit either a running to the lip of the burrow and standing at the burrow entrance (coyote) or standing in place where the animal was feeding (domestic dog)" (Slobodchikoff 2002, p. 258). If confirmed, this level of semantic communication appears comparable to alarm calling by vervet monkeys and calls for further investigation.

Invertebrate communication

It is very widely assumed that only vertebrate animals can be conscious. But it is appropriate to ask how we can be certain that this is correct. Although most recent investigations of cognition have been restricted to mammals and birds, increasing evidence of complex cognition indicates that some invertebrates may take advantage of the effectiveness of conscious thinking when faced with challenging problems. Reed (1982) and Crist (2002) have reminded us that Darwin had no doubt that many animals are conscious of matters important to them, and that his studies of earthworms convinced him that they experience simple conscious thoughts about the tactile maneuvers by which they plug their burrows. Mather (2003) has reviewed evidence that cephalopods employ their complex color changes in social communication.

Wilcox and Jackson (1998, 2002) have found extensive experimental and observational evidence of complex cognition in jumping spiders of the genus *Portia*, which often prey on web-building spiders. To solve the challenges of preying on larger venomous spiders, *Portia* must reach moderately complex and appropriate decisions about spatial relationships, taking long detours around obstacles to reach a favorable location even when this requires losing visual contact with the goal. They engage in a complex form of communicative exchanges with their prey that include elements of deception. They approach the web quietly and set some of its threads into vibrations similar to the vibrations used in the courtship of the web-builder. The *Portia* adjusts its own vibratory signals in response to those of the web-builder in many subtle ways, tending to emit a wide variety of vibratory signals but to repeat those that attract the web-builder to the edge of the web. Wilcox and Jackson (2002) conclude that their investigations "bring us closer than we initially expected to something like the cognitive implications of verbal language" (Wilcox and Jackson 2002, p. 31).

Biesmeijer and Ermers (1999) have reviewed the social foraging behavior of neotropical stingless bees, which do not use waggle dances like those of honey bees but recruit nestmates to new food sources by transferring the odors of flowers. They also use scent marks placed on desirable food sources, and in some cases they mark the route between colony and food. One species, *Melipona panamica*, has been found by Nieh and Roubik (1995) and Nieh (1998) to recruit more nestmates to a food source on the ground or 40 m up on an observation tower in the rain forest, depending on which of the two the first bee had visited. Thus they have some method of indicating vertical location of a food source. This may be accomplished by means of acoustical signals in the nest cavity, as discussed by Nieh (1999) and Aguilar and Briceno (2002).

Recent investigations of the symbolic communication of honey bees have yielded new evidence of its versatility. Although Wenner (1998) continues to claim that no information is conveyed about the direction and distance to food sources, Polakoff (1998) has described new experiments showing that such information is transferred, even when the food is a kilometer from the hive, and regardless of the direction of the wind that might carry odors. This is a much greater distance than in previous experiments that led to the same conclusion.

Anderson and Ratnieks (1999) and Thom et al. (2003) have analyzed how tremble dances, stop signals and shaking signals fine-tune the basic message conveyed by waggle dances. Tautz (1996). Sandeman et al. (1996) and Tautz et al. (2001) have found increasing evidence that information from the waggle dances is transmitted from dancer to other bees by vibrations of the honeycomb substrate. Michelsen (2003), however, reports that both oscillating air currents and a jet of moving air directed straight behind a dancer may well provide bees following the dance with more useful information than substrate vibrations or direct contact between the dancer and the antennae of a follower. The jet appears to be sufficiently intense to stimulate the antennae of bees up to a few centimeters posterior to a dancer.

Weidenmüller and Seeley (1999) have found much smaller variability of direction indicated in waggle dances of swarming bees reporting locations of possible new home sites than in dances about food sources at the same distance. This provides support for the hypothesis of Towne and Gould (1988) that the increasing variation in the latter at increasing distances correlates with the typical size of flower patches, and may well serve to spread the searching efforts of newly recruited bees over a wider area than the immediate vicinity of the source the dancer had just visited. Waggle dances appear to vary in vigor or liveliness depending on how urgently the colony needs nectar or pollen. Although the number of times the dance is repeated clearly increases with the desirability of what the dancer is reporting, it has been difficult to detect any difference in the individual cycles of the waggle dance. Seeley and Buhrman (1999) have discovered that when signaling high levels of desirability, the bee shortens the time between the end of the straight waggle run and the beginning of the next run, hurrying to repeat the information-bearing portion of the dance.

After the dances on a swarm have narrowed down to almost complete unanimity about the chosen cavity (to which the swarm will move en masse), several additional activities are necessary to achieve a liftoff by the whole swarm, many members of which must first increase their body temperature. Seeley et al. (1998) and Visscher et al. (1999) have shown that this is accomplished by shaking signals in which one of the more active bees literally shakes a cooler sister by vigorous dorsoventral contact. Seeley and Tautz (2001) describe an acoustical piping signal by excited workers (many of which are nest-site scouts), who "scramble through the swarm cluster pausing every second or so to pipe. This also stimulates less active bees to raise their body temperature enough to join in the flight to the chosen cavity."

Seeley and Buhrman (1999) have confirmed and extended Lindauer's original observations that dancers on a swarm sometimes visit and dance about more than one cavity. They marked all the workers in three relatively small swarms (2,357–3,649 workers) and video-recorded all dances during the 2–3 days before the swarm flew off to the chosen cavity. The scouts had visited and danced about many cavities in different directions and at distances up to 3 km, but within about an hour almost all dances indicated the cavity to which the swarm flew off. Out of 113 bees that initially danced about a nonchosen cavity, 34 changed their dances to indicate the chosen cavity. Most of the others stopped dancing, but a few changed to a different nonchosen site. Nine continued dancing about a nonchosen cavity, but 42% of the 156 bees that danced initially about the chosen site continued to do so until the swarm flew off.

Camazine et al. (1999) and Visscher et al. (1999) confirmed Lindauer's discovery that a few bees first dance about one cavity then follow dancers describing a different cavity and later dance about the latter. Several bees were observed to visit and dance about both of two cavities located in desert terrain where there were almost no natural cavities A few visited both cavities, many followed dances about both, and a few interspersed dancing, dance following, and cavity visiting in a way that provided opportunities to compare dance messages and the cavities themselves. In some cases, dancers changed their dances to match dances they had followed *without visiting the second cavity*. In other words an exchange of communicative signals resulted in a change of subsequent dances. This is a rare case of chain communication and means that the whole sequence of visiting cavities and dancing about them is not rigid and inflexible, but is sometimes changed on the basis of information learned by following dances.

All of this new evidence narrows slightly but significantly the enormous gap between honey bee communication and human language. Many find it difficult even to conceive of the possibility that honey bees could be conscious to any degree at all. But the dance communication system provides us with the same general kind of evidence that we routinely use to infer human conscious experiences.

Of course the content of any conscious experiences of bees must be very different from any human thoughts. But if this category of evidence is valid for us, it must, in principle, be valid for other animals as well.

One reason for the widespread skepticism that bees could be conscious is that they do not learn their communication system. But many basic components of human speech have a genetic basis, and bees must learn the specific content of messages they communicate. Furthermore bees are capable of most types of learning found in vertebrates, as reviewed by Bitterman (1996, 2000). Giurfa et al. (2001) report evidence that bees can learn to distinguish the categories of same and different. The accumulating evidence of communicative versatility has led Seeley (2003) to conclude that "Although there is no evidence that worker bees possess reflective consciousness, I feel that the impressive cognitive abilities shown by worker bees in producing their communication signals are strong evidence that these creatures possess a degree of perceptual consciousness... (They) do not merely respond to objects and events in the environment, but are conscious of them in the sense that they experience perceptions and memories of these things."

Discussion

Although no single piece of evidence provides a "smoking gun" that proves with total certainty that pA, the probability of awareness, is 1.0, the cumulative impact of the data reviewed above, together with abundant evidence previously available, renders it far more likely than not that animal consciousness is real and significant. The basic nature of central nervous system function is much the same in all animals with central nervous systems, despite wide variation in gross anatomy and concentration of particular functions in specific areas of the brain. No uniquely human correlate of consciousness has been discovered.

A truly comparative neuroscience of consciousness has begun to develop. Many interesting animal brains are too small for adequate localization of function by the currently available imaging procedures; but this formidable difficulty is beginning to be overcome (Logothetis et al. 1999, 2002). Along with new electrophysiological methods (Rees et al. 2002; Crick and Koch 2003), imaging techniques may eventually be adapted to search in a variety of animals for the neural correlates of consciousness if and when these are convincingly identified in human and monkey brains. If this proves possible, the results will add a new dimension to cognitive ethology. Although identification of the NCC is highly desirable, it is not absolutely essential. For once we open our minds to the possibility that versatility in response to unpredictable challenges, and communication – broadly conceived – reveal some of the conscious experiences of animals, we can gather abundant and significant objective data on which to base scientific investigations. The next major challenge and opportunity for students of animal mentality is to learn what

particular animals are aware of, that is, the content of their conscious experience and what their lives are actually like, to them.

References

Aguilar I, Briceno D (2002) Sounds of *Melipona costaricensis* (*Apidae: Meliponini*): effects of sugar concentration and nectar source distance. Apidologie 33:375–388

Anderson C, Ratnieks FLW (1999) Worker allocation in insect societies: coordination of nectar foragers and nectar receivers in honey bee (*Apis mellifera*) colonies. Behav Ecol Sociobiol 46:73–81

Baars RJ (2002) The conscious access hypothesis: origins and recent evidence. Trends Cogn Sci 6:47–52

Baeyens F, Eelen P, Van den Bergh O, Crombez G (1990) Flavor-flavor and color-flavor conditioning in humans. Learn Motiv 21:434–455

Balda, RP, Pepperberg IM, Kamil, AC (eds) (1998) Animal cognition in nature. Academic, San Diego

Bekoff, M, Allen C, Burghardt GM (eds) (2002) The cognitive animal, empirical and theoretical perspectives. MIT Press, Cambridge, Mass.

Biesmeijer JC, Ermers MCW (1999) Social foraging in stingless bees: how colonies of *Melipona fasciata* choose among nectar sources. Behav Ecol Sociobiol 46:129–140

Bitterman ME (1996) Comparative analysis of learning in honeybees. Anim Learn Behav 24:123–141

Bitterman ME (2000) Cognitive evolution: a psychological perspective. In: Heyes C, Huber L (eds) The evolution of cognition. MIT Press, Cambridge, Mass., pp 61–79

Boysen S, Hines GT (1999) Current issues and emerging theories in animal cognition. Annu Rev Psychol 50:683–705

Büchel C, Morris JS, Dolan RJ, Friston KJ (1998) Brain systems mediating aversive conditioning: an event-related MRI study. Neuron 20:947–957

Büchel C, Dolan RJ, Armony JL, Friston KJ (1999) Amygdala-hippocampal involvement in human aversive trace conditioning revealed through event-related functional magnetic resonance imaging. J Neurosci 19:10869–10876

Byrne RW (2002) Imitation of novel complex actions: what does the evidence from animals mean? Adv Stud Behav 31:77–105

Camazine S, Visscher PH, Finley J, Vetter RS (1999) House-hunting by honey bee swarms: collective decisions and individual behaviors. Insect Soc 46:348–360

Capaldi EA, Robinson GE, Fahrbach, SE (1999) Neuroethology of spatial learning: the birds and the bees. Annu Rev Psychol 50:651–682

Cartmill M, Lofstrom I (eds) (2000) Animal consciousness: some philosophical, methodological, and evolutionary problems. Am Zool 4:835–846

Chapell JA, Kacelnik A (2002) Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). Anim Cogn 5:71–78

Cheney DL, Seyfarth RM (1990) How monkeys see the world, inside the mind of other species. University of Chicago Press, Chicago

Churchland PM (2002) Brain-wise. MIT Press, Cambridge, Mass.

Clark RE, Squire LR (1998) Classical conditioning and brain systems: the role for awareness. Science 280:77–81

Clark RE, Squire LR (1999) Human eyeblink conditioning: effects of manipulating awareness of the stimulus contingencies. Psychol Sci 10:14–18

Clark RE, Zola S (1998) Trace eyeblink classical conditioning in the monkey: a nonsurgical method and behavioral analysis. Behav Neurosci 112:1062–1068

Clark RE, Manns JR, Squire LR (2002) Classical conditioning, awareness, and brain systems. Trends Cogn Sci 6:524–531

Clayton NS, Dickinson A (1998) Episodic-like memory during cache recovery by scrub jays. Nature 398:272–74

Clayton NS, Griffiths DP, Dickinson A (2000) Declarative and episodic-like memory in animals: personal musings of a scrub jay. In: Heyes C, Huber L (eds) The evolution of cognition. MIT Press, Cambridge, Mass., pp 273–288

Clayton NS, Yu KS, Dickinson A (2001) Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. J Exp Psychol Anim Behav Process 27:17–29

Clayton NS, Yu KS, Dickinson A (2003) Interacting cache memories: evidence for flexible memory use by western scrub-jays (*Aphelocoma californica*). J Exp Psychol Anim Behav Process 29:14–22

Cowey A, Stoerig P (1992) Reflections on blindsight. In: Milner D, Rugg MD (eds) The neurophysiology of consciousness. Academic, London, pp 11–37

Cowey A, Stoerig P (1995) Blindsight in monkeys. Nature 373: 247–249

Cowey A, Stoerig P (1997) Visual detection in monkeys with blindsight. Neuropsychologia 35:929–939

Crick F, Koch C (1998) Consciousness and neuroscience. Cereb Cortex 8:97–107

Crick F, Koch C (2000) The unconscious homunculus. In: Metzinger T (ed) Neural correlates of consciousness, empirical and conceptual questions. MIT Press, Cambridge, Mass., pp 103–110

Crick F, Koch C (2003) A framework for consciousness. Nat Neurosci 6:119–126

Crist E (1999) Images of animals: anthropomorphism and animal mind. Temple University Press, Philadelphia

Crist E (2002) The inner life of earthworms: Darwin's argument and its implications. In: Bekoff M, Allen C, Burghardt GM (eds) The cognitive animal, empirical and theoretical perspectives on animal cognition. MIT Press, Cambridge, Mass., pp 3–8

Damasio AR (1999) The feeling of what happens: body and emotion in the making of consciousness. Harcourt, Orlando, Fla.

Damasio AR (2000) A neurobiology for consciousness. In: Metzinger T (ed) Neural correlates of consciousness, empirical and conceptual questions. MIT Press, Cambridge, Mass., pp 111–120

Dawkins MS (2000) Animal mind and animal emotions. Am Zool 40:883–888

Dawson ME, Schell AM (1987) Human autonomic and skeletal classical conditioning: the role of conscious cognitive factors. In: Davey G (ed) Cognitive processes and Pavlovian conditioning in humans. Wiley, New York, pp 27–55

Dehaene S, Naccache L (2001) Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. Cognition 79:1–37

Dickinson A, Balleine BW (2000) Causal cognition and goal-directed action. In: Heyes C, Huber L (eds) The evolution of cognition. MIT Press, Cambridge, Mass., pp 185–204

Donald M (2001) A mind so rare, the evolution of human consciousness. Norton, New York

Edelman GM, Tononi G (2000) Reentry and the dynamic core: neural correlates of conscious experience. In: Metzinger T (ed) Neural correlates of consciousness, empirical and conceptual questions. MIT Press, Cambridge, Mass., pp 139–151

Eichenbaum H (1997) Declarative memory: insights from cognitive neurobiology. Annu Rev Psychol 48:547–572

Emery NJ, Clayton NS (2001) Effects of experience and social context on prospective caching strategies by scrub jays. Nature 414:443–446

Engel AK, Singer W (2001) Temporal binding and the neural correlates of sensory awareness. Trends Cogn Sci 5:16–26

Fichtel C, Kappeler PM (2002) Referential alarm calls in lemurs. Behav Ecol Sociobiol 51:267–275

Fouts RS (1997) Next of kin: what chimpanzees have taught me about who we are. Morrow, New York

Fouts RS, Jensvold MLA (2002) Armchair dilusions versus empirical realities: a neurological model for the continuity of ape and human languaging. In: Goodman M, Moffat MLA (ed) Probing human origins. American Academy of Arts and Sciences, Cambridge, Mass., pp 87–101

Frith D, Perry R, Lumer E (1999) The neural correlates of conscious experience: an experimental framework. Trends Cogn Sci 3:105–114

Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of "sameness" and "difference" in an insect. Nature 410:930–933

Goschke T (1997) Implicit learning and unconscious knowledge: mental representations, computational mechanisms, and brain structures. In: Lamberts K, Shanks D (eds) Knowledge, concepts and categories. Psychology Press, Hove, England, pp 247–333

Green JT, Woodruff-Pak DS (2000) Eyeblink classical conditioning: hippocampal formation is for neutral stimulus associations as cerebellum is for association response. Psychol Bull 126:138–158

Griffin DR (1976) The question of animal awareness. Rockefeller University Press, New York

Griffin DR (1984) Animal thinking. Harvard University Press, Cambridge, Mass.

Griffin DR (1998) From cognition to consciousness. Anim Cogn 1:3–16

Griffin DR (2001) Animal minds, beyond cognition to consciousness. University of Chicago Press, Chicago

Griffiths D, Dickinson A, Clayton, NS (1999) Episodic memory: what can animals remember about their past? Trends Cogn Sci 3:74–80

Hampton RR (2001) Rhesus monkeys know when they remember. Proc Natl Acad Sci USA 98:5359–5362

Hart BL, Hart LA, McCoy M, Sarath CR (2001) Cognitive behaviour in Asian elephants; use and modification of branches for fly switching. Anim Behav 62:839–847

Hauser MD (2000) Wild minds, what animals really think. Holt, New York

Hauser MD, Konishi M (eds) (1999) The design of animal communication. MIT Press, Cambridge, Mass.

Heinrich B (1999) The mind of the raven, investigations and adventures with wolf-birds. Cliff Street Books (Harper-Collins), New York

Herman LM (2002) Exploring the cognitive world of the bottlenose dolphin. In: Bekoff, M, Allen C, Burghardt GM (eds) The cognitive animal, empirical and theoretical perspectives. MIT Press, Cambridge, Mass., pp 275–283

Hesslow G (2002) Conscious thoughts as simulation of behaviour and perception. Trends Cogn Sci 6:242–247

Heyes C, Huber L (eds) (2000) The evolution of cognition. MIT Press, Cambridge, Mass.

Hunt GR (1996) Manufacture and use of hook-tools by New Caledonian crows (*Corvus moneduloides*). Nature 379:249–251

Hunt GR (2000a) Tool use by the New Caledonian crow (*Corvus moneduloides*) to obtain *Cerambycidae* from dead wood. Emu 100:109–114

Hunt GR (2000b) Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. Proc R Soc Lond B 267:403–413

Hunt GR, Gray RD (2003) Diversification and cumulative evolution in New Caledonian crow tool manufacture. Proc R Soc Lond B 270:867–874

Inman A, Shettleworth SJ (1999) Detecting metamemory in nonverbal subjects: a test with pigeons. J Exp Psychol Anim Behav Process 25:389–395

Kanwisher N (2001) Neural events and perceptual awareness. Cognition 79:89–113

Kentridge RW, Heywood CA (1999) The status of blindsight. J Conscious Stud 6(5):3–11

Koch C, Laurent G (1999) Complexity and the nervous system. Science 284:96–98

Logothetis NK (1999) Vision: a window on consciousness. Sci Am Nov:69–75

Logothetis NK, Schall JD (1989) Neuronal correlates of subjective perception. Science 245:761–763

Logothetis NK, Guggenberger H, Peled S, Pauls J (1999) Functional imaging of the monkey brain. Nat Neurosci 2:555–562

Logothetis NK, Merkle H, Augarth M, Trinath T, Ugurbul K (2002) Ultrahigh-resolution fMRI in monkeys with implanted RF coils. Neuron 35:227–242

Lovibond PF, Shanks DR (2002) The role of awareness in Pavlovian conditioning: empirical evidence and theoretical implications. J Exp Psychol Anim Behav Process 28:3–26

Manns JR, Clark RE, Squire LR (2000a) Awareness predicts the magnitude of single-cue trace eyeblink conditioning. Hippocampus 10:181–186

Manns JR, Clark RE, Squire LR (2000b) Parallel acquisition of awareness and trace eyeblink conditioning. Learn Mem 7:267–272

Manns JR, Clark RE, Squire LR (2002) Standard delay eyeblink classical conditioning is independent of awareness. J Exp Psychol Anim Behav Process 28:32–37

Manser MB (2001) The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proc R Soc Lond B Biol 268:2315–2324

Mather J (2003) Cephalopod skin displays: from concealment to communication. In: Oller K, Griebel U (eds) Evolution of communication (Theoretical biology series). MIT Press, Cambridge, Mass. (in press)

Matsuzawa T (ed) (2001) Primate origins of human cognition and behavior. Springer, Berlin Heidelberg New York

Menzel R, Giurfa M, Gerber B, Hellstern F (2001) Cognition in insects: the honey bee as a study case. In: Roth G, Wullimann MF (eds) Brain evolution and cognition. Wiley, New York, pp 333–366

Metzinger T (ed) (2000) Neural correlates of consciousness, empirical and conceptual questions. MIT Press, Cambridge, Mass.

Michelsen A (2003) Signals and flexibility in the dance communication of honeybees. J Comp Physiol A 189:165–174

Mitchell RW (2002) Imitation as a perceptual process. In: Dautenhahn K, Nehanivc L (eds) Imitation in animals and artifacts. MIT Press, Cambridge, Mass., pp 441–469

Natsoulas TN (1983) Concepts of consciousness. J Mind Behav 4:13–59

Nelson TO, Rey G (eds) (2000) Metacognition and consciousness. Conscious Cogn 9:147–327

Nieh JC (1998) The food recruitment dance of the stingless bee, *Melipona panamica*. Behav Ecol Sociobiol 43:133–145

Nieh JC (1999) Stingless-bee communication. Am Sci 87:428–435

Nieh JC, Roubik DW (1995) A stingless bee *Melipona panamica* indicates food location without using a scent mark. Behav Ecol Sociobiol 37:63–70

Öhman A, Esteves F, Soares JJF (1995) Preparedness and preattentive association learning: electrodermal conditioning to masked stimuli. J Psychophysiol 9:99–108

Pepperberg IM (1999) The Alex studies, cognitive and communicative abilities of grey parrots. Harvard University Press, Cambridge, Mass.

Pepperberg IM, Lynn SK (2001) Possible levels of animal consciousness with reference to grey parrots (*Psittacus eritiacus*). Am Zool 40:893–901

Piggins D, Phillips CJC (1998) Awareness in domesticated animals – concepts and definitions. Appl Anim Behav Sci 57:181–200 (and related papers pp 201–325).

Placer J, Slobodchikoff CN (2000) A fuzzy-neural system for identification of species-specific alarm calls of Gunnison's prairie dogs. Behav Process 52:1–9

Polakoff LM (1998) Dancing bees and the language controversy. Integr Biol 1:187-194

Povinelli DJ (2000) Folk physics for apes, the chimpanzees' theory of how the world works. Oxford University Press, New York

Pryor, K, Haag R, O'Reilly J (1969) The creative porpoise: training for novel behavior. J Exp Anal Behav 12:653–661

Reed ES (1982) Darwin's earthworms: a case study in evolutionary psychology. Behaviorism 10:165–185

Rees G, Kreiman G, Koch C (2002) Neural correlates of consciousness in humans. Nature Rev 3:261–270

Rescorla RA (1988a) Pavlovian conditioning: it's not what you think it is. Am Psychol 43:151–160

Rescorla RA (1988b) Behavioral studies of Pavlovian conditioning. Annu Rev Neurosci 11:329–352

Roberts LE, Young R (1971) Electrodermal responses are independent of movement during aversive conditioning in rats, but heart rate is not. J Comp Physiol Psychol 77:495–512

Roth G (2000) The evolution and ontogeny of consciousness. In: Metzinger T (ed) Neural correlates of consciousness, empirical and conceptual questions. MIT Press, Cambridge, Mass., pp 77–97

Roth G, Wullimann MF (eds) (2001) Brain evolution and cognition. Wiley, New York

Sahraie A, Weiskrantz L, Barbur JL, Simmons A, Williams SCR, Brammer MJ (1997) Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. Proc Natl Acad Sci USA 94:9406–9411

Sandeman DC, Tautz J, Lindauer M (1996) Transmission of vibration across honeycombs and its detection by bee leg receptors. J Exp Biol 199:2585–2594

Savage-Rumbaugh S, Shanker SG, Taylor TJ (1998) Apes, language, and the human mind. Oxford University Press, New York

Schacter DL (1998) Memory and awareness. Science 280:59–60

Seager W (1999) Theories of consciousness, an introduction and assessment. Routledge, London

Searle JR (1998) How to study consciousness scientifically. Brain Res Rev 26:379–387

Searle JR (2000) Consciousness. Annu Rev Neurosci 23:557–578

Searle JR (2002) Consciousness and language. Cambridge University Press, New York

Seeley TD (2003) What studies of communication have revealed about the minds of worker honey bees. In: Kikuchi T (ed) Behavior and evolution in social insects. University of Hokkaido Press, Sapparo (in press)

Seeley TD, Buhrman SC (1999) Group decision making in swarms of honey bees. Behav Ecol Sociobiol 45:19–31

Seeley TD, Tautz J (2001) Worker piping in honey bee swarms and its role in preparing for liftoff. J Comp Physiol A 187:667–676

Seeley TD, Weidenmüller A, Kühnholtz S (1998) The shaking signal of the honey bee informs workers to prepare for greater activity. Ethology 104:10–26

Seward T, Seward MA (2000) Visual awareness due to neuronal activities in subcortical structures: a proposal. Conscious Cogn 9:86–116

Seyfarth D, Cheney D, Marler P (1980) Vervet monkey alarm calls: evidence for predator classification and semantic communication. Anim Behav 28:1070–1094

Shanks DR, Lovibond PF (2002) Autonomic and eyeblink conditioning are closely related to contingency awareness: reply to Wiens and Öhman (2002) and Manns et al. (2002). J Exp Psychol Anim Behav Process 28:38–42

Shanks DR, St. John MF (1994) Characteristics of dissociable human learning systems. Behav Brain Sci 17:367–447 (including commentaries and authors' response)

Sheinberg DL, Logothetis NK (1997) The role of temporal cortical areas in perceptual organization. Proc Natl Acad Sci USA 94:3408–3413

Shettleworth SL (1998) Cognition, evolution, and behavior. Oxford University Press, New York

Slobodchikoff CN (2002) Cognition and communication in prairie dogs. In: Bekoff, M, Allen C, Burghardt GM (eds) The cognitive animal, empirical and theoretical perspectives. MIT Press, Cambridge, Mass., pp 257–264

Smith JD, Shields WE, Washburn DA (2003) The comparative psychology of uncertainty monitoring and metacognition. Behav Brain Sci (in press)

18

Sousa C, Matsuzawa T (2001) The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). Anim Cogn 4:213–221

Stevenson RJ, Boakes RA, Prescott J (1998) Change in odor sweetness resulting from implicit learning of a simultaneous odor-sweetness association: an example of learned synesthesia. Learn Motiv 29:113–132

Stoerig P, Zontanou A, Cowey A (2002) Aware or unaware: assessment of cortical blindness in four men and a monkey. Cereb Cortex 12:565–574

Tautz J (1996) Honeybee waggle dance: recruitment success depends on the dance floor. J Exp Biol 199:1375–1381

Tautz J, Casas J, Sandeman D (2001) Phase reversal of vibratory signals in the honeycomb may assist dancing honeybees to attract their audience. J Exp Biol 204:3737–3746

Taylor JG (1999) The race for consciousness. MIT Press, Cambridge, Mass.

Thom C, Gilley DC, Tautz J (2003) Worker piping in honey bees (*Apis mellifera*): the behavior of piping nectar foragers. Behav Ecol Sociobiol 53:199–205

Thompson NS, Derr PG (2000) Intentionality is the mark of the vital. In: Tonneau F, Thompson NS (eds) Evolution, culture and behavior. Perspectives in ethology. Kluwer, Dordrecht 13:213–229

Tong F, Nakayama K, Vaughan JT, Kanwisher N (1998) Binocular rivalry and visual awareness in human extrastriate cortex. Neuron 21:753–759

Tononi G, Edelman GM (1998) Consciousness and complexity. Science 282:1846–1851

Tononi G, Srinivasan R, Russell DP, Edelman GM (1998) Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. Proc Natl Acad Sci USA 95:3198–3203

Tonooka R (2001) Leaf-folding behavior for drinking water by wild chimpanzees (*Pan troglodytes*) at Bossou, Guinea. Anim Cogn 4:325–334

Towne WF, Gould JL (1988) The spatial precision of honey bee dance communication. J Insect Behav 1:129–155

Tully T, Quinn WG (1985) Classical conditioning and retention in normal and mutant *Drosophila melanogaster* J Comp Physiol A 157:263–277

Tulving E (1972) Episodic and semantic memory. In: Tulving E, Donaldson W (eds) Organization of memory. Academic, New York, pp 382–403

Tulving E (2002) Episodic memory: from brain to mind. Annu Rev Psychol 53:1–25

Visscher PK, Shepardson J, McCart L, Camazine S (1999) Vibration signal modulates the behaviour of house-hunting honey bees (*Apis mellifera*). Ethology 105:759–769

Waal FBM de (2001) The ape and the sushi master, cultural reflections of a primatologist. Basic Books, New York

Waal FBM de, Tyack PL (2003) Animal social complexity: intelligence, culture, and individual societies. Harvard University Press, Cambridge, Mass.

Weidenmüller A, Seeley TD (1999) Imprecision in waggle dances of the honey bee (*Apis mellifera*) for nearby food sources: error or adaptation? Behav Ecol Sociobiol 46:190–199

Weir AAS, Chappell J, Kacelnik A (2002) Shaping of hooks in New Caledonian crows. Science 297:981

Weiskrantz L (1986) Blindsight, a case study and implications. Oxford University Press, New York

Weiskrantz L (1997) Consciousness lost and found. Oxford University Press, New York

Weiskrantz L, Warrington EK, Sanders MD, Marshall J (1974) Visual capacity in the hemianopic field following a restricted cortical ablation. Brain 97:709–728

Wenner A (1998) Honey bee dance language controversy. In: Greenberg G, Haraway MM (eds) Comparative psychology, a handbook. Garland, New York, pp 823–836

Wickens DD, Meyers PM, Sullivan SW (1961) Classical GSR conditioning, conditioned discrimination, and interstimulus intervals in cats. J Comp Physiol Psychol 54:572–576

Wiens S, Öhman A (2002) Unawareness is more than a chance event: comment on Lovibond and Shanks (2002). J Exp Psychol Anim Behav Process 28:27–31

Wilcox RS, Jackson RR (1998) Cognitive abilities of Areneophagic jumping spiders. In: Balda RP, Pepperberg IM, Kamil AC (eds) Animal cognition in nature: the convergence of psychology and biology in laboratory and field. Academic, San Diego, pp 411–434

Wilcox S, Jackson R (2002) Jumping spider tricksters: deceit, predation, and cooperation. In: Bekoff M, Allen C, Burghardt GM (eds) The cognitive animal, empirical and theoretical perspectives on animal cognition. MIT Press, Cambridge, Mass., pp 27–45

Williams LM, Brammer MJ, Skerrett D, Lagopolous J, Rennie C, Peduto A, Gordon E (2000) Neural activity associated with electrodermal orienting: an integrated fMRI and GSR study. Psychophysiology 37: S105 [Suppl]

Xitco MJ Jr, Gory JD, Kuczaj SA II (2001) Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). Anim Cogn 4: 115–123

Zuberbühler K (2000) Interspecies semantic communication in two forest primates. Proc R Soc Lond B 267:713–718

Zuberbühler K (2001) Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. Behav Ecol Sociobiol 50: 414–422

Zuberbühler K, Cheney DL, Seyfarth RM (1999a) Conceptual semantics in a nonhuman primate. J Comp Psychol 113:33–42

Zuberbühler K, Jenny D, Bahary R (1999b) The predator deterrence function of primate alarm calls. Ethology 105:471–490