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7                   **Comparative Cognition: Perspectives, Challenges, and Prospects**

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**Abstract**

24 The publication of the centennial year of the *Journal of Comparative Psychology* is an occasion  
25 to reflect on the state of our discipline. In this article, I focus on one aspect of comparative  
26 psychology, namely comparative cognition. This focus stems from my long-standing interest in  
27 comparative cognition. The trends and challenges in comparative cognition share many of the  
28 trends and challenges in the broader field of comparative psychology. In the first part of this  
29 article, I outline my perspective on the field. Next, I consider challenges. I end with a section on  
30 prospects for the future.

31           Keywords: comparative psychology, comparative cognition, interdisciplinary research

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# Comparative Cognition: Perspectives, Challenges, and Prospects

34 The publication of the centennial year of the *Journal of Comparative Psychology* is an  
35 occasion to reflect on the state of our discipline. In this article, I focus on one aspect of  
36 comparative psychology, namely comparative cognition. This focus stems from my long-  
37 standing interest in comparative cognition. I view comparative cognition as a hub at the  
38 intersection of animal behavior, ecology, evolutionary biology, cognitive science, neuroscience,  
39 and philosophy. I note a limitation at the outset that the trends and challenges in comparative  
40 cognition are likely to overlap incompletely with those of the broader field of comparative  
41 psychology. I also write from a particular vantage point, university-based research in the United  
42 States, recognizing that conditions are different in other parts of the world. In the first part of  
43 this article, I outline my perspective on the field. Next, I consider challenges. I end with a  
44 section on prospects for the future.

## Perspectives

46 Where will new and exciting advances come from in the future? What factors can be  
47 harnessed to promote these advances? The future is always uncertain, but I attempt to outline  
48 my outlook on these questions. Some projections about the future examine the past. But other  
49 projections focus on new approaches.

50 One answer to the questions posed above focuses on interdisciplinarity (Crystal &  
51 Glanzman, 2013). Comparative Psychology has always borrowed from related fields, such as  
52 animal behavior, experimental psychology, and developmental science. Increasingly, science is  
53 accomplished with teams. A broader outline of interdisciplinarity integrates comparative  
54 psychology with ecology, evolutionary biology, neuroscience, cognitive science, informatics,

55 philosophy and other disciplines. Comparative psychologists are experts in behavioral  
56 approaches. In many cases, neuroscientists seek a functional endpoint in behavior but lack  
57 expertise in behavioral approaches. A behavioral endpoint in neuroscience research ensures  
58 that the insight gained on the neuroscientific front has a connection to something functional.  
59 Comparative psychologists can improve neuroscience research by bringing expertise in  
60 understanding the natural behaviors of animals and an evolutionary perspective. Integration  
61 with neuroscience is likely an important factor in future research. But integration with  
62 neuroscience is not without challenges. In collaborations with neuroscientists, the  
63 neuroscientist often wants the behavioral endpoint to be efficient; one day of behavior is ideal  
64 from this perspective, two days is tolerable. Experts in behavioral approaches typically invest a  
65 significantly longer amount of time. Many interesting behavioral phenomena cannot be  
66 investigated in a day or two. A potential solution to disagreements about time horizons focuses  
67 on a division of labor across labs; for example, an agreement may be reached in which long-  
68 term behavioral studies are conducted in the comparative cognition lab, and the animals are  
69 transferred to the neuroscience lab for brief periods (e.g., surgeries, tissue collection, etc.).

70 Many individuals do most of their research with members of their own labs (e.g., grad  
71 students) and like-minded colleagues. Large interdisciplinary teams are uncommon in our field  
72 in the United States. Projects in Europe and Japan are ahead of the US in this respect.  
73 Integration with philosophers is another promising avenue for future research. Philosophers  
74 bring expertise in analysis of problems that can transform the experimental techniques of  
75 comparative psychology. For example, theory of mind research has benefited from the critical

76 analysis of philosophers (Allen & Bekoff, 1999; Andrews, 2020; Bugnyar et al., 2016). Again,  
77 Europe and Japan are ahead of the US in advancing this type of collaboration.

78 I will describe two examples of large interdisciplinary projects. The first case comes from  
79 “The Science of Mental Time: Investigation in the past, present and future” which is led by  
80 Shigeru Kitazawa in Japan. They refer to mental time as an awareness of time over past,  
81 present, and future. The project involves an active collaboration of neuroscientists,  
82 psychologists, clinical neurologists, linguists, philosophers, and comparative ethologists.

83 Examples of diverse accomplishments of this project include a better understanding of how the  
84 hippocampus encodes locations of self and others (Danjo et al., 2018), how novelty is encoded  
85 in the hippocampus (Mizunuma et al., 2014), and insights into the dysfunction of time  
86 perception and counting in patients with Parkinson disease (Honma et al., 2016). A second  
87 example comes from “Constructing scenarios of the past: A new framework in episodic  
88 memory” which is led by Sen Cheng in Germany. The project combines computational  
89 neuroscience, psychology, and philosophy, in an effort to answer fundamental questions about  
90 scenario construction during episodic memory recall. An example of an accomplishment of this  
91 project is an improved understanding of the interplay between episodic memory and sensory  
92 processing (Görler et al., 2020).

93 More broadly, new, cutting-edge developments in interdisciplinary research are difficult  
94 to track. Some of this work is published in interdisciplinary, high-impact journals such as  
95 *Science*, *Nature*, *Proceedings of the National Academy*, and others. These articles are a small  
96 proportion of the research published in these outlets. In the past, most researchers stayed  
97 abreast of new developments by reading a small number of journals in the field, *JCP* among

98 them. Of course, this is a valuable source of information. However, monitoring cutting-edge  
99 developments in interdisciplinary research has the potential to open new opportunities for  
100 comparative psychologists to contribute to cutting-edge interdisciplinary research. To address  
101 this problem (important developments but difficult to find), I undertook an initiative when I  
102 became the editor of *Learning & Behavior* (Crystal, 2016). The journal launched a new section  
103 of the journal, called *Outlook*. The goal of Outlook papers is to allow readers to stay up to date  
104 on the latest findings, trends, important developments, and new ideas in the field. Outlook  
105 papers offer a short review (limited to 2 pages) of groundbreaking work reported in a recent  
106 target article, allowing the Outlook author to say something about the target article and expand  
107 to the author's views on this part of the field. By the time that this article is published, we will  
108 have published about 60 Outlook papers on varied topics. A measure of the impact of this effort  
109 includes over 100,000 accessions and downloads of Outlook papers.

110 One limitation of the focus on cutting-edge developments is that they sometimes lack a  
111 clearheaded assessment of alternative explanations. The effort to draw bold conclusions  
112 sometimes leads to a rush to judgment before adequate experimentation can restrain the  
113 conclusions. Theory of mind is a domain that has become more critical of itself over time (Call &  
114 Tomasello, 2008) Ultimately, to have a lasting impact on the field, converging lines of evidence  
115 are needed (Crystal & Suddendorf, 2019). A balance between critical judgments and promoting  
116 the field is needed; for example, it is important to not “eat the young” researchers, which may  
117 adversely impact their career development. Finding a balance along this continuum is not a  
118 unique problem for comparative cognition.

119 Another perspective focuses on selection of questions, problems, and approaches.

120 Although variation along these lines is substantial across disparate domains of comparative

121 psychology, I will outline my perspective on comparative cognition. I advocate the view that

122 comparative cognition is primarily focused on comparisons of animals with human cognition.

123 Research seeks to explore the evolution of cognition by identifying aspects of cognition that are

124 widely distributed across species, although some aspects of cognition may be unique to people.

125 This focus is not anthropocentric, in the sense that researchers adopt human-oriented ideas

126 about animals. Instead, it is a perspective that views human cognition as a well-developed

127 discipline to prompt questions about the evolution of cognition in animals. A wide range of

128 views have been espoused about the role of a human-oriented perspective in animal behavior

129 (Burghardt, 2004; Smith et al., 2012; Williams et al., 2020; Wynne, 2004). Animals may not

130 have the same level of the capacities exhibited by humans, but it is likely that animals have

131 important evolutionary precursors. The exact degree of similarity or dissimilarity remains to be

132 empirically established.

133 A final perspective focuses on identifying limits in comparative cognition. Finding that

134 animal X has process Y is an advance. This advance may be leveraged to explore the range and

135 limits of the process in animals. For example, we recently described evidence that rats replay a

136 stream of episodic memories (Panzica-Brown et al., 2018). This development prompts new

137 questions about the similarities and differences in the replay of episodic memories in rats and

138 humans. Insights in the evolution of cognition may come from identifying where the limits lie in

139 this, and other, aspects of cognition (Crystal & Suddendorf, 2019). To identify limits, one needs

140 to not be afraid of failure because the outer limits of a phenomenon are defined by the  
141 boundary between successes and failures.

142 **Challenges**

143 The field of comparative cognition faces significant challenges in the future. One  
144 challenge stems from different traditions in interdisciplinary research. An example above noted  
145 that neuroscientists sometimes seek behavioral endpoints that do not match the traditions in  
146 behavioral approaches. Comparative psychologists can contribute as equal partners to this type  
147 of interdisciplinary research, but success hinges on aligning styles and traditions adequately to  
148 make the undertaking successful for multiple parties.

149 Funding to support comparative psychology has been a significant challenge for a long  
150 period of time, and the problem is likely to intensify in the future. As funding to support  
151 pursuits of fundamental questions (i.e., basic research) declines, focusing on applications offers  
152 a pathway forward. Indeed, the prospect of interdisciplinary research is appealing because it  
153 offers a route to integrating comparative psychology with applications, such as animal models  
154 of human health (Crystal, 2012).

155 Training new scientists to be prepared to effectively carry out research with  
156 interdisciplinary teams is an additional challenge. Many senior investigators were trained in a  
157 model in which they were on track to self-replicate their mentors. This trend was sustainable  
158 when funding for basic science was more plentiful. However, this model will only intensify  
159 isolation of comparative psychology from interdisciplinary opportunities. Training in graduate  
160 school should emphasize team-science while preparing future researchers to collaborate with  
161 individuals with diverse skillsets.

162 A final challenge comes from the aversion of being labeled anthropocentric. I view  
163 comparative cognition as an effort to leverage our knowledge about the species of animal to  
164 enable us to ask questions about advanced cognitive abilities in animals and the evolution of  
165 cognition. For example, rats have exceptional spatial cognition and olfaction. We (and others)  
166 have leveraged these propensities to graft complex problems onto domains in which rats  
167 naturally excel. I will give two broad examples of this approach. The first example focuses on  
168 spatial navigation. In a number of studies, we have investigated episodic memory in rats  
169 navigating on radial mazes. We do not teach rats about spatial cognition; rather they come to  
170 the experiments with naturally occurring foraging competencies. Our strategy was to layer  
171 elements of episodic memory on top of spatial navigation. By layering, I mean that we start  
172 with task requirements that tap into naturally occurring behaviors and abilities, and then we  
173 add additional features; this strategy has been used effectively by others (e.g., Clayton &  
174 Dickinson, 1998). This is a natural fit for one approach to episodic memory, which focuses on  
175 what-where-when memory (i.e., memory of an event or episode is demonstrated by knowledge  
176 of what happened, where did it occur, and when did it happen). Rats pass a number of tests of  
177 episodic memory in these preparations (Babb & Crystal, 2005, 2006a, 2006b; Naqshbandi et al.,  
178 2007; Roberts et al., 2008; Zhou & Crystal, 2009, 2011; Zhou et al., 2012). Again, this is a natural  
179 fit for a different approach to episodic memory, which focuses on the source (or origin) of  
180 memories (i.e., source memory). Rats pass a number of tests of source memory in these  
181 preparations (Crystal & Alford, 2014; Crystal et al., 2013; Crystal & Smith, 2014).  
182 The second example focuses on olfaction. Again, rats come to the experiments with  
183 remarkable olfactory abilities. In a number of studies, we have investigated episodic memory in

184 rats making judgments about odors that they previously encountered. Again, our strategy was  
185 to layer elements of episodic memory on top of olfactory decision making. This is a natural fit  
186 for approaches to episodic memory that investigate the capacity to remember many episodic  
187 memories and the sequential order of episodic memories (Panoz-Brown et al., 2018; Panoz-  
188 Brown et al., 2016).

189 In both of these examples, we tend to agonize over the details of the design to ensure  
190 that we optimize conditions for the animals to succeed. Our view is that there are many ways to  
191 do these studies wrong, which provide limited insights. For example, treating rats as if they  
192 were little primates may lead investigators to place a rat in front of a touchscreen. Although  
193 rats are able to perform relatively simple discriminations in these preparations (e.g., Horner et  
194 al., 2013), it is unlikely that we would succeed in layering more complex problems in this  
195 approach. Visual acuity (unlike spatial cognition and olfaction) is not a strength in rats.

### 196 **Prospects**

197 Prospects for the future are linked to challenges (described above) and our response to  
198 challenges. One challenge focuses on the declining investment in basic research by funding  
199 agencies. In the US, the decline in funding for basic research has accelerated as the focus on  
200 applications have increased. An illustration comes from comparing the growth in budgets for  
201 the National Institutes of Health and the National Science Foundation; in 2020, the NIH budget  
202 was over five times the budget of NSF. Advocacy in the field may try to mitigate this trend, but  
203 the focus on application is widespread in society and unlikely to abate. Thus, team science  
204 approaches to interdisciplinary research provides a route forward.

205        A promising prospect for the future of comparative psychology focuses on institutional  
206    support especially at universities that focus on undergraduate education (Highfill & Yeater,  
207    2018; Krause, 2018). Research in this setting can be done using institutional support for  
208    undergraduate research. A subset of these institutions continues to invest in animal facilities to  
209    support training and research. It will be important to maintain this institutional support in the  
210    future. Vigilance and advocacy are needed to retain and increase resources. One strategy for  
211    securing resources focuses on connecting our training in research to entry into STEM fields. For  
212    example, the Center for the Integrative Study of Animal Behavior at Indiana University has  
213    operated an NSF-funded Research Experiences for Undergraduates program for 25 years. Our  
214    interns engage in rigorous, cutting-edge research in a faculty member's lab during a 10-week  
215    summer program. After completing our program, about 39% of recent interns presented their  
216    research at national meetings, and 26% presented at their home institutions or at regional  
217    conferences. An impressive 97% of recent interns say that they are more likely to pursue  
218    graduate study in science because of their participation in our program, and 78% of recent  
219    interns are currently pursuing or intend to pursue graduate degrees. These latter percentages  
220    are noteworthy because 77% of recent interns come from minority groups underrepresented in  
221    STEM, 80% are women or other-gendered, 41% are from low income families, and 38% are  
222    first-generation college students.

223        A final prospect for the future focuses on achieving a balance between repetition of  
224    well-established approaches and creativity to develop new approaches. Our confidence in a  
225    phenomenon is increased by replication, and converging lines of evidence requires some  
226    degree of continued focus on similar problems. Sometimes a field gets stuck in continual

227 repetition of the same experiments (Crystal, 2014). However, new advances will come from  
228 creative approaches to old and new problems. The creativity of new investigators is one of the  
229 most exciting prospects for the future of comparative psychology.

230 **Conclusions**

231 A lot of comparative cognition research can be done relatively inexpensively. This  
232 strength may propel comparative cognition research as an exciting avenue of animal behavior  
233 research at smaller state schools and liberal arts colleges. More large scale research may be  
234 fostered by developing larger interdisciplinary and international research teams. Comparative  
235 psychologists can bring an understanding of the natural behavior of organisms and an  
236 evolutionary context that can strengthen neuroscience research. Team science is more likely to  
237 include comparative psychologists when we train our students to be conversant in more than  
238 one discipline. Knowing the language, methods, and problems of multiple disciplines will allow  
239 us to play a central role in new scientific endeavors. Along these lines comparative psychology  
240 has much to contribute to science as we progress toward the next centenary.

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