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Comparative Cognition: Past, Present, and Future

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Abstract

Comparative cognition is the field of inquiry concerned with understanding the cognitive abilities and mechanisms that are evident in nonhuman species. Assessments of animal cognition have a long history, but in recent years there has been an explosion of new research topics, and a general broadening of the phylogenetic map of animal cognition. To review the past of comparative cognition, we describe the historical trends. In regards to the present state, we examine current “hot topics” in comparative cognition. Finally, we offer our unique and combined thoughts on the future of the field.

“Man with all his noble qualities... still bears in his bodily frame the indelible stamp of his lowly origin.”

Charles Darwin

“Intelligence is based on how efficient a species became at doing the things they need to survive.”

Charles Darwin

Comparative psychology was born from the idea that there are psychological qualities, attributes, and processes that are shared across species, likely in part because of our common biology and histories. Darwin noted that species shared not only a biological history (first quote above) but also perhaps a psychological one and that the psychological evolution of species might well select for increases in intelligence, primarily as such intelligence would afford adaptation of minds as well as bodies to changing environments (second quote).

Comparative psychology is now well into its second century, is thriving as an area of inquiry

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Portions of this paper were prepared to mark the 50th anniversary of Bitterman’s (1960) “Toward a comparative psychology of learning” and were presented in an American Psychological Association symposium organized following Bitterman’s death to honor his many career contributions.

in the social sciences, and it has contributed to a fuller understanding of the principles above.

What is the state of comparative psychology as it pertains to issues relevant to the field of Cognition? This was the mission we were given, to provide a relatable and concise answer regarding the (relatively brief) history, current status, and future directions for the area of research commonly called comparative cognition. It is a daunting mission, in part because it is highly unlikely that any two comparative psychologists writing such an article would come to the same conclusions. The diversity of opinions on what we, as comparative psychologists interested in cognition, do well, and on what is, and should be, our primary focus is likely very large. And so we began the effort by recognizing that the best way of providing something of value was to not have one opinion, or even two. What you read here is an attempt to present coherently (we hope!) the opinions of four comparative psychologists at different points in their careers. Parrish is a graduate student nearing completion of her doctoral studies, Perdue is an assistant professor a few years out of graduate school, Beran is a mid-career researcher, and Washburn is a senior scientist. Each of us brings our own experiences and our own perspectives to this task. Because of our shared interests and shared resources as researchers working with primates, this means we also will bring certain biases.

We begin with an historical overview of comparative psychology and its contributions to cognitive science. We then survey the field today with regard to what topics are within the purview of the field, where those data are reported, and what changes in this field have occurred in just the past couple of decades. Our goal here is not to provide a comprehensive overview of every species tested in every area of comparative cognition but rather to give the reader some sense of what the current field of comparative cognition entails. Finally, we offer the unique perspectives we each have on what the future of this field should be and why comparative psychology has such a promising future in furthering our understanding of the cognitive sciences.

A (Relatively Brief) History of Comparative Psychology

Knowledge regarding the animal mind, like knowledge of human minds other than our own, must come by way of inference from behavior. Two fundamental questions then confront the comparative psychologist. First, by what method shall he find out how an animal behaves? Second, how shall he interpret the conscious aspect of that behavior? (Washburn, 1908, p. 4)

One would stimulate little debate by calling Darwin's (1871) *Descent of Man* (or perhaps his *Expression of the Emotions in Man and Animals* published the following year) the first textbook of comparative psychology, although the birthday of psychology itself as a separate scientific discipline is generally accepted as 1879, and although one can cite much earlier reports of animal behavior that include some aspects of cognition (for example, Aristotle's *History of Animals*). The point here is that the history of comparative psychology is about as long as the history of psychology itself. Shortly after Professors Wundt, James, Hall, and others established the laboratories, wrote the influential books, and founded the academic departments, scholarly journals, and professional organizations that defined the new

discipline, some of their academic offspring were describing the methods and findings of psychology with respect to animal behavior and animal consciousness. Noteworthy early contributions to this field include classic publications by Romanes (1882, 1883), Morgan (1894), Thorndike (1898, 1911), Small (1900, 1901), Mills (1899), Hobhouse (1901), von Uexküll (1957), and numerous contributions by Yerkes (which we represent with citation of his first book, *The Dancing Mouse* (1907), that he envisioned as a kind of laboratory manual for courses in comparative psychology, comparable to supplements on frog physiology that were once common in courses on comparative anatomy).

As indicated by the quotation above, we have taken Margaret Floy Washburn's (1908) influential *The Animal Mind: A Text-Book of Comparative Psychology* as a starting point for our discussion. Washburn's textbook was obviously not the first publication in comparative psychology; indeed, even in its first edition, Washburn referenced more than 400 studies, including the contributions cited above and many others that would properly be classified as comparative psychology. We highlight the importance of *The Animal Mind* in the history of comparative cognition because of its impact. Updated through four editions, the last published in 1936, Washburn's text has been a highly influential reference for generations of comparative psychologists. Even in the 1957 second edition of his classic *A History of Experimental Psychology* Boring described (1929), *The Animal Mind* as "the classical text" (pg. 659). But it is not just the longevity of Washburn's synthesis and review that encourages us to highlight its historical importance; we also recognize the unapologetic boldness with which Professor Washburn approached the topics of animal cognition—including animal consciousness—without deviating from the experimental method or the reliance on behavior as the source of our data. While acknowledging the methodological difficulties associated with the study of animal minds, Washburn steadfastly defended that these difficulties are not different in kind (although they may be in degree) than the challenges of studying mental processes in our own species.

Must we accept the statement that no knowledge whatever of the animal mind is attainable? If so, we must also admit that human psychology is impossible. Our acquaintance with the mind of animals rests upon the same basis as our acquaintance with the mind of our fellow-man; both are derived by inference from observed behavior. The actions of our fellow-men resemble our own, and we therefore infer in them like subjective states to ours: the actions of animals resemble ours less completely, but the difference is one of degree, not of kind....The mental processes in other minds, animal or human, cannot indeed be objectively ascertained facts; the facts are those of human and animal behavior; but the mental processes are as justifiable inferences as any others with which science deals. (Washburn, 1908, p. 23)

Margaret Floy Washburn's *The Animal Mind* also serves to illustrate *why* there is a comparative psychology. Whereas her own motivation to write the textbook stemmed from her great love of animals and nature (Washburn, 1930), the volume is a comprehensive, process-focused review of the behavioral evidence for mental activity associated with sensation and perception, attention, learning, memory, reasoning, tool use, affect and motivation. Within each topic, a wide range of species get discussed—amoebas, ants, bees,

caterpillars, cats, chickens, chubs, clams, cockroaches, cows, crabs, crayfish, dogs, dragonflies, earthworms, elephants, flies, frogs, goldfish, grasshoppers, guinea pigs, horseshoe crabs, jellyfish, lancelets, leeches, mice, minnows, monkeys, pigeons, pike, planarians, potato beetles, raccoons, rats, salamanders, sea anemones, seurchins, shrimps, silkworms, snails, spiders, tortoises, wasps, and water beetles. The clear goal of these discussions is to analyze evidence of animal minds, wherever this evidence is manifest in behavior, irrespective of species. The goal of comparative psychology is psychology, and the assumption (given that humans are not unique in the capacity to behave) is that psychology is inherently comparative.

Thus, through this point in history, we can trace the field's efforts to study, to describe, to explain, and to predict the behavior of a wide range of nonhuman animals, as well as attempts by many of these comparative psychologists to make reasonable inferences about the unobservable cognitive or mental processes that underlie some of these behaviors. A comprehensive review of the history of comparative psychology, or even just comparative cognition, is beyond the scope of this article -- and is, in any case, unnecessary as there are already numerous excellent scholarly reviews in the literature. For many of these, we are indebted to the careful scholarship of Donald Dewsbury (2013). Thus, the history of the discipline has been told chronologically (Dewsbury, 1984; Wasserman, 1997), biographically (Innis, 1998), geographically (Dewsbury, 1992; Malakhovskaya, 1992; Takasuna, 2010), conceptually (Wasserman, 1993), and as an epic tale of triumphs and tragedies (Dewsbury, 1992; Lockard, 1971).

We have previously discussed the history of comparative psychology, using apparatus innovations as milestones in this journey (Washburn, Beran, Evans, Hoffman & Flemming, 2013; Washburn, Rumbaugh & Putney, 1994). A disadvantage of this approach would be any implication that comparative psychology required apparatus. Certainly this is not true, and a great number of outstanding contributions to the comparative literature relied on little or no apparatus (unless, in the playful spirit of the famous comparative psychologist Emil Menzel one chooses to refer to natural objects like trees and rivers as apparatus; see Menzel, 1969). An advantage of organizing a discussion of the history of comparative psychology (or any branch of psychology) using developments of apparatus and paradigms is that it emphasizes the way that research answers are inextricably tied to the methods used to ask the research questions. That is, the study of human and nonhuman animal minds depends critically on how "mind" is measured. This is the first part of the Washburn (1908) quotation that began this section of the present article, and remains as true now as it was a century ago. Thorndike's (1898) views on animal intelligence were driven by clear data showing trial-and-error learning as a function of the consequences of behavior; however, these data were constrained by the selection and design of the problem-box apparatus which prevented Thorndike's animal subjects from learning any way other than by trial-and-error. Similarly, the operant chamber or Skinner box was an elegant and powerful apparatus for investigating changes in the rate of responding under highly simplified and controlled conditions. Is it really any surprise that simple associative principles could describe and predict behavior in these contexts, where only simple competencies could be manifest?

Contemporary comparative research at many laboratories uses computer-based apparatus (what we have called the “Rumbaughx” in honor of comparative psychologist Duane Rumbaugh who was, and remains, a pioneer in the use of computers to study cognition comparatively; see Washburn et al., 2013). This computerized hardware and associated software allows animals to respond to a wide range of stimuli and game-like task demands. The paradigm allows the testing of animals under conditions that mimic those for Thorndike’s cats or Skinner’s pigeons (for example); but the paradigm also yields possibilities for demonstrating cognitive competencies that are not easily described by classical and operant conditioning—as indeed previous investigators (Kohler, 1925; Tolman, 1932, 1948) have shown with their own apparatus innovations.

Because the Rumbaughx provides an apparatus, task software, and set of research procedures for studying cognition in nonhuman animals that are the same as the apparatus, task software, and research procedures used for studying cognition in humans, there is unsurpassed comparability and opportunity to argue, with appropriate tentativeness and precautions and convergence, from analogy. This speaks to the second part of Washburn’s (1908) quote, and the defense that she and many others (Burghardt, 1985; Rumbaugh, 1994) have repeatedly made about the heuristic value of a critical anthropomorphism. Given the strong opposition that many comparative psychologists, from Thorndike (1911) to Wynne (2007) have directed toward anthropomorphism, quite often with justification, perhaps it would be better to describe the position advocated by Washburn (1908) and others as “critical comparativism.” That is, it seems important to use the same standards for inferring cognitive processes from behavioral evidence, whether the subjects of interest are human or nonhuman. As Wynne (2007) asks in the title of his paper, “What are animals?” Margaret Floy Washburn would respond, “Humans are animals” and the present authors would concur—as indeed would Professor Wynne. In every case, Wynne’s cautions about the perils of inference are well taken and important, as are the historical lessons about clever animals and the role of cuing in animal performances (Pfungst, 1911), and so forth. But these are equally potent cautions with respect to studies of human cognition as of animal cognition.

The “Rise” of Comparative Cognition

Although Beach (1950) famously decried the state of comparative psychology, Dewsbury (1984, 1998, 2000) has contested this point. Apparatus innovations by Yerkes, Tolman, Lashley, Harlow and others helped to sustain comparative psychology through the middle of the last century, the heyday of behaviorism in North America. Nevertheless, Beach’s criticism that comparative psychology was insufficiently comparative (i.e., it studied too few species, and too few topics within psychology) had plenty of bite, and rang too true. A decade after Beach declared “the snark was a boojum,” Bitterman (1960) reached the same conclusion in a classic paper, “Toward a comparative psychology of learning.” In this publication, Bitterman described two broad strategies for comparative investigation: one involved testing multiple species on one or more standard tests, well-illustrated by the research traditions of Harlow, Rumbaugh and others (see also Maier and Schneirla, 1964); the other involved development of a comprehensive theory (of learning, for example) in two different species, with the goal of comparing the theories rather than the animals per se. In support of this latter strategy (and demonstrating the creativity that marked his career),

Bitterman proceeded to describe apparatus innovations that made it possible to include studies of fish, crabs, blowflies, and earthworms into a truly comparative psychology of learning.

Bitterman examined publications in the decade following Beach (1950) and concluded that there was no change in the pattern of findings: about 60% of the papers reported studies with rats. Indeed, Bitterman noted, if one examined additional journals and counted only those studies on learning, about 90% had rats as the subject. On the fiftieth anniversary of Bitterman (1960), we examined the recent literature to determine whether comparative cognition was doing any better at being truly comparative—that is, in investigating a range of species and phenomena. Figure 1 shows the result of our examination of the decade 2001–2010. Note the diversity of animals being studied, although there are still many publications in which rats or pigeons are the species of choice. These studies appear primarily, but not exclusively, in *Journal of Experimental Psychology: Animal Behavior Processes* and *Journal of the Experimental Analysis of Behavior* with investigations of the behavior and cognition of primates and other animals appearing predominantly in the other two journals surveyed. Note that Shettleworth (1993) had echoed Beach's (1950) criticisms by questioning whether comparative cognition was truly comparative when she examined three of these same journals for the 2005–2007 period and reached a similar conclusion to the one we report here (Shettleworth, 2009).

As noted above, comparative psychology has long embraced the challenge of studying animal intelligence and animal minds, and this literature is fraught with both accomplishment and failure—just as is characteristic of studies of these same topics with human animals. And just like the landmark studies of comparative psychology that emerged in the literature a decade or two after the first studies of human psychology, it was a decade or two after the so-called “cognitive revolution” in psychology first began before publications about cognitive animals boldly appeared (e.g., Honig & Fetterman, 1992; Hulse, Fowler, & Honig, 1978; Roitblat, Bever, & Terrace, 1984). The 1990s saw the blossoming of a comparative cognition, and the introduction of new societies and journals dedicated to that area of research. Prior to this time, the main outlets for this research were the *Journal of Comparative Psychology* (formerly the *Journal of Comparative and Physiological Psychology*), *Animal Learning and Behavior* (now *Learning and Behavior*), and the *Journal of Experimental Psychology: Animal Behavior Processes* (now the *Journal of Experimental Psychology: Animal Learning and Cognition*), although by no means were these journals publishing large numbers of papers in comparative cognition. Since the 1990s, new journals have emerged, including *Animal Cognition*, *Comparative Cognition and Behavioral Reviews*, the *International Journal of Comparative Psychology*, and *Animal Behavior and Cognition* (soon to be released). In addition, reports about animal cognition appeared in journals such as *Science*, *Nature*, *Psychological Science*, *Cognition*, *Animal Behaviour*, and *Psychonomic Bulletin & Review*.

How does comparative cognition fare with respect to the second criticism levied by Beach (1950), Bitterman (1960), and others (i.e., too few different problems studied)? It would be difficult to convey accurately the raw numbers of articles published over the last 20 years, given that many research reports can be difficult to classify as being about cognitive

processes in animals versus other processes, but we made an attempt to provide approximate numbers for some topics that we will discuss in more detail, if only to highlight the trend for increasingly greater numbers or lesser numbers of such reports during this time. Figure 2 presents the numbers of papers in successive 2-year periods over the past 20 years from the journals *Animal Cognition* and the *Journal of Comparative Psychology*. As can be seen, in general there have been increases in each of these areas, although it is also easy to see that broader topic areas such as spatial cognition are represented much more in these literatures than more specific topic areas. Before one assumes that a topic like spatial cognition has dominated recent comparative cognition, one needs to view that area against the broader topic of social cognition, as shown in Figure 3. Clearly, social cognition in animals is a dominant theme in current comparative psychology (although, of course, spatial cognition is just one aspect of the larger area of physical cognition that is sometimes contrasted against social cognition). We examined the social cognition area in even greater detail, so that we might provide some means of representing the diverse range of species that are tested in contemporary comparative psychology in one dominant area of research. Table 1 presents these data for just the last 5 years and just in the journal *Animal Cognition*, which represents the broader comparative literature and also indicates how robust the investigation of the social-cognitive lives of animals has become.

Beyond just these example areas, what is the range of topics covered in comparative cognition? The answer is simple – the same range covered in human cognition. Take any Cognitive Psychology textbook that you can find, and flip through the chapters (and subchapters within chapters), and it is likely that many of the processes or phenomena you see there are similar to the processes that have been or are being studied in nonhuman animals. Typically, these things will be studied using primates (and, more specifically, in most cases this will be apes or rhesus monkeys, and in fewer cases perhaps capuchin monkeys or baboons), rats, or pigeons. We know a lot about how stimuli are perceived, how they are processed using attention resources, how they are categorized, stored in memory, retrieved, and used to guide decision making in both social and physical domains. Excellent volumes now exist as starting points to get deeper into the theoretical and empirical aspects of these areas (Bekoff, Allen, & Burghardt, 2002; Maestripieri, 2003; Shettleworth, 2009; Tomasello & Call, 1997; Vonk & Shackelford, 2012; Zentall & Wasserman, 2012). The information processing approach that has been so influential in human cognitive psychology has had equal influence in comparative cognition, although it has been far less well integrated into a holistic perspective as has been done in human psychology. And, most recently, advances in neuroimaging techniques and other neurobiological approaches (for example, transcranial magnetic stimulation, PET, MRI, DTI) have been applied to tests of nonhuman behavior and cognition so those results could be related back to work with humans (Hopkins, Russell, & Schaeffer, 2012; Hopkins, Tagliabata, Russell, Schaeffer, & Nir, 2010; Marzluff, Miyaoka, Minoshima, & Cross, 2012; McCoy & Platt, 2005; Nieder, 2009; Nieder, Diester, & Tudusciuc, 2006; Nieder & Miller, 2003; Phillips & Hopkins, 2012; Sawamura, Shima, Tanji, 2002; Schenker, Desgouttes, & Semendeferi, 2005).

One thing that is worth noting (and that we thank one of our anonymous reviewers for pointing this out) is that much of what is studied in comparative cognition is not found in

human cognitive psychology texts. For example, there is little mention of numerical cognition in standard human cognition texts (although language and other symbolic processes often are featured). There is also little coverage of social cognitive processes, or the emergence of capacities such as self-recognition or metacognition, despite those being studied in great detail in nonhuman animals. This suggests that work remains to be done integrating comparative cognition into the broader cognitive science framework, although some recent volumes have made progress in that area (Zentall & Wasserman, 2012).

Comparative Cognition – Then and Now

The comparative cognition of 20–30 years ago was dominated by some still-popular research questions (perception, attention, memory), but many of the focal topics have changed. Critically, there has been a shift towards more so-called “higher-order” topics of cognition that might reveal important similarities and critical differences between human and nonhuman cognition. We outline just a few key topic areas within comparative cognition here. Thirty years ago (and more), one of the most hotly debated questions pertained to whether animals had anything remotely resembling the language that is ubiquitous among humans (Herman, Richards, & Wolz, 1984; Gardner & Gardner, 1969; Savage-Rumbaugh, 1986; Savage-Rumbaugh et al., 1993; Schusterman & Gisinger, 1988). This was an extremely contentious and high-profile area of research (Roitblat, Herman, & Nachtigall, 1993; Seidenberg & Pettito, 1979; Terrace et al., 1979). Today, there is a general consensus in the field that, given the right early environment, some species develop communicative capacities that show many of the basic but important qualities of human languages, albeit not all of those hallmarks, and perhaps not the most critical ones. Very little research with “animal language” projects remain, although a number of the animals involved in that research are still participating in studies of comparative cognition, helping to shed light on the impact of language-immersed enculturation on development and the emergence of other cognitive competencies (Beran et al., 2000; Beran, Smith, & Perdue, 2013; Beran, Washburn, & Rumbaugh, 2007; Bodamer & Gardner, 2002; Jensvold & Gardner, 2000; Menzel, 1999; Menzel, Savage-Rumbaugh, & Menzel, 2002; Pepperberg & Carey, 2012). Rather, recent research efforts have focused on other aspects of referential communication by animals (Cartmill & Byrne, 2010; Herman et al., 2001; Leavens, Hopkins, & Thomas, 2004; Miklosi et al., 2005; Pepperberg, 2002, 2010, 2013; Tagliatalata et al., 2009).

Twenty to thirty years ago, the question of self-awareness and self-recognition was a hot topic (Gallup, 1970; Suarez & Gallup, 1981). In attempts to understand what animals understand of their own minds and the minds of others, mirror self-recognition and theory-of-mind studies were highly publicized and heavily debated (Bard et al., 2006; Epstein, Skinner, & Skinner, 1981). Recently, similar studies have been conducted using these tests with a variety of species (Delfour & Marten, 2001; Pepperberg, Garcia, Jackson, & Marconi, 1995; Plotnik, de Waal, & Reiss, 2006; Prior, Schwarz, & Güntürkün, 2008; Reiss & Marino, 2001; Roma et al., 2007). A closely related capacity involves understanding the mental states of others as separate and potentially different from one’s own mental states - what is referred to as theory of mind. Comparative approaches to theory of mind examine which species might achieve a human-like level of ‘mind-reading’, or how other capacities

such as behavior-reading might also be beneficial for understanding and predicting the actions of conspecifics (Hare, Call, & Tomasello, 2001; Leslie, 1987; Lurz, 2011; Penn & Povinelli, 2007; Premack & Woodruff, 1978).

There has been a shift to greater emphasis on understanding how animals see conspecifics and their role in cooperative or competitive contexts and on how a theory of mind would reveal itself in social interactions, including those in which deception or “mindreading” would be necessary (Bugnyar, 2007; Bugnyar & Heinrich, 2005; Call, Brauer, Kaminski, & Tomasello, 2003; Kaminski, Call, & Tomasello, 2008; Krachun, Call, & Tomasello, 2009; Krachun, Carpenter, Call, & Tomasello, 2010; Tempelmann, Kaminski, & Liebal, 2011; Tomasello, Call, & Hare, 2003; Tomonaga, Uwano, Ogura, & Saito, 2010). Organisms may engage in passive or active forms of deception via withholding valuable information from group members (for example, about the location of a foraging site) or providing faulty information (for example, alarm calls in the absence of a predator), respectively (Byrne & Whiten, 1992; Cheney & Seyfarth, 1990). As one might expect, there remains a vigorous debate about what these kinds of tests exactly reveal about self-awareness and theory of mind in animals (Call & Tomasello, 2008; Horowitz, 2011; Penn, Holyoak, & Povinelli, 2008; Roberts & MacPherson, 2011; Udell & Wynne, 2011).

A related topic that was nonexistent in the field of comparative psychology 20 years ago regards metacognitive abilities in animals. This area focuses on whether nonhuman animals monitor their own cognitive states and can seek information, monitor uncertainty, and even adjust their estimates of confidence in their own knowledge. Although there have been many suggestive reports, particularly with primate species (Beran & Smith, 2011; Call, 2010; Hampton, 2001; Kornell, Son, & Terrace, 2007; Smith, Beran, Redford, & Washburn, 2006; Smith, Redford, Beran, & Washburn, 2010; Smith, Shields, Schull, & Washburn, 1997; Suda-King, 2008), but also some non-primate species (Adams & Santi, 2011; Foote & Crystal, 2007; Smith et al., 1995), this too is a contested area of research with an active ongoing debate about the appropriate interpretation of these programs of research and the data they generate (Carruthers, 2008, 2009; Crystal & Foote, 2009; Hampton, 2009; Kornell, 2009, 2013; Le Pelley, 2012; Jozefowicz, Staddon, & Cerutti, 2009; Smith, 2009; Smith, Beran, Couchman, & Coutinho, 2008).

Twenty years ago, another “hot” topic was whether animals could count, and whether number even was a relevant stimulus dimension to which animals responded (Boysen & Capaldi, 1993; Davis & Perusse, 1988; Pepperberg, 1994). At the time, the jury was out, and it seemed difficult to know how salient numerosity was for animals (Davis & Memmott, 1982). We now know fairly definitively that number is salient, and that animals make use of number in many circumstances (Brannon & Roitman, 2003; Gallistel & Gelman, 2000; Pepperberg, 2006). Performances of animals in various quantitative tasks can look very much like the performances of young children, and in some cases can even be quite similar to the performance of adult humans (Cantlon & Brannon, 2006; Cordes, Gallistel, Gelman, & Whalen, 2001; Menzel, 1960; Tomonaga & Matsuzawa, 2002; Whalen, Gallistel, & Gelman, 1999). But, we also know that animals do not count, at least not without massive efforts to instill such counting routines (Beran & Rumbaugh, 2000; Boysen & Berntson, 1989; Matsuzawa, 1985; Pepperberg, 1994, 2012; Pepperberg & Carey, 2012; Pepperberg &

Gordon, 2005), and even then performance is underwhelming compared to what a 4- or 5-year-old child can do (Gelman & Gallistel, 1978). The more recent controversy has been about the nature of nonverbal representation of number and quantity, and whether animals require and access one or two “core systems of number,” and a large amount of research has been conducted as part of this debate (Beran, 2004, 2007, 2008, 2012; Beran & Beran, 2004; Feigenson, Dehaene, & Spelke, 2004; Gomez-Laplaza, & Gerlai, 2011; Hanus & Call, 2007; Hauser, Carey, & Hauser, 2000; Jordan & Brannon, 2006; Nieder, 2005; Piffer, Agrillo, & Hyde, 2012; Perdue, Talbot, Stone, & Beran, 2012; Rugani, Cavazzana, Vallortigara, & Regolin, 2013; Tomonaga, 2007; Ujfalussy, Miklósi, Bugnyar, & Kotrschal, in press; Vonk & Beran, 2012).

In a trajectory that mimics the evolution of research into human memory, the study of animal memory has diversified through the years. Assessments of memory for short and long durations remain a focus of priority in comparative cognition, in large part because of their importance in many relevant areas of intervention with different groups of humans (for example, Alzheimer’s patients). Early research was focused on general memory processes, such as working and reference memory (Olten & Papas, 1979; Olten & Samuelson, 1976), but this focus has gradually diverged into several areas including, but certainly not limited to, spatial, episodic and prospective memory (Balda & Kamil, 1992; Balda & Wiltscheko, 1995; Bednekoff, Balda, Kamil, & Hile, 1997; Checke & Clayton, 2012; Clayton & Dickinson, 1998, 1999; Clayton, Yu, & Dickinson, 2003; Griffiths, Dickinson, & Clayton, 1999; Perdue, Evans, Williamson, Gonsiorowski, Beran, 2013; Perdue, Snyder, Pratte, Marr, & Maple 2009; Perdue, Snyder, Zhihe, Marr & Maple, 2011). Accordingly, there has been a fairly stable representation of “general” memory in the literature, while areas such as episodic and prospective memory have increased in recent years (see Figure 2).

Episodic memory is memory for personally experienced events (Tulving, 1972). There has been an intense debate about whether animals are capable of experiencing the auto-noetic feelings associated with the true recollection of a personally experienced episode (Wheeler, Stuss & Tulving, 1997). Thus, animal researchers have focused on what is referred to as episodic-like memory, or memory for the what-where-when of an event (Clayton & Dickinson, 1998; Correia, Dickinson, & Clayton, 2007; Feeney, Roberts, & Sherry, 2009; Griffiths et al., 1999; Hampton, Hampstead, & Murray, 2005; Hoffman, Beran, & Washburn, 2009; Menzel, 1999). This has spurred a great deal of research that includes a continued pursuit of the idea of agency and awareness.

Prospective memory refers to remembering to engage in some behavior at a specified time in the future (Cheke & Clayton, 2012; Clayton, Salwiczek & Dickinson, 2007; Schacter, Addis, & Buckner, 2007). This area of research is still developing in the comparative literature, but there is growing evidence that animals show similar, albeit less complex, forms of prospective memory and planning ability to that observed in humans (Beran, Perdue, Bramlett, Menzel, & Evans, 2012; Perdue, Evans, Williamson, Gonsiorowski, Beran, 2013; Raby & Clayton, 2009; Wilson & Crystal, 2012; Wilson, Pizzo & Crystal, 2013).

Finally, spatial memory, or more broadly, spatial cognition, has spurred a great deal of research within animal cognition (Gould, 1986, 1990; Gresack, & Frick, 2003; Healy, Braham, & Braithwaite, 1999; Kelly & Gibson, 2007; Lacreuse, Herndon, Killiany, Rosene, & Moss, 1999; Langley, 1994; Lipp et al., 2001; MacDonald, 1994; Morris, Garrud, Rawlins & O'Keefe, 1982; Washburn & Astur, 2003). From the early work of Tolman (1932) suggesting that rats constructed cognitive maps, there has been substantial interest in how animals navigate through the world and remember and respond to information about location. Spatial cognition has remained a constant presence in the animal literature for the last 20 years and continued research explores how neural systems underlie these abilities and how ecological pressures have shaped these processes in many species (Gaulin & Fitzgerald, 1989; Sherry, Jacobs & Gaulin, 1992).

Comparative Social Cognition

Another area of research that is dominant in comparative cognition pertains to social cognitive processes. Social cognition consists of the suite of cognitive skills used for interacting with other individuals, including individuals that are related and nonrelated, opponents and collaborators. The complexity of a species' social group will dictate the level of cognitive skill required to effectively navigate one's social world. For species that form relatively long-term, complex, and stable social groups comprised of multiple individuals of variable social status, the ability to recognize individuals and their relationships is a key component to social living. Although early experimental psychology primarily focused on the cognitive capacities of animals in isolation of their larger social network, the shift to a comprehensive approach to cognition, including both physical and social domains has become highly emphasized. Within comparative psychology and ethology, the study of social cognition has transformed over the past several decades into a multi-faceted and integrative field that incorporates multiple species and a variety of experimental approaches, including field and laboratory studies (for reviews, see Shettleworth, 2010; Zentall & Wasserman, 2012).

The in-depth study of social cognition gained momentum with early long-term field studies of nonhuman primates that inhabit relatively large and complex social groups (Cheney & Seyfarth, 1990; de Waal, 1982; Goodall, 1986; Kummer, 1982). Several hypotheses regarding the evolution of higher-order cognitive abilities arose from this work, suggesting that intelligence among highly social species was selected for in response to an unstable and fluctuating social environment in comparison to the animals' relatively static physical world. The Social Intelligence Hypothesis predicts that the evolution of intelligence among primates is a direct result of group living with multiple individuals of varying relations (Humphrey, 1976; Jolly, 1966). The related Machiavellian Intelligence Hypothesis suggests that the unique nature of competition among conspecifics drove the evolution of primate intelligence as individuals not only cooperate with one another, but also must compete and outmaneuver their social counterparts (Byrne & Whiten, 1988). The growing literature assessing social cognition among non-primate mammals and birds suggests that social theories of intelligence may not be exclusive to primates. Additionally, whether social and physical cognition are truly distinct entities is an important and related question within this field. It has been suggested that cognition evolved in response to a variety of selective

pressures (both social and nonsocial), and social cognition reflects the application of a larger and more general suite of cognitive capacities to explicitly social settings and problems (Gigerenzer, 1997; Healy & Rowe, 2007; Holekamp 2007; Shettleworth, 2010).

We have space here to provide only a selective list of key topic areas within social cognition, and then consider how the field has developed and transformed over the past ten years. An organism's ability to identify and recognize conspecifics and their relationships (related/nonrelated; dominant/subordinate; ally/opponent; in-group/out-group) is an important factor in socially living species. Additional areas of research within social cognition include cooperation, social learning, communication, deception, and theory of mind.

Individual recognition and relationship classification has been a large focus of social cognition studies among a wide variety of species, ranging from studies of mother/offspring recognition to third party relationships and transitive inference. Methodologies within this topic area are diverse (for example, face perception tasks, field playback experiments, etc.), providing information on whether organisms require and subsequently utilize individual recognition, what they understand about the nature of their own relations and others' relations within and outside of their social hierarchy, and how this knowledge translates to novel settings and individuals (Colgan, 1983; Falls, 1982; Holmes & Sherman, 1983).

Beyond individual recognition, social cognition investigates the relationships that develop between conspecifics and how information transfers between individuals. Many species (for example, nonhuman primates, dolphins) are known for their ability to form coalitions and alliances that are often maintained through long-term affiliative interactions (Connor, Smolker, & Richards, 1992; de Waal, 1982; Goodall, 1986; Packer & Pusey, 1982). Studies on cooperation investigate whether, and under what circumstances, species work together with related and nonrelated individuals, including topic areas such as mutualism, reciprocity, and altruism (see Brosnan & Bshary, 2010; Dugatkin, 1997). Social learning, or the transfer of information between conspecifics, also may occur among group-living species, which would facilitate the rapid transfer of information within a social group. Social learning studies examine a range of interactions including learning basic information from others via local or stimulus enhancement or more interactive and directed learning via emulation (replicating end-states) and imitation (copying actions) (Byrne, 2002; Heyes, 1994; Whiten & Ham, 1992; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). In some species, social learning may culminate into more advanced culture or culture-like traditions that are also a key area of inquiry in comparative cognition (Krützen, Mann, Heithaus, Connor, Bejder, & Sherwin, 2005; Whiten et al., 2002).

How social species transfer information between individuals via multiple sensory modalities (visual, auditory, olfactory, tactile) is investigated within the field of communication (Bradbury & Vehrencamp, 1998). Research investigating the production and reception of communicative information (for example, alarm calls) provides rich information on the type of material conveyed between individuals, and the level of control that an organism might have over such interactions (Cheney & Seyfarth, 1990; Owren & Rendall, 1997). Communication also may be gestural in nature and is often studied as the precursor to

human language, leading to the investigation of language or language-like abilities in nonhuman species (Heimbauer, Beran, & Owren, 2011; Leavens & Hopkins, 1998; Rumbaugh, 1977; Savage-Rumbaugh, 1986).

Future Research Goals for Comparative Cognition

Comparative cognition needs to continue on a three-pronged path. First, it must continue to broaden its comparative approach – more species, more tests, and more replication. The focus should not be only on the comparative cognition of primates (or rats, or pigeons) but on the comparative cognition of all animals, even though, of course, individual research teams may focus more heavily on some species than others (as is true with our own research with primates). Our interest in any psychological phenomenon should not be through how it manifests in a single assessment or single test, but how it manifests across contexts and across tests, thereby providing a more robust database on the cognitive abilities of animals. And, our confidence in what animals can (and cannot) do can only grow when we replicate the singular findings that often are held as benchmarks for the cognitive capacities of whole species. It is through replication that we can more confidently apply descriptions using cognitive constructs to the behavior of nonhuman animals. This is not a unique issue to comparative psychology, but to science in general, and is an issue that is gaining strength through increased emphasis on valuing replication (including new initiatives to report replication attempts in journals such as *Perspectives on Psychological Science*), and an awareness of how often research reports are difficult to replicate and may be false (Ioannidis, 2005).

Second, the field of comparative cognition must intensify its understanding of the processes that underlie performances that, at the surface, appear to be cognitive in their manifestation. This means that it is not simply enough to show what animals can (or cannot) do, but rather to devise clever methods that allow us to understand how and why they do the things that they do. Here, the measures used must be sensitive to delineating the mechanisms that underlie behavior and must be sensitive to the proper contexts in which these behaviors are likely to occur in the natural settings in which animals evolved and currently live.

Third, the field of comparative cognition must continue to look across research topics to broader research areas. This has happened in the past, as when ape language studies complemented more ethologically based assessments of the communicative abilities of animals, including in terms of referential communication (Seyfarth, Cheney, & Marler, 1980; Zuberbuhler, Cheney, & Seyfarth, 1999). Another example is the broadening of the search for counting behavior to the more inclusive understanding of how magnitudes and quantities of all types are represented by a variety of species (Brannon & Roitman, 2003; Gallistel & Gelman, 2001; Pepperberg, 2006). Today, we take the perspective that many of the cognitive skills that we study in animals may fall under broader areas than we tend to study. For example, our research team sees the value in approaching our individual topic areas (for example, self-control, attentional control, memory retrieval, planning, prospective memory, perceptual processing and decision-making) as they relate to the notion of behavioral inhibition, and the emergence of cognitive control. This “forest” instead of “trees” approach has led to greater cross-talk among our team, and we expect it would do the

same for the field as a whole. For example, greater attention to what one means by “social cognition versus physical cognition” could help situate and maximize the value of data from a variety of tasks given to animals. Greater attention to the role of individual differences across research topics also could serve the same purpose (Matzel, Wass, & Kolata, 2011; Vonk & Povinelli, 2011), as could more focus on the ontogenetic emergence of any of the topics traditionally held as part of comparative cognition.

Our Individual Perspectives on the Future of Comparative Cognition

What should the future of comparative cognition be in general? Here, our opinions varied, and although we found some common ground, we also had unique perspectives that are outlined below. The reader will also recognize some familiar themes, some of which are now more than 100 years old.

Parrish

As the field advances, my hope is for the continuing development of a more inclusive and comprehensive construction of an animal’s psychology. As is common among most psychological literatures (including in our own current review!), physical and social cognition are typically subdivided and studied independently of one another. As we progress, I anticipate a more integrative outlook on these traditionally isolated areas of comparative cognition. Although this approach serves practical and functional purposes, we are beginning to see cross talk among these subfields, and this is exciting. Cognition results from the inevitable interplay between an organism’s physical and social domains; thus, in constructing the mental minds’ of others, we must study their psychology from a holistic perspective. Additionally, I suspect there will be a stronger emphasis on a multifaceted approach towards similar questions within comparative psychology, including both the inclusion of more animal species and a wider range of methodologies. By definition, comparative cognition strives to investigate the psychological mechanisms and behavioral manifestations among multiple species and, critically, how those compare and contrast with one another. Moreover, multiple methodological approaches to similar questions will help elucidate whether and how cognition differs between species and even among species. Thus, for the future, I anticipate a particular emphasis on issues of integration and collaboration within the field of comparative cognition.

Perdue

In the coming years, a priority within animal cognition will be to protect our science by rekindling and retaining the methodologically rigorous roots from which the field has grown. Early behaviorists were focused only on observable, overt behavior in an effort to establish a replicable science grounded in observation. The cognitive revolution opened the door for more in depth exploration of the cognitive processes underlying an animal’s behavior, but this door may be swinging too far open, allowing for too highly anthropomorphized and untestable suppositions about the causes of behavior. It is imperative that the field of comparative cognition remain rigorous in the scientific methodology and peer-review process to avoid the paradigmatic pendulum swinging too far to one side. Animals do not have to be identical to humans in all aspects to be fascinating

and worth studying. Additionally, with the rise of cognitivism, there seems to be a demonization of “associationism” within comparative psychology that is not only unnecessary, but potentially harmful to the field. Much of any animal’s behavior, including that of humans, can indeed be explained by principles of classical and operant conditioning. More focus should be made on how cognition overlays learning to yield the fascinating feats of some organisms, rather than a harsh dismissal of learning processes as if they are irrelevant to understanding animal behavior. The field will benefit from a greater focus on understanding the interactions and relation between learning and cognition rather than a swing towards fully embracing one while ignoring the other. By developing stringent methods that prevent cuing, avoiding overinterpretation of results, and focusing on cognition as complementary and supplemental to learning, the field of comparative cognition will continue to thrive and grow in the coming years.

Beran

The comparative perspective informs our understanding of human uniqueness as much as it does of humans’ relatedness to other animals’ psychologies. This is its purpose – to illustrate what we alone may be capable of in terms of our cognitive capacities by discounting those things that are not uniquely human, and then by looking at what remains. Comparative cognition needs to be agnostic. It needs to be objective. It cannot be driven by a desire to elevate (or reduce) the cognitive abilities of animals, per se, and it cannot be driven by ignorance of species’ unique perceptual and cognitive mechanisms, or by ignorance of the role of other, non-cognitive processes (such as associative learning) that complement or, in some cases, compete with cognitive ones.

The future of comparative cognition must be in the delineation and description of those processes that complement the associative processes which presumably account for so much of animal (and human!) behavior, but cannot account for all it. A comparative cognition that ignores the role of associative processes is like a theory of economic decision making that ignores what people really do and focuses only on what they should do, given that they “*must be* rational.” It would be like a physics that advances only the consequences of a general relativity without a special relativity.

Comparative cognition must embrace its “comparative” charter – we need more data, from more species. These data must come from species-fair tests, and from tests that are designed with a sensitivity to (and memory of) our mistakes of the past in terms of cuing animals (Beran, 2012). Comparative cognition must do a better job of recognizing the changes in cognition that occur within the lifespan of a given animal. We know beyond doubt that there is no single “human cognition.” There is the cognition of the infant, of the toddler, of the school child, of the human version of the white lab rat (college kids, age 18–22), of the adult, and of the aged. Cognitive psychology addresses these critical issues, in conjunction with developmental psychology, and comparative cognition must do the same. Some efforts have been made, but more are needed (see Thornton & Lukas, 2012).

We also run the risk of overselling the cognitive abilities of animals. We run the risk that, through over-inclusion, we may reduce the impact of finding human-like cognitive abilities in species or individuals for whom such evidence is truly informative about how those

abilities emerged in our species. In some cases, this over-inclusion is warranted. For example, it seems beyond question that nearly all species yet to be tested will show some sensitivity to the quantitative and even numerical properties of stimuli, given that all species tested to date have shown this. And, we see great similarities across species in the existence of memory stores, although the content and processes that access those stores is likely quite different, including for things such as episodic memory and future oriented behavior. But, the point is that comparative cognition serves little or no value if its goal becomes to work to admit as many species as possible into “the club” of thinking creatures. And, comparative cognition betrays its mission when it panders to the desires of the public who simply want to find that animals are “smart” so as to boost beliefs about the “worth” of that species. The value of any species should not be related to its intellectual ability, or to its similarity to how humans perceive and interact with the world, and a comparative cognition that takes that as its mission is misguided, and even dangerous. We have been down that road before, and the blatant anthropomorphism and over-interpretation (along with weak methodological designs that allowed for cuing of animals) set the stage for the strong pushback that was radical behaviorism. This risk still exists, and grows stronger whenever weak results are over-interpreted, and whenever animal behavior that has multiple possible causes is automatically assumed to be of the “highest form” that most closely approximates human behavior.

Washburn

There are tremendous benefits to the study of cognition comparatively. (As an aside, it is significant how much less controversial it feels to say that one studies animal cognition than to say that one studies animal *minds*—the former seems to allow one to be agnostic with respect to the question of consciousness! But are the terms really that different?) Humans surely categorize. Monkeys surely attend. Rats surely remember. Bees surely communicate. Even cats surely learn! Understanding the cognitive processes (concept formation, attention, memory, language, and so forth) that correspond to these behavioral statements and that may mediate stimulus-response relations must then embrace behavioral data across species. This is the strength and promise of contemporary “cognitive science,” which incorporates information from computer science and neuroscience and philosophy and psychology (cognitive, developmental, cross-cultural, and—yes—comparative). Moreover, there are opportunities for replication, for experimental control, and for convergence/divergence in the comparative method that are more elusive when studying cognition only in humans.

That said, a cognitive psychology that includes nonhuman animals is still cognitive psychology, and accordingly is subject to all the same criticisms and threats that have plagued cognitive research for the last five decades. Cognitive psychology, whether comparative or not, tends to be highly fractionated, phenomenon-driven, and theoretically circular. Cognitive psychologists, comparative or otherwise, sometimes forget that our constructs (such as attention, episodic memory) are shorthand for collections of behaviors as measured on specific groups of tests; rather, these constructs become reified, giving truth to Skinner’s (1985) criticism that cognitive psychologists treat descriptions as explanations and invent “explanatory systems which are admired for a profundity which is more properly called inaccessibility” (p. 42). Cognitive psychology, comparative or otherwise, has a self-confidence problem, and so runs to neuroscience or to applied fields for support whenever

someone challenges its necessity or utility. In truth, I believe that comparative strategies for cognitive research can help with all of these criticisms, helping to ground our theory and to challenge our assumptions. Moreover, I am encouraged by developments within cognitive psychology that suggest that some of the diverse and tangled threads are starting to form a coherent fabric: recent publications in the attention (Posner, 2012) and working-memory (Redick & Engle, 2011) literatures, for example, suggest that the answers are emerging to some complicated and long-asked cognitive questions. I believe that the team-science approach where groups of scholars tackle common questions using various tools, strategies, and levels of analysis has great promise within cognitive psychology, comparative or otherwise. However, any future for cognitive psychology, and for comparative cognition more specifically, requires resolution of the aforementioned criticisms and concerns.

I was born the year after Bitterman (1960) was published. I was trained as an undergraduate by a behaviorist in an operant laboratory, and entered graduate school at a time when it was ok to say that one was studying animal cognition. Indeed, it was encouraged by the funding opportunities, publication outlets, and the like, which by the 1980s were more receptive to “attention and memory” than to “orienting behavior and remembering behavior.” I consider myself fortunate to have experienced the best of both of these worlds— rigorous methodological and theoretical behaviorism married with the challenges of making inferences about the processing of information by humans and other animals. I think also of a mentor, Duane Rumbaugh, who began his career in psychology as a Hullian and who has been a leader in the field of comparative cognition, forging a unified theory that embraces respondent, operant, and emergent behavior (Rumbaugh, 2013). Consider the other leaders in the field of comparative cognition: Wasserman, Zentall, Shettleworth, and too many others to list. Each was trained in a behaviorist tradition that provided a theoretical and empirical foundation and a repertoire of research strategies that can be applied to the study of animal cognition. It seems to me that these examples of how the field has changed across each of our lifetimes yield at least two implications for the future: First, I am concerned that we are not leaving the field in better shape than we found it. Science is supposed to be cumulative, and I hope that the current and future generations of comparative-cognition researchers are getting as solid a foundation in behavioral science as did their academic parents. I worry also about the future of comparative cognition in light of the funding climate, academic job prospects, and many political pressures at work against comparative psychology now versus when I entered the field.

The dramatic changes in comparative psychology over the last half-century suggest a second implication for the future. Fifty years hence, as psychology approaches its bicentennial birthday, comparative cognition (or whatever it is called then) seems likely to be much different than can be predicted based on its current state!

All Authors

In the end, we promote an optimistic perspective for the future of comparative cognition, and comparative psychology more broadly. We remain committed to the promise of greater knowledge through comparative approaches to cognition, and we remain committed to the promise that the science of human psychology cannot exist without understanding its

comparative and evolutionary foundations. And, we remain committed to one final idea – that we are fortunate to be able to learn from animals, and that we will continue to enjoy doing so with the same passion shown by those who established this area of scientific inquiry.

Since all the sciences, and especially psychology, are still immersed in such tremendous realms of the uncertain and the unknown, the best that any individual scientist, especially any psychologist, can do seems to be to follow his own gleam and his own bent, however inadequate they may be. In fact, I suppose that actually this is what we all do. In the end, the only sure criterion is to have fun. (Tolman, 1959, p. 374)

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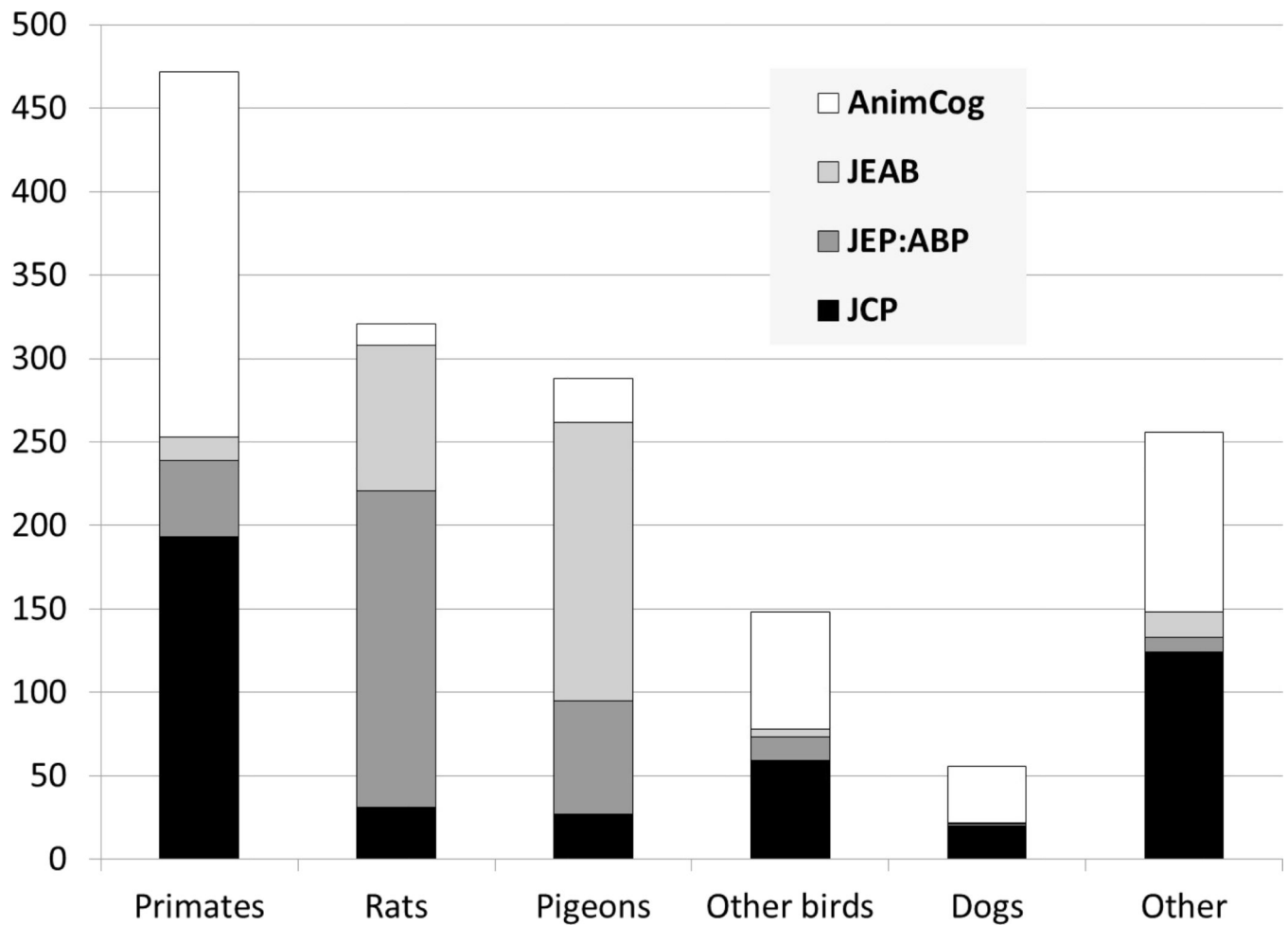


Figure 1.
 Number of publications (2001 – 2010) by animal of study, grouped by journal outlet
 (AnimCog= *Animal Cognition*; JEAB = *Journal of the Experimental Analysis of Behavior*;
 JEP:ABP = *Journal of Experimental Psychology: Animal Behavior Processes*; JCP =
Journal of Comparative Psychology).

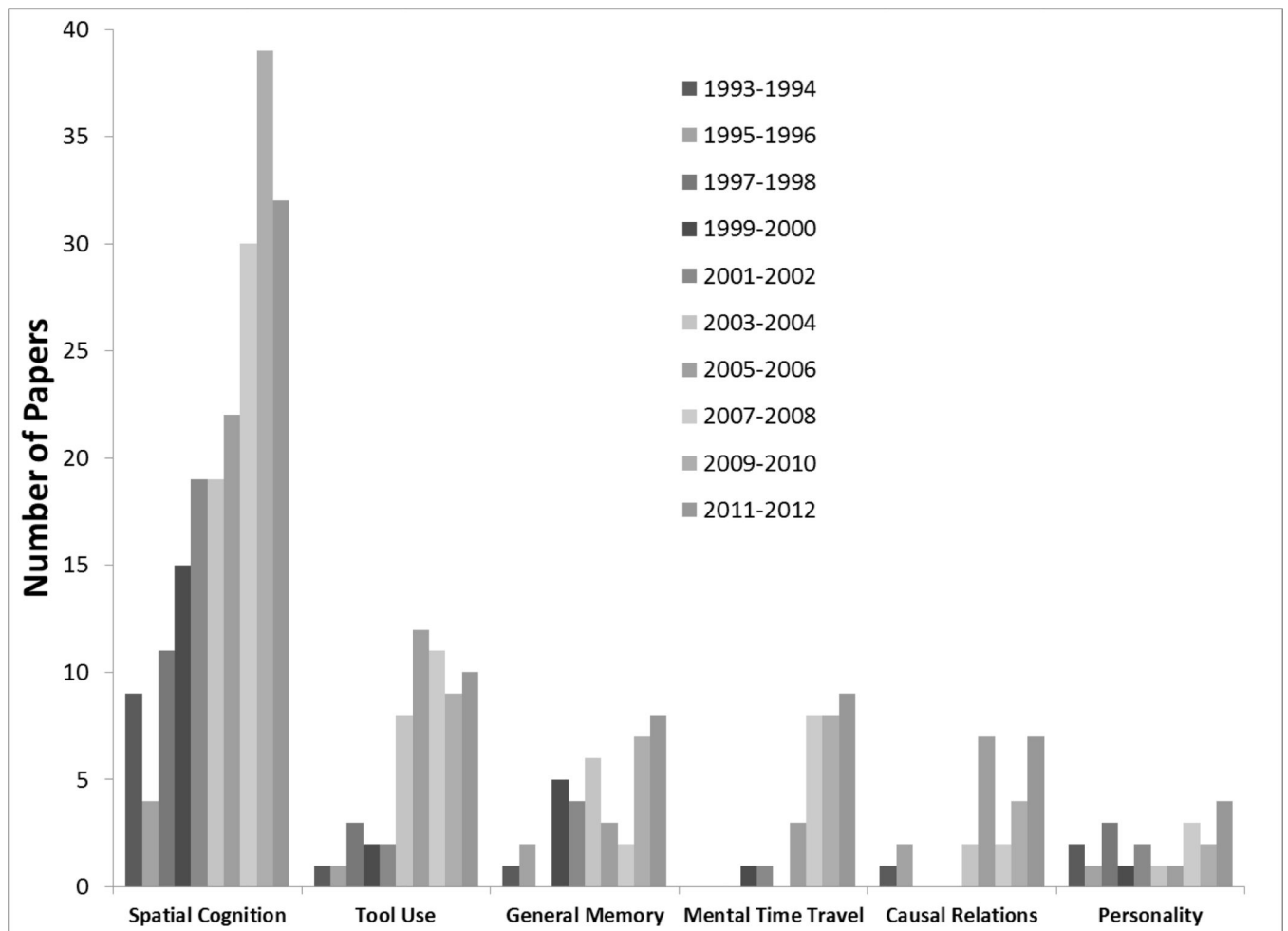


Figure 2. Numbers of publications in selected research areas, shown in successive two-year periods for the last 20 years. Data come from the *Journal of Comparative Psychology* and *Animal Cognition*.

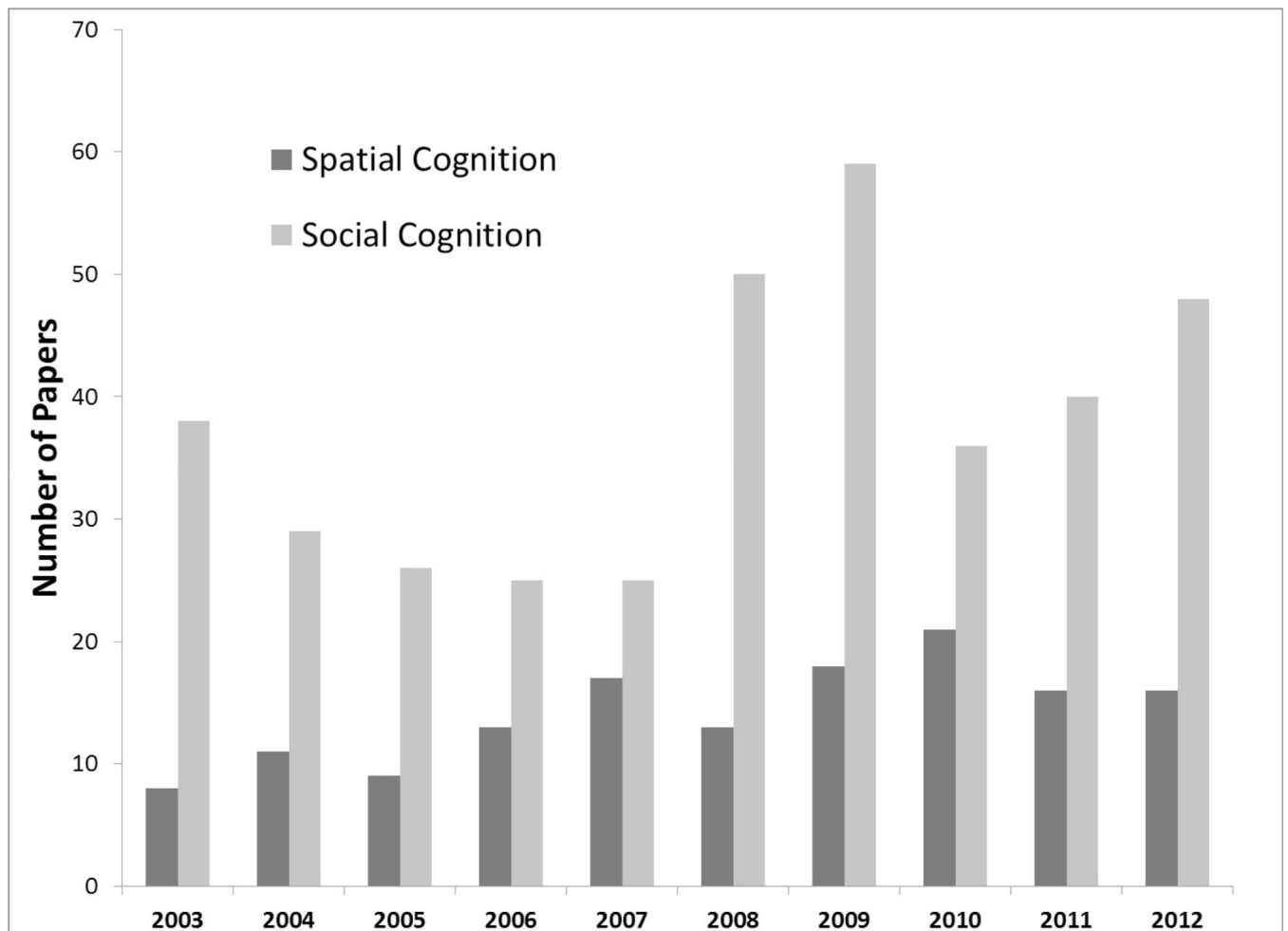


Figure 3.

A comparison of the relative numbers of papers about spatial cognition or social cognition in nonhuman animals, 2003–2012. Data come from the *Journal of Comparative Psychology* and *Animal Cognition*.

Table 1Species represented and topic areas reported during the last five years for the journal *Animal Cognition*

Year	Species Represented		Topic Areas	
2008	Dogs	Mandrills	Social Learning	Social Foraging
	Bowerbirds	Horses	Dominance Rank	Face Discrimination
	Chimpanzees	Degus	Culture	Reputation Learning
	Lemurs	Wolves	Theory of Mind	Kin Recognition
	Ravens	Rhesus Monkeys	Deception	Self-Recognition
	Capuchin monkeys	Sticklebacks	Social Orienting	Gestural Communication
	Marmosets	Pigeons	Gaze Following	Enculturation Effects
	2009	Gray Parrots	Orangutans	Experimenter Cues
Ants		Bonobos	Collective Problem Solving	Imprinting
Mangabeys		Gorillas	Emotional Perception	Gestural Communication
Dolphins		Lemurs	Social Learning	Inequity
Dogs		Prairie Dogs	Attention to Conspecifics	Gaze Following
Keas		Zebra Finches	Social Attention	Cross-Fostering
Rhesus Monkeys		Quail	Face Recognition	Reciprocity
Capuchin Monkeys		Horses	Self-Recognition	Token Transfer/Competition
Chimpanzees		Canaries	Capability of Others	ID recognition
Chicks		Cichlid fish	Song Sharing	Contagious Yawning
2010	Beetles	Walrus	Kin recognition	Play
	Humans	Rooks	Face recognition	Altruism
	Capuchin Monkeys	Tortoise	Cooperative Breeding	Gaze following
	Dingoes	Chimpanzees	Attentional states	Reciprocity
	Gorillas	Baboons	Theory of Mind	Culture
	Horses	Ungulates	Gestural communication	Animal Communication
	Dogs	Orangutans	Human Cue Reading	Triadic and Collaborative
	Macaques	Tamarins	Cooperation	
	2011	Nutcrackers	Fish	Gestural communication
Dogs		Pigeons	Conflict	Vocal recognition
Chimpanzees		Magpies	Human Cue Following	ID recognition
Rhesus Monkeys		Bees	Facial Recognition	Social Learning
African Grey Parrot		Geese	ID recognition	Helping Behavior
Gorillas		Ungulates	Facial Expression Discrimination	Prosocial behavior
Capuchin Monkeys		Horses		
2012	Dogs	Bonobos	Social Referencing	Recognition of humans
	Deer	Marine Fish	Attention/Communication with Humans	Vocal recognition
	Human Children	Canaries	Facial/kin recognition	Empathy
	Capuchin Monkeys	Horses	Emotional Recognition	Bonding
	Diana Monkeys	Invertebrates	Social Learning	Theory of Mind
	Rhesus Monkeys	Goats	Courtship	Visual Perspective Taking
Squirrel Monkeys	Gibbons	Contagious Yawning	Point Following	

Year	Species Represented	Topic Areas
Lemurs	Crocodiles	