

The evolution of comparative cognition: Is the snark still a boojum?

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ARTICLE INFO

Article history:

Received 28 August 2008

Accepted 2 September 2008

Keywords:

Animal cognition
Comparative psychology
Memory
Numerical cognition
Theory of mind

ABSTRACT

In “The Snark is a Boojum”, Beach [Beach, F.A., 1950. The snark was a boojum. *American Psychologist*, 5, 115–124] famously asserted that animal psychology embraced too few species and too few problems to deserve the name *comparative*. Later in the 20th century, others [e.g. Kamil, A.C., 1988. A synthetic approach to the study of animal intelligence. In: Leger, D.W. (Ed.), *Comparative Perspectives in Modern Psychology*. Nebraska Symposium on Motivation, vol. 35. University of Nebraska Press, Lincoln, NE, pp. 230–257; Shettleworth, S.J., 1993. Where is the comparison in comparative cognition? *Alternative research programs*. *Psychological Science*, 4, 179–184] expressed similar concerns about the new subfield of comparative cognition, suggesting that a more biological approach to choice of species and problems was needed to balance a dominant anthropocentrism. The last 10–15 years have seen many new developments, and a recent survey like Beach’s reveals a very different picture. Not only are many more species being studied, contributions by researchers from different backgrounds are increasing, and research on comparative cognition is better connected with developmental psychology, behavioral neuroscience, primatology, behavioral ecology, and other fields. Contemporary research addresses three major aspects of cognition about equally: basic processes, physical cognition, and social cognition. This article describes a selected research program from each area, chosen to exemplify current trends and challenges for the field.

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1. Introduction: the snark and the boojum

As many readers will recognize, the title of this article alludes to two classics in the literature. The primary source is Lewis Carroll’s long nonsense poem, *The Hunting of the Snark*, the story of a Bellman, a Banker, a Beaver, a Baker and a few other hardy souls who go hunting the snark. Snarks have various qualities, but the important one in the present context is noted when the Baker’s ancient uncle warns, “O beamish nephew, beware of the day/If your Snark be a boojum! For then/You will softly and suddenly vanish away,/And never be met with again! When the hunters do eventually encounter a snark, sad to say it proves to be a boojum, and the baker, who sees it first, does indeed “softly and suddenly vanish away.”

The relationship of Carroll’s poem to comparative cognition is clarified by the second classic to which the title alludes, Frank Beach’s 1950 *Psychological Review* article, “The snark was a boojum.” Of course comparative cognition had not been thought of in 1949, when Beach gave his presidential address about the snark to the experimental division of the American Psychological Association; he was talking about comparative psychology in general. In

Beach’s analogy, American psychologists who had spent the first part of the century in pursuit of something called comparative psychology were like the Baker and his friends in that their quarry was not what they thought. As a result they were in danger of “softly and suddenly” vanishing away, and unlike Lewis Carroll, Beach had a graph to prove it. His Fig. 1 (Beach, 1950) showed the total number of articles published every second year between 1911 and 1947 in *The Journal of Comparative Psychology (JCP)*, along with its incarnations earlier as the *Journal of Animal Behavior* and later, as *The Journal of Comparative and Physiological Psychology*. The total number of articles was going up, but the total number of species represented in those articles was going down, to fewer than ten in an average year in the 1940s. And you can probably guess what the most popular of those species was. So, Beach argued, genuine comparative psychologists had vanished away because they had been pursuing the boojum of the white rat.

One can make all kinds of qualifications and comments on Beach’s analysis, and over the years people have (e.g. Adkins-Regan, 1990; Dewsbury, 1998). Nevertheless, the snark and the boojum are a good starting point for talking about recent developments not so much in comparative psychology as a whole but research on cognition in animals. We can begin by comparing Beach’s data with the results of a similar survey of articles in the last three years. The left-most panel in Fig. 1 displays Beach’s (1950, Fig. 2) breakdown of articles by groups of species for 1946–48 as a histogram. The

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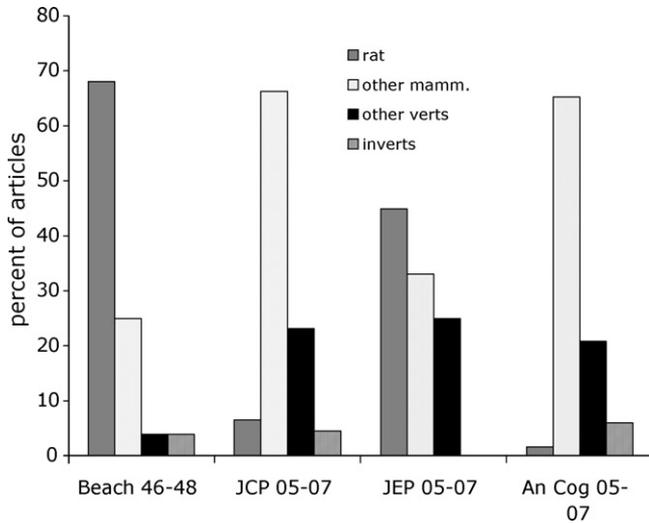


Fig. 1. Percent of all articles published in the given periods in each journal reporting data on rats (rat), mammals other than rats (other mamm), non-mammalian vertebrates (other verts), and invertebrates (inverts). Beach = data from Fig. 2 in Beach (1950) for 1946 + 1948; JCP = *Journal of Comparative Psychology*; JEP = *Journal of Experimental Psychology: Animal Behavior Processes*; An Cog = *Animal Cognition*; 05–07 = based on total for the three year period 2005–2007.

comparable analysis of the *Journal of Comparative Psychology* for 2005–2007 displayed beside it is a stunning contrast. Of course JCP might not be most relevant for comparative cognition, as it publishes quite a bit of straight animal behavior or ethology. But the profiles for two of the other leading outlets for animal learning and cognition research, the *Journal of Experimental Psychology: Animal Behavior Processes* (JEP:ABP) and *Animal Cognition*, in the rightmost two panels are also very different from the one based on Beach's data. The difference between them largely reflects JEP:ABP's status as an archival journal for the continuing development of basic theory with data from relatively few species. This kind of research,

which Beach and others (Dewsbury, 1998) might call simply animal psychology is considered in this article as part of the broader field of comparative cognition. Method and theory developed with in-depth studies of a few species are indispensable for explicitly comparative research, which in turn can feed back on the development of basic theory (for an example see Wright, 2006).

In itself the trend toward studying more species could represent just a mindless accumulation of data. But Beach (1950) also complained about the limited number of problems and kinds of behaviors being studied by so-called comparative psychologists. Those criticisms were echoed over the years by people such as Hodos and Campbell (1969), who added the complaint that the comparisons that were being made were not well grounded in evolutionary theory (see also Papini, 2002). So what is important is what this changing profile means, and to explore that I will focus on comparative cognition, mainly on developments in the last 15 years or so. Not only does this time frame correspond to the age of the Comparative Cognition Society, but also it is a little more than 15 years since Stu Hulse, one of the pioneers of the contemporary study of comparative cognition, organized a symposium on the topic at the meetings of the Psychonomic Society (Hulse, 1993). Echoing the complaints of Beach (1950) and Hodos and Campbell (1969) about the absence of biologically meaningful comparisons from so-called comparative psychology, my contribution to it (Shettleworth, 1993) was titled "Where is the comparison in comparative cognition?" It contrasted biological and anthropocentric approaches to comparison and suggested that at the time most comparisons being made by animal cognition researchers were implicitly with humans, i.e. anthropocentric. More research was needed with an ecological or adaptationist approach, testing for convergence and/or divergence in cognitive abilities based on how cognition functions in the wild. Comparisons of spatial memory in food-storing and nonstoring birds provided an example. Other people, especially Al Kamil (e.g. Kamil, 1988), were saying similar things at the time. Over the years many others have made their own thoughtful assessments of the field of comparative cognition (Terrace, 1984; Wasserman, 1997; Hulse, 2006; Church, 2001).

What follows is a personal view of what has been happening in the field in the past 10–15 years, a view developed while preparing an updated edition of my book (Shettleworth, 1998). Documenting all the new developments makes clear that there really have been some very big changes, so that complaints like those of Hodos and Campbell about lack of sophistication regarding evolution, neglect of natural behavior and more than a handful of species, or absence of connections with other areas in the psychology and biology of mind and behavior are becoming less and less appropriate. But before surveying a few examples of these developments, let us go back to a Beachian analysis of the proportions of articles on different groups of species in JEP:ABP (Fig. 2) and JCP (Fig. 3) at the beginning and end of this roughly 15-year period. The changes in JEP:ABP are most conspicuous. Although about the same number of articles was published in 2005–2007 as in 1991–1993 (126 and 113, respectively), the number of species studied doubled, from 10 to 20, as did the proportion of articles reporting new data on more than one species ("multi species"; see figure captions for further explanation). The increased number of species largely reflects studies on apes and monkeys and on more different species of birds. The trend toward more studies of nonhuman primates is even more conspicuous in the data for the JCP, where the total number of species hardly changed (66 species in 136 articles in 1991–93 and 73 species in 151 articles in 2005–2007), but the species represented shifted toward apes, monkeys, and humans. Indeed, a substantial number of the multi species articles in the latter period were explicit comparisons of two or more primates, sometimes including humans. Finally, as the simplified summary in Fig. 1 suggests, the journal

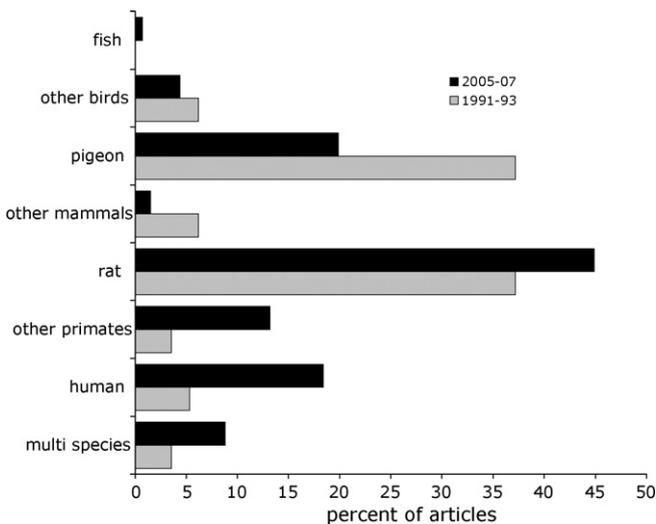


Fig. 2. Percent of all articles published in the *Journal of Experimental Psychology: Animal Behavior Processes* in 1991–1993 and in 2005–2007 reporting data on species in the given groups. Multi species = contains new data from more than one species. Multi species articles are also represented in one or more of the other categories. They were counted once in each species group represented. For example, an article comparing two or more monkey species counted as one article about "other primates" but one comparing monkeys with humans counted as one about humans and one about other primates. See Dewsbury (1998) for an alternative approach to this problem.

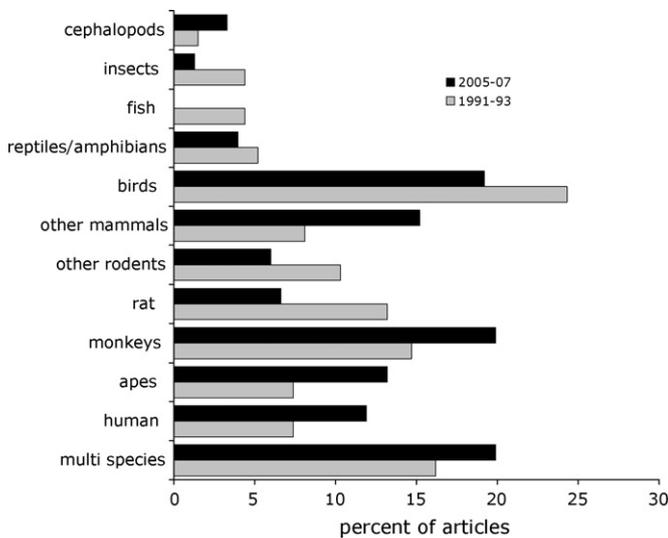


Fig. 3. Percent of all articles published in the *Journal of Comparative Psychology* in 1991–1993 and in 2005–2007 reporting data on species in the given groups. Multi species = contains new data from more than one species. Multi species articles are also represented in one or more of the other categories as explained in the caption to Fig. 2.

Animal Cognition has a profile similar to *JCP*'s in 2005–2007, with a small proportion of papers on rats and a large proportion on monkeys and apes. The very existence of this journal, which appeared first in 1998, says something about the growth of the field.

And people publishing on comparative cognition are not just talking to each other. Another revealing index is the number of articles that appear in prominent generalist scientific journals—*Proceedings of the Royal Society*, *PNAS*, *Biology Letters*, and most importantly perhaps, *Science* and *Nature*. As a rough measure, the database of references for my book contains more than twice as many items from *Science* or *Nature* in 2005–2007 as in 1991–1993. The very recent ones include probably the largest single study of comparative cognition ever done (Herrmann et al., 2007), in which 106 chimpanzees, 32 orangutans, and 105 two-year-old children were each given a whole battery of tests of physical and social cognition. But what is going on is much more than larger numbers of articles about larger numbers of species. There has been a dramatic evolution in what comprises the study of comparative cognition.

2. What is comparative cognition?

So what is comparative cognition? In a sense the field began with Darwin, whose second great book, *The Descent of Man and Selection in Relation to Sex*, (Darwin, 1871) identified nearly every aspect of comparative cognition that has been investigated since, not to mention proposing the still-controversial (see Penn et al., 2008) hypothesis that human beings differ mentally only in degree, not in kind, from other animals. But to confine ourselves to contemporary research stimulated by the cognitive revolution in psychology, a good way to see how comparative cognition has evolved is to consult some landmark edited books (see also Hulse, 2006). The collection by Hulse et al. (1978) that is often seen as having proclaimed the beginning of the field has fourteen chapters: five on conditioning, two each on memory and spatial cognition, one each on attention, serial learning, time, and abstract concepts. The research described therein represents a total of three nonhuman species: rat, pigeon, and chimpanzee. But even within a few years this profile began to change. The animal cognition conference held at Columbia University in the spring of 1982 resulted in a book

(Roitblat et al., 1984) with 33 chapters. New topics included number, evolution, and neuroscience. And the species contributing data now included Clark's nutcrackers and other songbirds and many more nonhuman primates. One might continue this survey and extend it to textbooks, many of which reflect the historical development of the field with titles mentioning "animal learning and cognition" and organizations with the chapters on cognition at the end.

But it seems to me that if done without too many historical blinders, an inclusive survey of current work in comparative cognition reveals that the field encompasses three major sets of mechanisms for the acquisition, processing, and representation of information about the environment. Basic cognitive processes cut across all kinds of content; these are the ones that were the main focus in the 1970s. They include perception, attention, memory, associative learning, category and concept learning. In addition, following the taxonomy proposed by Tomasello and Call (1997), is research on two sets of possibly specialized processes of acquisition, representation, and behavioral control, or cognitive modules, defined largely in terms of their functions, i.e. what aspects of the world they are about, namely physical cognition and social cognition. Some aspects of physical cognition like time, space, and number have been studied for quite a long time within experimental animal psychology, whereas others like tool using and causal learning have emerged or re-emerged into prominence recently. Social cognition includes social knowledge, the kind of thing so beautifully studied in the field by Cheney and Seyfarth (2007), i.e. what animals know about their social networks and how they come to know it. It also includes theory of mind, imitation and other forms of social learning, and the representational and other processes involved in communication.

So part of what has changed since the 1970s is that the study of cognitive processes in animals now encompasses a much broader set of problems. They are also being studied by researchers from a much wider variety of backgrounds. Behavioral ecologists, field biologists, developmental psychologists, and others are all contributing, and in some integrative research the lines between them are nearly invisible. But more important are the major conceptual and theoretical issues being addressed. The next part of the article briefly reviews some key issues common to different aspects of cognition by taking one topic within each of the three major areas to exemplify some of the important new developments and challenges.

3. Basic processes: memory

To start with basic processes, we can go right back to memory, studies of which have been with us since well before Roberts and Grant (e.g. 1974) and others started looking at pigeons' forgetting functions in operant paradigms. Like research on human memory in the 1970s, research on animal memory was focused on functional aspects of memory such as retention vs. time since training and perhaps information processing models of what was going on. Conscious aspects of memory were simply not an issue. But the analysis of human memory has evolved a good deal since then, and at the same time the study of consciousness has become respectable in the cognitive and brain sciences more generally. So the study of human memory now includes all sorts of questions about conscious aspects of memory: explicit vs. implicit memory, remembering vs. knowing, metamemory, episodic memory, and the latest (Addis et al., 2007), using memory to imagine the future. Along with these developments has come a compelling interest in the same kinds of processes in nonhuman animals. It is not mere anthropomorphism to ask, for example, whether animals are aware of their memories or engage in "mental time travel." These are also legitimate questions

about evolutionary continuity between humans and other species. In addition, advances in the brain sciences have made comparative research on memory much more rich and interesting by providing “animal models” for neurobiological studies potentially relevant for human welfare. So it is not surprising that the last decade has seen a huge upsurge in research on aspects of memory that in humans are accompanied by distinctive conscious experiences, especially episodic memory (Clayton et al., 2003a; Hampton and Schwartz, 2004) and metamemory (e.g. Smith and Washburn, 2005; Terrace and Metcalfe, 2005).

On one controversial definition (cf. Tulving, 2005) episodic memory, or memory for unique experiences in one’s personal part, is accompanied by the sense of traveling back in time to the event, consciously re-experiencing it. The fact that loss of episodic memory is one of the symptoms of Alzheimer’s disease and other pathologies helps to explain the intense interest of the neuroscience community in potential examples in animals. The landmark experiment (Clayton and Dickinson, 1998) that kicked off much of this work exploited the natural food-storing behavior of Western scrub jays (*Aphelocoma californica*). The birds stored both peanuts and wax worms and were allowed to retrieve them either after 4 h, in which case both items were fresh, or after 124 h, at which time the worms were “rotten” (i.e. made distasteful). At first the birds were given a number of opportunities to learn this contingency by actually encountering fresh and rotten worms. When they were then tested with no worms or nuts present, they chose as would be predicted if they remembered not only what they stored where, but also when (or how long ago, Roberts et al., 2008) the storing episode took place. That is, they searched for worms first after 4 h and for peanuts first after 124 h. Control birds for whom the worms were always fresh went first for worms at both times, showing that sites with worms are not simply forgotten more quickly than those with peanuts. So does this mean scrub jays have episodic memory?

Of course if episodic memory means traveling mentally back in time to the moment when the food was hoarded, we can never know the answer to this question. By same token, the question whether animals consciously imagine the future, the new wave of research in this area, is also unanswerable (Raby et al., 2007; Suddendorf and Corballis, 2007). But to the extent episodic memory encodes a specific place, thing, and time (or time ago), the birds could only do what they do if they have such a what–where–when memory. So Clayton and Dickinson (1998) wisely claimed no more that they had demonstrated “episodic-like memory” in the scrub jays; that is, they had gone as far as it is possible to go with non-verbal subjects. Further experiments, including some employing a third type of item, have provided evidence that the birds’ memories for what, where, and when have some other characteristics of human episodic memory. For example, they can be used flexibly, in that the animal’s evaluation of an item can change after it has been hoarded (Clayton et al., 2003b). This whole approach to animal episodic memory has been debated, however, and several alternative approaches suggested. For example, unlike with unique experiences in daily life, in Clayton and Dickinson’s experiment the birds could anticipate having their memory tested, and this may have affected encoding. Perhaps a better analogue involves asking the animals an unexpected question (Zentall et al., 2001). Maybe the temporal aspect of episodic memory is not time as such but spatial context or the context provide by surrounding events (Eichenbaum et al., 2005). Pigeons, rats, and mice all pass one or more tests of episodic memory based on such criteria.

Consideration of this research reveals several issues that often arise in attempts to document processes in animals that are already somewhat understood in humans. The first is that progress is often greatest if the process under study is well defined for humans. However, among researchers studying human memory, conscious

re-creation of rich personal experiences in everyday life is not universally seen as the key feature of episodic memory. Memory for familiar images seen in the laboratory a few minutes ago is also studied under the rubric of episodic memory (e.g. Kohler et al., 2001). Such ambiguities leave the way open for the multiple approaches to testing animals sketched above.

Second, attempts to investigate human-like processes in other species often begin with asking yes/no questions and designing pass/fail tests to answer them. For example, “do animals have episodic memory” translated into “do scrub jays exposed to decaying worms behave significantly differently from controls?” More powerful and convincing are cases in which a more extensive pattern of data can be sought, in effect functional similarity in the mathematical sense of similar relationships between dependent and independent variables, and predictions from different theories of the mechanisms involved pitted against each other in experiments (see Wasserman, 1984; Heyes, 2008). In the case of episodic memory this has been achieved by Howard Eichenbaum and his group (cf. Eichenbaum et al., 2005) using tests of rats’ remarkable olfactory memory modeled on tests for people that dissociate “remembering” vs. “knowing” (or recollection, i.e. episodic memory, vs. a mere sense of familiarity with previously encountered material). Although this approach (Yonelinas, 2001) is not controversial, it does predict different patterns of data from two independent kinds of memory tests when factors such as retention interval and the subjects’ reporting bias are varied. These patterns can be replicated in rats. They also change in hippocampally lesioned rats in ways that parallel changes in amnesic humans. This whole package of parallels thus constitutes strong evidence that rats share with humans a process with the functional properties of episodic memory. It is an also excellent example of how comparative research can be connected with cognitive neuroscience in important and productive ways.

Finally, when it comes to aspects of cognition such as episodic memory and metamemory that are accompanied by distinctive conscious experiences in humans, the best we can do is agree on criteria for functional similarity. In the tests of scrub jays’ episodic-like memory, for instance, appropriate choice among cache sites is taken as evidence for the kind of integrated memory of what, where, and when that people report on verbally. But as to whether the jays or any other animals have the same conscious memory processes as humans, as Hampton (2005) said of work on metamemory in monkeys, “It will . . . always remain a matter of conjecture whether monkeys experience conscious states of knowing like our own . . . We need to adopt a performance-based view of natural selection, from which cognition is seen through what it does, not through how it is experienced.” This viewpoint has the somewhat paradoxical implication that although asking whether animals are aware of their memories appears to be a legitimate comparative question about cognitive and brain processes, and although it has led to fascinating and important discoveries about animal memory, in some sense it is unanswerable.

4. Physical cognition: number

In the area of physical cognition, the study of spatial cognition might be taken as a prime example of tremendous recent change. Beginning with Gallistel’s (1990) landmark book, research on spatial behavior has become a leading example of integration of both data and theory across species, from invertebrates to humans, and from the field to virtual reality to neurobiology (cf. Jeffery, 2003). Research on tool using and on causal learning (Penn and Povinelli, 2007a) has also seen many recent developments, for example in the discovery that birds may rival apes in their use of tools. And some of what began as the study of foraging has evolved

into a rich integration of biological optimality modeling, analysis of behavior on reinforcement schedules, and theories of economic decision making (Kacelnik, 2006; Shapiro et al., 2008). But the study of numerical cognition may have changed the most in that its theoretical framework has been transformed and comparative research seamlessly integrated with research on child development and cognitive neuroscience, sometimes all in the same laboratory or research group (cf. Brannon, 2006; Feigenson et al., 2004).

Investigations of numerical cognition in animals go back at least to Clever Hans, but until about a decade ago, they very often focused on the question, “can animals count?” (see Chapter 8 in Shettleworth, 1998). As suggested in the last section, this is not the most productive kind of question for comparative psychologists because it presupposes a yes or no answer. The history of research on such questions – “can animals learn a human language” is another – shows that claims to have produced answers to them usually lead only to debate about what the question means and what actually needs to be demonstrated. The transformation in the study of numerical cognition consists of beginning to look at it as encompassing several core components, each of which may or may not be shared across species. One core component is a widely shared ability for fuzzy discrimination among sets of different sizes. Both nonverbal subjects (animals and human babies) and human adults prevented from counting by rapid stimulus presentation and the like discriminate among sets of different numerosities in a way described by Weber’s Law. For instance, sets of 6 vs. 8 items are discriminated about as well as sets of 60 vs. 80. Because error increases proportionately with set size, sets that differ by a given absolute amount are better discriminated when they are small (e.g. 7 vs. 9) than when they are large (87 vs. 89).

In addition, at least in some situations monkeys and babies display a core ability for precise discrimination among small sets of items, where “small” is 3 or 4 depending on species and age. For example, when free-ranging rhesus monkeys have seen up to three apple pieces placed one by one into each of two containers, they choose the container with more pieces, but they choose randomly when either container has more than three pieces (Hauser et al., 2000). In a task copied directly from the one for monkeys, human babies choose similarly when allowed to crawl toward one or another of two containers in which they have seen crackers deposited (see Feigenson et al., 2004). Unlike with the approximate large number system, performance changes abruptly at a particular set size. These set size limits are thought to reflect the operations of a primitive object tracking system, although the conditions under which it operates are not yet entirely clear. For instance, on some numerical tasks requiring extensive training there is little if any evidence for anything other than the Weber’s Law based system (Brannon, 2006). Nevertheless, the two core processes can both be demonstrated in human adults. The Brazilian Mundurucu, whose language does not have words for precise quantities greater than about four, behave essentially the same as numerate French adults both in precise judgments about quantities lower than four and in relative comparisons of quantities (clouds of dots) up to 80 or more. However, when precise quantities greater than four are to be judged, the tribes people’s performance falls substantially below that of the French adults, who count the items (Pica et al., 2004).

In summary, the central comparative question about numerical cognition in the early 21st century is not “do animals count?” but something more like “what are the components of numerosity discrimination, how are they shared across species, and what is the role of language in the numerical competence of numerate human adults?” All three aspects of this question have provisional answers, the products of fertile two-way exchanges of method and theory between comparative and developmental psychologists. Neuroimaging and other methods of neuroscience are also

being used to investigate key theoretical issues here, such as the nature of the mental number line and differences between the precise small and approximate large number systems (Nieder, 2005).

5. Social cognition: theory of mind

Turning to changes in the understanding of social cognition, one might mention the new insights being contributed by studies of birds and non primate mammals such as hyenas and meerkats (cf. de Waal and Tyack, 2003; Emery et al., 2007). One might also mention the evolution of a diverse and lively community of researchers studying social learning, in species from rats and fish to chimpanzees and children, and topics from mathematical models of social transmission to the possibility of animal cultures (Galef and Heyes, 2004; Galef and Laland, 2005). And of course there are exciting and controversial proposals about the potential contributions of comparative research to understanding the nature and evolution of human language (Fitch, 2005; Hauser et al., 2002). But for the purposes of this article, the development of research on animal theory of mind is particularly instructive as an illustration of general issues not discussed in the two preceding sections.

In psychology, having a theory of mind means understanding that other individuals have minds, i.e. that they can have knowledge, beliefs, desires, and so on. The concept originated in an influential article by Premack and Woodruff (1978), “Does the chimpanzee have a theory of mind?” However, although Premack and Woodruff presented some initial data from tests in which the language-trained chimpanzee Sarah behaved as if understanding the intentions and desires of people in films, the study of theory of mind took off first in developmental psychology, where it soon became a lively and controversial topic (e.g. Carruthers and Smith, 1996). Research with chimpanzees followed along in the early 1990s, especially in the extensive work of Daniel Povinelli and colleagues. Many of their studies involved a paradigm in which a chimpanzee was confronted with two people from whom it could beg for food by reaching through a barrier toward one or the other. Only one of the people could see the animal; the other might have a blindfold, be looking away, or the like, and would not give food if chosen. In effect this was a test of whether chimpanzees understand something like, “S/he can see me, therefore s/he knows what I want.” But because the animals had many trials in any given condition, they could have come to perform successfully simply by learning to discriminate on the basis of some observable predictive cue. One early series of studies seemed to rule out this possibility by showing that the animals transferred above-chance performance to a novel situation. However, an analysis of the trial by trial data done in response to a sharp-eyed behaviorist critic (Heyes, 1993) showed that the animals did not transfer immediately but acquired the correct response during the test (Povinelli, 1994). As a result, subsequent work focused specifically on what cues the animals used or learned to use in this and related tests. One important point underlined by this work is that whether in contrived laboratory situations or in natural social groups, inferences about the minds of others are necessarily based on their behavior. Therefore Premack and Woodruff’s question “Is the chimpanzee a behaviorist or a mentalist?” cannot have an all-or-nothing answer. Chimpanzees may or may not interpret other’s behavior with mentalist constructs like those invoked by humans, but it is impossible to be only a mentalist.

The generally negative conclusions from the chimpanzee theory of mind research of the 1990s were not universally accepted. Rather, several critiques of the early paradigms inspired a new and still ongoing wave of research. Two prominent critiques were that, first, the chimpanzees were being tested on their theory of the human mind; perhaps they would perform differently if tested with other chimpanzees. Second, they were being asked to

understand a cooperative individual, but in nature chimpanzees more often compete than cooperate over food. And indeed, as these ideas predict, chimpanzees do behave as if having theory of mind when competing with a dominant animal over food (Hare et al., 2001). Again, however, what is going on in such tests can be deconstructed into use of particular observable cues, including memory for who was present and where they were directing their gaze when food was hidden (Povinelli and Vonk, 2003; but see Tomasello et al., 2003). These social skills are not confined to chimpanzees; ravens and scrub jays also show them when protecting their food caches (Bugnyar and Heinrich, 2005; Dally et al., 2006).

Another line of deconstruction is based on the observation that the original paradigms required chimpanzees to use human communicative cues such as pointing and gazing. Perhaps due to a history of domestication other animals, particularly dogs, do this better than chimpanzees (Hare and Tomasello, 2005; Miklósi et al., 2004). This intuition turns out to be correct, an excellent example of how behavior that seems to be “smart” in human terms is not necessarily confined to primates but may be an adaptation to a particular social niche. However, exactly how and why domestication has resulted in responsiveness to human gestures and other cues and whether it has anything to tell us about the evolution of human sociality is still a matter of debate, made the more interesting by the finding that domestic goats and foxes selected merely for tameness show the same tendencies as dogs (Hare, 2007).

Although in exploring these diverging avenues, researchers may seem to have lost sight of Premack and Woodruff’s original question, it continues to be debated. On one view, in principle no paradigm from which data has yet been reported can distinguish behavior based on theory of mind from use of observable cues, and new kinds of tests are called for (Penn and Povinelli, 2007b). On another (Call and Tomasello, 2008), based on new sorts of data, evidence for at least some components of theory of mind in chimpanzees has never been stronger. Like numerical cognition, theory of mind may be best understood as having various components. For example, Call and Tomasello (2008) suggest that chimpanzees understand the perceptions and goals of others but not their beliefs and desires. Controversy surrounding this issue seems unlikely to abate any time soon. In the meanwhile, one general principle that can be derived from the history sketched here is that explaining what animals do as the expression of memories, concepts, representations, and the like does not preclude explaining it in terms of observable factors such as past history and present cues. The challenging business of attempting to infer cognitive processes from behavior cannot be conducted successfully without taking into account what ethology and behavior analysis have to say about the control of behavior *qua* behavior.

Introductions to animal behavior for biology students traditionally begin by defining Tinbergen’s (1963) four questions – proximate cause, current function, evolutionary history, and development in the individual – and go on to emphasize that they must not be confused with one another. Particularly insidious is the ease with which cause can be confused with function and functional answers given to causal questions. For instance, a scrub jay’s reaching may function to deceive a competitor, but this does not mean that the jay has theory of mind and an intention to deceive. During the last 30–40 years, the tendency to such confusions has been exacerbated by theoretical developments in both the biology and the psychology of animal behavior. With the rise of behavioral ecology in the 1970s, traditional ethological causal analyses in terms of sign stimuli, fixed action patterns and the like seemed increasingly old fashioned and theoretically uninteresting (Dawkins, 1989). The answer to “what is this animal doing?” was more likely to be “choosing a mate” than “bowing and cooing in response to cues from a female.” As a result, students were

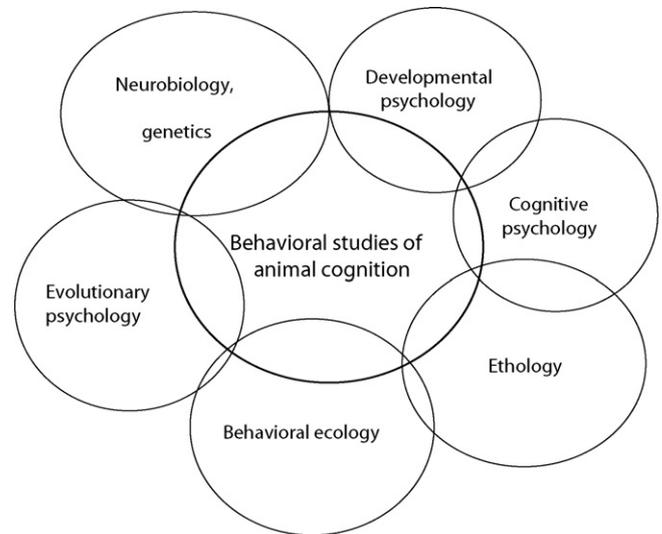


Fig. 4. Schematic depiction of how comparative cognition intersects with other sciences.

not always taught to look at behavior as such. At more or less the same time, the shift within psychology from behaviorism to cognitivism meant that psychology students were not so often exposed to behavior analysis as a valuable aid to causal understanding. Here “what is this animal doing?” became “expressing its theory of mind” rather than “responding to cues that predicted reinforcement in the past.” But just as Tinbergen emphasized keeping all four questions in mind and seeking to answer them in an integrated way, so it is important to know about and keep in mind alternative ways of answering causal questions. The participation in comparative cognition research of scientists from more diverse backgrounds has increased the importance of such thinking. As we have seen in this section, a test of theory of mind may be at the same time a discrimination learning experiment and a situation in which a species has been selected for responding in one way rather than another. In a sense, then, the take-home message from this section is that the lessons of Tinbergen and Skinner should not be forgotten in the excitement of seeking human-like cognitive processes in other species.

6. Conclusions: the snark is no longer a boojum

The study of cognitive mechanisms of animal behavior, or cognitive ethology in the broad sense (Kamil, 1998), is an energetic and growing interdisciplinary enterprise (Fig. 4). Figs. 1–3 reveal that the classic criticisms of Beach and others regarding undue focus on a small number of species simply do not apply to contemporary research on comparative cognition. The brief summaries of research on basic cognitive processes, physical, and social cognition elsewhere in this article indicate that the range of problems being studied is also much broader than in the past. As for the sophistication of comparisons that are being done, many of the examples touched on here involve comparisons between distantly related species, scrub jays and humans for example. The classic methods of biological comparison include comparing both close and distant relatives, and much can be learned from work of both kinds (see Papini, 2002). In current research on comparative cognition, for example, the suggestion that some birds among the corvids may have convergently evolved aspects of social cognition long thought to be exclusive to primates (Emery and Clayton, 2004) provides both an antidote to anthropocentric assumptions about the “specialness” of primates and possibilities for testing hypotheses about

the evolution of social intelligence. Comparisons of close relatives may be part of the same enterprise, as in the tests of transitive inference abilities in corvids differing in sociality (Bond et al., 2003). As another example of testing close relatives, comparing chimpanzees with humans to discover “what makes us human” and eventually connect the findings with comparative genetics and neuroanatomy is a very active area in itself (Penn et al., 2008; Herrmann et al., 2007).

Although the argument by analogy (or anthropomorphism) undoubtedly still plays a role in suggesting problems for study, the mainstream of research on comparative cognition can be characterized, to borrow a phrase from Heyes (2008) as experimental tests of functionally defined processes and mechanisms. The current sketch of selected recent developments has highlighted a few challenges for this enterprise. One is to start with clear functional definitions of the processes under study, something that may not be possible when the process is not already well understood in some reference species, very often humans. (But when it is not, sometimes research with animals will suggest new and revealing tests with people, as in Silva et al., 2005.) Especially productive are cases in which rather than a simple yes/no answer, rich functional relationships between dependent and independent variables can be sought. Instead of setting up one-off critical tests that members of a species either pass or fail, more progress may be made by breaking a broadly defined capability down into components, asking which are shared among species, and under what conditions and why. One way to resist the seductions of anthropomorphism or folk psychology is to keep in mind that animals may solve problems in very different ways than we do or believe we do. What Tinbergen and Skinner taught us about the causes of behavior is an indispensable part of understanding the cognitive mechanisms underlying that behavior. Finally, Fig. 4 is not meant to be reminiscent of Wilson's (1975) infamous depiction of the biological sciences swallowing up the behavioral sciences. Rather, it is meant to indicate that comparative cognition intersects with nearly all the other subfields of cognitive science and the biology of behavior and that exploiting and nourishing those connections, and teaching our students to do the same, is an essential part of the future of the field.

Acknowledgements

Preparation of this article was supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada. Many thanks to Caroline Strang, who did all the work on the survey presented in Figs. 1–3. I am deeply grateful to the members of the Comparative Cognition Society for the honor represented by the invitation to give the 2008 Master Lecture on which this article is based and especially honored by the contributions of Karen Hollis and so many other students, colleagues, and friends to the Society's 2008 conference and this wonderful special issue.

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