**Animal minds: from computation to evolution**

Alex Thornton[1]*, Nicola S. Clayton[1] and Uri Grodziski[1]

[1] Department of Experimental Psychology, University of Cambridge

* Email for correspondence: jant2@cam.ac.uk

In the great Darwinian struggle for existence, all animals must tackle the problems posed by variable environments, be it finding and processing food, recognising and attracting potential mates, avoiding predators, outcompeting rivals or navigating back to nesting sites. Though the mental processes by which different species deal with such challenges are varied, all animals share the fundamental problem of having to cope with the sheer abundance of information in the environment, much of which is likely to be irrelevant to the task at hand. The first step, therefore, is to attempt to sift through the mass of data and attend to that which may inform adaptive decision making. Having acquired the relevant data, animals may then benefit from establishing how the different pieces of information relate to one another. Do yellow flowers reliably indicate the presence of nectar? Does the presence of a dominant silverback male signal impending danger? In complex environments, it may be advantageous not only to take into account statistical co-occurrence of different stimuli, but to also extract general rules, making it possible to act flexibly and solve a wide variety of problems across different contexts [1,2]. Certain animal species might also form mental representations or models of the way the world works. These internal representations may be used to reason about the desirability of alternative actions or scenarios, based on expectations of their likely outcome, thus guiding the individual's behaviour [3,4]. Thus, for instance, an animal with a mental representation of the action of gravity on objects could use it to reason that a food item will fall out of its reach if pushed towards a precipice [5,6]. The possibility that animals may employ such human-like reasoning

25  has intrigued observers throughout the centuries, from Aesop's fables to Romanes's

26  anthropomorphic anecdotes. However, careful scientific exploration of the mental faculties of

27  other animals, and their relation to our own, did not commence in earnest until the last century,

28  with the rise of comparative psychology and ethology. Contemporary comparative cognition,

29  which grew from these two disciplines, aims to determine the mental processes underpinning

30  animal behaviour, and to understand how these processes have evolved over the generations and

31  develop over an animal's lifetime.

32

33  Recent years have seen a great burgeoning of studies of comparative cognition, building on

34  earlier advances in our understanding of basic processes of perception, attention, associative

35  learning and memory [4,7]. Elegant experimental work is generating insights into disparate

36  cognitive abilities across a wide range of taxa, from path integration in ants and spatial memory

37  in rats [8,9] to mental faculties that were considered uniquely human, such as mental state

38  attribution and mental time travel in apes and corvids [10–13]. Nevertheless, despite these

39  important empirical advances, the field suffers from a lack of theoretical underpinning, and

40  conceptual debates abound. For example, how might we discriminate between alternative

41  cognitive mechanisms underpinning behaviour? Do the abilities seen in cognitive experiments

42  reflect domain-specific 'adaptive specialisations' or domain-general problem solving capacities?

43  How and why do humans differ cognitively from other animals? This special issue brings

44  together a variety of developmental, mechanistic and functional approaches to the study of

45  cognition with the goal of synthesizing this emerging body of work, and beginning to build a

46  theoretical framework to facilitate further progress towards our understanding of animal minds.

47

**1. DELVING INTO ANIMAL MINDS: DETERMINING MECHANISMS OF ANIMAL COGNITION**

The range of possible mental processes through which animals may interact with their environments poses a major challenge to students of animal minds. We can observe a non-verbal creature solving a problem, but how can we infer the processes by which it does so? This issue is particularly problematic given that seemingly complex behaviour may often be generated through relatively simple mechanisms. Meerkats, for instance, teach their young to hunt by responding to age-related changes in pups' begging calls, provisioning dead or disabled prey to young pups and live prey to older pups. A simple stimulus-response mechanism thus allows adults to provide pups with prey-handling opportunities appropriate for the pups' age and competence, without needing Theory of Mind to attribute ignorance to their pupils [14]. Similarly, reflexive responses coupled with associative learning processes enable many animals, from insects to primates, to use tools effectively without understanding their physical properties. For example, larval antlions (*Myrmeleon* spp.), insects of the order Neuroptera, knock passing prey into their pit-traps by flinging grains of sand in response to vibrational cues [15]. How might we discriminate between such low-level mechanisms and other, more complex cognitive processes? It may be tempting to assume that species that are more closely related to us may share more "human-like" cognitive faculties. However, numerous examples of evolutionary convergence in unrelated taxa, along with abundant evidence of the importance of relatively simple, evolutionarily ancient mental processes in human behaviour [16–18] caution against this archaic view of a mental *scala naturae*. Instead, the contributors to this volume urge a more careful, bottom-up approach to determine the minimal computational requirements needed to

70  generate particular behavioural outcomes and to use careful experimentation to tease apart

71  alternative explanations.

72

### *1.1 Bottom-up approaches: building models and robots*

74  It is common in comparative cognition to use folk psychological intuitions of how humans solve

75  certain problems when designing experiments to test the cognitive abilities of other animals.

76  While this approach has clear value in helping to derive hypotheses, it suffers from two major

77  weaknesses. First, our intuitions of how we solve problems have repeatedly been shown not to

78  reflect psychological reality (e.g. [19,20]). Secondly, a reliance on folk psychological intuitions

79  may detract from considering other, arguably more "killjoy" explanations based on simpler

80  mechanisms [17,18]. A fundamentally different approach advocated by some of the contributors

81  to this issue is to build models of simple neural networks to determine the minimal necessary

82  requirements to solve a specific task. These models often yield rather surprising results,

83  suggesting that abilities that are commonly considered to be complex may in fact be

84  implemented by very simple networks (see [21], this issue). A circuit of only a few hundred

85  neurons, for example, has been shown to suffice for reliable face recognition [22]. This approach

86  is clearly of great value in quantifying basic computational complexity, undermining the

87  assumption that many cognitive feats require big brains [21,23]. Indeed, recent studies have

88  revealed a number of striking cognitive feats in small-brained animals such as insects and, as

89  Webb discusses in this issue [3], there is evidence that insects may employ internal mental

90  representations of the outside world. However, given that even miniscule invertebrate brains

91  contain more neurons than the theoretical neural thresholds predicted by computational models

92  for many tasks, this 'minimal cognition' approach may be limited in explaining observed

93   cognitive differences between species. Moreover, the computational requirements for solving a

94   specific, isolated problem may underestimate those needed to solve the same task in the real

95   world, let alone solve multiple different tasks using the same network. One way to build up

96   complexity towards that faced by an animal in the physical world is to build a robot that must

97   replicate the animal's behaviour using the hypothesised neural mechanism to solve a given task.

98   As Webb points out, robotics thus forces us to face real world difficulties such as perceiving and

99   attending to relevant stimuli in addition to the abstract computational aspects of a problem, thus

100  generating more realistic demonstrations of minimal sufficiency. For example, a robotic female

101  cricket may be able to discriminate between male songs and approach only those who sound like

102  members of a given species without needing to rely on an internal computational mechanism for

103  evaluating and comparing songs [3]. Unlike a real cricket, however, it cannot deal with the

104  additional complexities involved in finding food and avoiding predators.  The development of

105  ever more complex robots, capable of computing solutions to multiple problems, may generate

106  important insights into the computational requirements needed for biological systems to respond

107  adaptively to the multitude of challenges they face in their natural environments. A related

108  challenge is to determine how organisms may integrate currently available information with

109  previously acquired knowledge of how the world works, bringing all the necessary cognitive

110  resources to bear when faced with a novel problem. How are parallel processing units in the

111  brain integrated to create a coherent, structured system capable of responding appropriately when

112  encountering a problem for the first time? How might a New Caledonian crow (*Corvus*

113  *moneduloides*) or a rook (*Corvus frugilegus*), for example, have the wherewithal to

114  spontaneously manufacture a hook to pull up a bucket containing food [24,25]? In this issue,

115  Shanahan takes a bottom-up approach, drawing on recent advances in brain connectivity to

116   propose a cognitive architecture that can generate such seemingly insightful solutions to novel

117   problems in the physical world [26]. This consists of a number of discrete modules with

118   extensive internal connectivity (a "modular small-world network"), which are in turn connected

119   to one another through nodes known as connector hubs to form a "connective core". Such a

120   system may enable the unanticipated integration of mental processes to produce a coherent

121   sequence of actions to achieve a goal. This theoretical approach thus holds the great promise of

122   allowing us to move beyond current vague conceptions of insight as a sudden, magical "Eureka

123   moment", to a tangible computational process that is amenable to research. An important

124   question arising from this work is how and why, given that the brains of humans, macaques, cats

125   and pigeons are all known to possess a connective core, these species may nevertheless differ

126   radically in their ability to plan their actions when solving a task. Answers to this question will

127   emerge from a more detailed understanding of differences in neural connectivity in the brains of

128   different species and their resulting computational power, coupled with behavioural tests of what

129   different animals are capable of.

130

131   **1.2 Top-down approaches: inferring cognitive mechanisms from behaviour**

132   *(a) Associative learning as a candidate explanation*

133   For behavioural researchers, a principal challenge is to devise experiments capable of

134   discriminating between alternative mechanistic explanations for observed behaviour. The

135   bottom-up approach exemplified by neural network models using computer simulations and

136   robotics cannot yet provide testable predictions for the range of behaviours examined in

137   contemporary comparative cognition research. Learning theory, in contrast, is grounded in

138   behavioural research and provides concrete hypotheses that can be readily examined by

139  empiricists. Indeed, associative learning is found throughout the animal kingdom and is known

140  to play a role in generating even seemingly complex behaviour in both non-human animals and

141  in our own species. Nevertheless, associative explanations are sometimes overlooked, perhaps as

142  a result of knee-jerk reactions to the overambitious claims of behaviourism, leading to a focus on

143  what Heyes [17] calls "super-cognitive" explanations derived from folk psychological intuitions.

144  In fact, modern learning theory is considerably more nuanced than the caricature of

145  behaviourism would suggest. Unlike behaviourism, it does not claim that anything can be

146  learned (or that all behaviour is learned), but instead incorporates constraints that limit learning

147  of coincidental associations and promote learning of biologically relevant associations.

148  Moreover, learning theory has the distinct advantage over folk psychology in that it rests on

149  well-described, general theories such as the Rescorla-Wagner [27] and Mackintosh [28] models.

150  One interesting development discussed by Dickinson [29] is his 'associative-cybernetic' theory

151  [30,31] which postulates that, if embedded in a constraining processing architecture, associative

152  learning may give rise to rational goal-directed action. That is, rather than simply learning that a

153  certain action is rewarded, an animal may also learn that its action causes a specific beneficial

154  outcome. This theoretical prediction has considerable empirical support. For example, rats

155  trained to obtain a reward by pressing a lever will reduce their lever pressing if the value of the

156  reward is reduced, indicating that they represent the causal relation between their own lever-

157  pressing actions and the outcome (reviewed in [29]). Thus, associative learning theory provides a

158  powerful and tractable framework for research on animal (including human) minds. Indeed,

159  rigorous research in comparative cognition often uses associative learning as a null hypothesis,

160  making considerable efforts to derive candidate explanations from learning theory to be tested

161  through behavioural experiments (e.g. [32]). There will, of course, be instances when behaviour

162  cannot be understood purely in terms of associative processes. Human behaviour, for instance, is

163  guided to a large extent by reasoning and inference about abstract causal relations in the physical

164  and social worlds [33–35]. The possibility that animals may employ similar cognitive processes

165  has attracted great interest from students of animal minds, but lacks the theoretical grounding of

166  associative theory and so is more difficult to pin down. If associative processes are found to be

167  lacking as explanations of animal behaviour, how might we make progress in determining

168  alternatives?

169

170  *(b) Beyond associative learning: individual-level approaches*

171  One common and powerful experimental approach is to use a series of training trials in which

172  subjects learn the basic requirements of the task, followed by transfer tests in which the causal

173  properties of the problem are kept constant, but arbitrary visible stimuli are changed. Thus, in

174  theory, subjects that have learned a simple rule based on visible features will fail transfers, while

175  those that have abstracted a generalizable understanding of the causal structure of the task should

176  apply it to solve the transfer [36, 37]. However, as Thornton & Lukas point out, the fact that

177  transfer tests typically involve the same binary choice over multiple trials means that a subject

178  might learn a rule based on the visible properties of the transfer test itself [38]. Thus, subjects

179  may reach a given criterion (say nine correct trials out of ten) using nothing but associatively

180  learned rules. Conversely, reliance on crude binary criteria of success or failure leads us to

181  ignore potentially valuable data. Instead, several of the contributors to this issue advocate a more

182  fine-grained analytical approach that focuses specifically on individual differences in

183  performance on a trial by trial basis to shed light on the cognitive mechanisms employed when

184  solving tasks [33,38,39]. Seed and colleagues, drawing on insights from developmental

185 psychology, point out that a detailed focus on individual behaviour, taking into account failed

186 trials as well as successes, may provide valuable insights into why subjects may fail, and the

187 precise mechanisms required for success. Using this approach, they show that chimpanzees (*Pan*

188 *troglodytes*) that failed a task requiring them to discriminate between a complete and a broken

189 tool failed not because of an inability to represent "connectedness" but rather because of

190 limitations in memory and attention [33]. Thus, an individual-based analytical approach may

191 allow us to determine the set of cognitive processes that must be employed together when

192 solving tasks.

193

194 The individual-level approach may also benefit from using formal planning theory used in

195 artificial intelligence (AI) research. In this issue, Chappell & Hawes explored a four-trap variant

196 of the classic 'trap tube' test in which the precise characteristics of the task (e.g. which of the

197 four traps was functional) varied systematically across a series of 64 trials. Using an AI planning

198 language, they generated a series of possible computational rules or "plans" an animal could

199 employ to solve the task. They then simulated how each of these plans would perform in each of

200 the different trials, and compared these simulations to the actual trial-by-trial performance of

201 orangutans (*Pongo pygmaeus*) [39]. The advantage of this method is two-fold. First,

202 decomposing the problem into its constituent parts may be valuable in designing experiments.

203 Second, in common with Seed et al.'s approach, it forces us to move away from the simplistic

204 and statistically problematic [38] dichotomy of success and failure and instead to harness the rich

205 data emerging from all the actions of all individuals in all trials to assess how animals solve

206 problems. In the future, we hope that such individual-based approaches will be combined with

207 insights from learning theory to determine the role of associative processes in within-task

208 learning, and to discriminate between alternative mechanistic explanations. We also envisage

209 great potential in linking this top-down approach of decomposing and simplifying specified

210 problems with bottom-up approaches that specify the components and connectivity of the

211 computational systems implementing the solutions. For instance, specifying the computational

212 components and connectivity of a neural system (c.f. [26]) may allow us to constrain the possible

213 range of plans the system might implement to solve a cognitively challenging task in a

214 biologically realistic way.

215

216 **2. THE EVOLUTION OF ANIMAL MINDS**

217 *2.1 Fitness consequences of individual cognitive variation*

218 Through a combination of experimental and theoretical approaches, comparative cognition is

219 beginning to provide important insights into the mental processes of different animals. However,

220 existing approaches tend to place relatively little emphasis on the central goal of understanding

221 how these processes evolve. In this issue, Thornton & Lukas point out that researchers

222 commonly assume that the cognitive traits they find in laboratory animals are the adaptive

223 products of natural selection, but they very seldom assess whether the basic tenets of Darwinian

224 theory apply to the trait in question [38]. For natural selection to act, there must be heritable

225 variation in the trait, leading to variation in reproductive success [40]. Consequently, if we want

226 to understand how cognitive traits evolve, we must ask whether they vary between individuals,

227 are heritable and influence fitness. Laboratory studies commonly reveal substantial variation in

228 individual performance, but rarely consider its causes. Thornton & Lukas's meta-analyses of

229 individual performance across a series of cognitive tasks suggest that much of this variation may

230 be explained by laboratory rearing conditions, with enculturated individuals with extensive

231  previous experience of laboratory tests typically outperforming the rest [38]. It is therefore

232  unclear to what extent this variation may be heritable, or indeed how cognitive traits may be

233  manifested in the natural conditions in which they evolved. In some short-lived animals it may

234  be possible to explore cognitive evolution using selection experiments in the laboratory [41], but

235  for many of the birds and mammals of interest to students of comparative cognition, such

236  experiments are less feasible. Laboratory studies must therefore be complemented by field

237  research to examine links between individual cognitive variation and reproductive fitness.

238  Unfortunately, the difficulties in examining cognition in the wild have led to a recent trend for

239  field researchers to assume that individuals that succeed in any experimentally presented

240  "problem-solving task" possess elevated cognitive abilities, without testing the underlying

241  mechanisms. Given this trend, there is a danger that, for example, the action of a pigeon pecking

242  a key to obtain a reward in the field would be regarded as a measure of "cognition", while no one

243  would consider the same action to be cognitive if done in a laboratory setting. If field studies are

244  to provide productive insights into cognitive evolution, it is therefore critical that they

245  incorporate the valuable lessons of psychological research concerning cognitive mechanisms into

246  the task design. For instance, Visalberghi and colleagues have used elegant experiments inspired

247  by laboratory tests of physical cognition to establish that capuchin monkeys recognise the

248  physical properties that render objects for use as hammers to crack nuts [42]. Similarly, studies

249  by Healy and colleagues have elegantly adapted laboratory tests of spatial memory and timing

250  for use in the field (reviewed in[43]), while Cheney & Seyfarth, McComb and others have

251  devised tests of social cognition incorporating expectation violation paradigms from

252  developmental psychology [44,45]. Such experimental approaches, as well as novel statistical

253  tools allowing mechanisms of learning and cognition to be inferred from natural behaviour [46]

254    hold great promise in enabling us to understand the cognitive processes used by animals in their

255    environments. A key challenge now is to determine whether individual animals in the wild vary

256    in their cognitive abilities, to use advances in quantitative genetics to assess the heritability of

257    this variation and to begin to examine its fitness consequences.

258

259    It may be tempting to assume that elevated cognitive abilities ought always to confer fitness

260    benefits, and are therefore subject to positive selection. However, any benefits associated with

261    improvements in cognition will be balanced against the costs they may carry. In *Drosophila*, for

262    example, there is evidence that selection for improved associative learning abilities among adults

263    comes at a cost of reduced ability to compete for food resources at the larval stage [47]. In

264    addition, at the individual level, the potential benefits of cognition will depend on behavioural

265    phenotypes. As Sih & del Giudice discuss in this issue, there is extensive evidence that

266    individual animals differ consistently in their behaviour over time and across contexts, and this

267    behavioural consistency may place important constraints on the ways in which cognitive abilities

268    are manifested [48]. Consider, for example, two individuals that have equal cognitive abilities

269    but differ in their behaviour, with one being very bold and exploratory while the other is shy and

270    slow to investigate unknown places or objects. While the bolder individual is likely to encounter

271    novel stimuli more often, the shier individual may have a greater tendency to pause and attend to

272    changes in the environment and update its assessment of a given situation. Behavioural

273    differences may therefore generate a trade-off between speed and accuracy when dealing with

274    novel problems, and influence the benefits that individuals can derive from their cognitive

275    abilities.

276

277 Just as individuals commonly exhibit suites of inter-correlated behaviours (termed "behavioural

278 syndromes" [48]) they may also exhibit consistency in cognitive abilities across different

279 contexts. Indeed, there is a longstanding debate as to whether animal behaviour is underpinned

280 by cognitive specialisations that have evolved to fulfil specific ecological functions (e.g.

281 retrieving cached food [49–51]), or rather is governed by domain-general mechanisms that

282 operate across contexts. Herrmann and Call, using large datasets of the individual cognitive

283 performance of chimpanzees across a test battery of multiple different tasks, suggest that the

284 truth may lie somewhere in between the two views [50]. Their analyses reveal that while some

285 exceptional chimpanzees consistently outperformed their conspecifics across a range of tasks,

286 there is no evidence for one single "general intelligence" factor, but neither were performances

287 entirely unrelated across different tasks. Rather, the data appear to support the existence of a

288 number of distinct clusters of abilities, such as spatial knowledge and discrimination learning

289 [52]. Further work is needed to determine whether the cognitive abilities of other organisms will

290 exhibit similar clustering, but the evidence from chimpanzees suggests that there may be

291 common mechanisms that animals apply to different tasks within particular clusters of abilities.

292 An understanding of cognitive evolution will therefore benefit from explicit theoretical models to

293 consider not only how overt, measurable behavioural abilities evolve, but also how selection may

294 act on the underlying mechanisms [53].

295

296 *2.2 Modelling the evolution of cognitive mechanisms*

297 As Lotem & Halpern discuss, rigorous theoretical analyses of cognitive evolution must consider

298 how different components of cognitive processing interact and co-evolve [54]. For example, to

299 understand how learning mechanisms evolve, we must also consider the evolution of the

attentional and motivational mechanisms. Whereas traditional learning models assume that data

are presented to the animal as discrete, distinguishable stimuli, Lotem & Halpern's model

explicitly considers the fact that animals must sift through and obtain relevant information from

the morass of data in their environments. The model assumes that, when animals encounter

biologically relevant stimuli such as food, they will also attend to other information in the

immediate environment. This array of data is then compared to previously encountered datasets.

Segments of data that are rarely encountered tend to be forgotten and decay, while links between

commonly encountered segments increase in weight and may become fixed in memory. Thus, by

segmenting and linking chunks of data according to encounter rates and allowing irrelevant data

to decay, the animal may build up a structured representation of the environment without the

heavy computational burden of learning and remembering connections between all possible

segments of data. Natural selection may act to tweak the parameters of both the data acquisition

and learning mechanisms, resulting in organisms that are well adapted to handle the natural

distribution of biologically relevant data in their environment. Lotem & Halpern argue that this

process of co-evolution of data acquisition and learning may generate incremental cognitive

change, allowing organisms to extract relevant data even when faced with dynamic and complex

arrays of information such as those that characterise some social systems. In their view, this

process might even facilitate key human cognitive characteristics such as theory of mind and

language acquisition [54–56].

## 3. THE QUESTION OF HUMAN UNIQUENESS

321 Of course, the quest to understand how and why the cognitive abilities of our own species may

322 differ from those of other animals has long been a central motivating force for much of

323 comparative cognition. What cognitive processes make us unique, and what are the origins of

324 these processes? As Shettleworth discusses in her contribution to this issue, there have been a

325 multitude of theories of human uniqueness throughout the years [57]. Some of these suggest that

326 the difference between humans and other animals lies in broad, domain-general processes that

327 are manifested across a wide range of behavioural contexts [58,59]. In contrast, evolutionary

328 psychologists have tended to view human cognition as comprising a suite of discrete modules,

329 some of which may exist in our species alone [60]. Both of these approaches appear to

330 emphasise dichotomous distinctions between "us and them". Is a given cognitive faculty (be it

331 domain-general or specific) uniquely human, or might it be found in other animals? Such human

332 vs. non-human comparisons suffer from two main problems. First, comparative studies have

333 tended to apply tests designed for adult, verbal humans and thus may often risk underestimating

334 the abilities of non-verbal creatures [61]. Second, an emphasis on the presence or absence of

335 particular cognitive capacities may detract attention from the possibility that, even if an animal

336 fails a test of some human ability, some of the cognitive processes it applies may still be shared

337 with humans. Instead, Shettleworth [57] and Spelke [35] argue that important insights may lie in

338 examining the development of cognitive abilities over individual lifetimes. Just as in

339 evolutionary biology it is recognised that seemingly different traits may share important

340 developmental commonalities [62], it is increasingly clear that considering developmental

341 cognitive trajectories may reveal important elements of similarity and difference. For example,

342 experiments by Spelke and colleagues [35] suggest that human spatial cognition develops in two

343 distinct stages. From infancy, children exhibit two systems for representing objects and vectors.

344 These are largely shared with other animals and are thus likely to be evolutionarily ancient

345 cognitive adaptations for navigation. Later in development, the acquisition of language and

346 culture enables children to combine the two systems in uniquely human ways to form abstract

347 geometrical concepts (reviewed in [35]). Tomasello, Call and colleagues place a similar

348 emphasis on developmental processes as being at the heart of human socio-cognitive uniqueness

349 (reviewed in [63]). Their extensive comparative experiments suggest that while human children

350 and apes show similar performance on tests of physical, spatial and numerical cognition, children

351 typically outperform apes on social tasks. In particular, they argue that, unlike our closest

352 relatives, humans are endowed from an early age with the motivation to engage with others in

353 joint activities involving shared goals and attention. Later in development, this tendency

354 facilitates the use of linguistic symbols and the creation of cultural norms [52,64,65]. As these

355 examples show, a continued emphasis on developmental processes in comparative cognition is

356 likely to yield further important insights into the similarities and differences between humans

357 and other species. To fully take advantage of this approach, it is important to extend the current

358 focus on comparing children with adult non-human animals to compare developmental

359 trajectories across species, acknowledging the fact that non-human cognition also develops.

360 Indeed, a common theme of this issue is that, as the field of comparative cognition matures, it

361 must incorporate careful comparative analyses across all levels - within individual lifetimes,

362 between individuals and between species. Understanding animal cognition is a deeply

363 challenging endeavour, not least because it requires investigation of multiple layers, from genes

364 and neurones to computational processes and the resulting behaviours to the developmental and

365 evolutionary processes shaping cognition over time. We hope that a synthesis of empirical and

366 theoretical tools from fields including robotics, neuroscience, psychology and biology, such as

367 those showcased in this issue, will help future research further unravel the mysteries of animal

368 minds.

369

378

379 **REFERENCES**

380 1    Murphy, R. A., Mondragón, E. & Murphy, V. A. 2008 Rule learning by rats. *Science* **319**,

381        1849-1851. (doi:10.1126/science.1151564)

382 2    Wilson, B., Mackintosh, N. J. & Boakes, R. A. 1985 Transfer of relational rules in

383        matching and oddity learning by pigeons and corvids. *Q. J. Exp. Psychol.* **37B**, 313-332.

384        (doi:10.1080/14640748508401173)

385 3    Webb, B. 2012 Cognition in insects. *Phil. Trans. R. Soc. B* **This issue**.

386 4  Pearce, J. M. 2008 *Animal learning and cognition: an introduction*, *3ʳᵈ edition*. New
387    York: Psychology Press.

388 5  Seed, A. M., Tebbich, S., Emery, N. J. & Clayton, N. S. 2006 Investigating physical
389    cognition in rooks, *Corvus frugilegus*. *Curr. Biol.* **16**, 697-701.
390    (doi:10.1016/j.cub.2006.02.066)

391 6  Hood, B. M., Hauser, M. D., Anderson, L. & Santos, L. 1999 Gravity biases in a non-
392    human primate? *Dev. Sci.* **2**, 35-41. (doi:10.1111/1467-7687.00051)

393 7  Shettleworth, S. J. 2010 *Cognition, evolution and behaviour, 2nd Edition*. Oxford: Oxford
394    University Press.

395 8  Broadbent, N. J., Squire, L. R. & Clark, R. E. 2004 Spatial memory, recognition memory,
396    and the hippocampus. *Proc. Natl. Acad. Sci. USA* **101**, 14515-20.
397    (doi:10.1073/pnas.0406344101)

398 9  Muller, M. & Wehner, R. 1988 Path integration in desert ants, *Cataglyphis fortis*. *Proc.*
399    *Natl. Acad. Sci. USA* **85**, 5287-5290.

400 10 Clayton, N. S., Dally, J. M. & Emery, N. J. 2007 Social cognition by food-caching
401    corvids. The western scrub-jay as a natural psychologist. *Phil. Trans. R. Soc. B* **362**, 507-
402    22. (doi:10.1098/rstb.2006.1992)

403 11 Clayton, N. S. & Dickinson, a 1998 Episodic-like memory during cache recovery by scrub
404    jays. *Nature* **395**, 272-274.

405  12    Call, J. & Tomasello, M. 2008 Does the chimpanzee have a theory of mind? 30 years

406        later. *Trends Cog. Sci.* **12**, 187-92. (doi:10.1016/j.tics.2008.02.010)

407  13    Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007 Planning for the future

408        by western scrub-jays. *Nature* **445**, 919-921. (doi:10.1038/nature05575)

409  14    Thornton, A. & McAuliffe, K. 2006 Teaching in wild meerkats. *Science* **313**, 227-229.

410  15    Devetak, D. 1998 Detection of substrate vibration in Neuropteriodea: a review. *Acta Zool.*

411        *Fennica* **209**, 87–94.

412  16    Seed, A. M., Emery, N. J. & Clayton, N. S. 2009 Intelligence in corvids and apes: a case

413        of convergent evolution? *Ethol.* **115**, 401-420. (doi:10.1111/j.1439-0310.2009.01644.x)

414  17    Heyes, C. 2012 Simple minds: a qualified defence of associative learning. *Phil. Trans. R.*

415        *Soc. B* **This issue**.

416  18    Shettleworth, S. J. 2010 Clever animals and killjoy explanations in comparative

417        psychology. *Trends Cog. Sci.* **14**, 477-481. (doi:10.1016/j.tics.2010.07.002)

418  19    Gigerenzer, G. 1999 *Simple heuristics that make us smart*. Oxford: Oxford University

419        Press.

420  20    Silva, F. J., Page, D. M. & Silva, K. M. 2005 Methodological-conceptual problems in the

421        study of chimpanzees' folk physics: how studies with adult humans can help. *Learn.*

422        *Behav.* **33**, 47-58.

423    21    Chittka, L., Rossiter, S. J., Skorupski, P. & Fernando, C. 2012 What is comparable in

424          comparative cognition? *Phil. Trans. R. Soc. B* **This issue**.

425    22    Strausfeld, N. J. 2009 Brain organization and the origin of insects: an assessment. *Proc. R.*

426          *Soc. B* **276**, 1929-37.

427    23    Chittka, L. & Niven, J. 2009 Are bigger brains better? *Curr. Biol.* **19**, R995-R1008.

428          (doi:10.1016/j.cub.2009.08.023)

429    24    Bird, C. D. & Emery, N. J. 2009 Insightful problem solving and creative tool modification

430          by captive nontool-using rooks. *Proc. Natl. Acad. Sci. USA* **106**, 10370-10375.

431          (doi:doi/10.1073/pnas.0901008106)

432    25    Weir, A. A. S., Chappell, J. & Kacelnik, A. 2002 Shaping of hooks in New Caledonian

433          crows. *Science* **297**, 981.

434    26    Shanahan, M. 2012 Serial and parallel processes in animal cognition. *Phil. Trans. R. Soc.*

435          *B* **This issue**.

436    27    Rescorla, R. & Wagner, A. 1972 Variations in the effectiveness of reinforcement and

437          nonreinforcement. In *Classical conditioning II: current research and theory* (eds. A. H.

438          Black & W. F. Prokasy), pp. 64-99. New York: Appleton-Century-Crofts.

439    28    Mackintosh, N. J. 1974 *The psychology of animal learning*. New York: Academic Press.

440    29    Dickinson, A. 2012 Associative learning and animal cognition. *Phil. Trans. R. Soc. B* **This**

441          **issue**.

442  30  de Wit, S. & Dickinson, A. 2009 Associative theories of goal-directed behaviour: a case

443      for animal-human translational models. *Psychol. Res.* **73**, 463-76.

444  31  Dickinson, A. 1994 Instrumental conditioning. In *Animal learning and cognition* (ed N. J.

445      Mackintosh), pp. 45-79. San Diego, CA: Academic Press.

446  32  Clayton, N. S. & Dickinson, a 1999 Memory for the content of caches by scrub jays

447      (*Aphelocoma coerulescens*). *J. Exp. Psychol.* **25**, 82-91.

448  33  Seed, A. M., Seddon, E., Greene, B. & Call, J. 2012 Chimpanzee "folk physics": bringing

449      failures into focus. *Phil. Trans. R. Soc. B* **This issue**.

450  34  Penn, D. C. & Povinelli, D. J. 2007 Causal cognition in human and nonhuman animals: a

451      comparative, critical review. *Annu. Rev. Psychol.* **58**, 97-118.

452      (doi:10.1146/annurev.psych.58.110405.085555)

453  35  Spelke, E. S. 2012 Core systems of geometry in animal minds. *Phil. Trans. R. Soc. B* **This

454      issue**.

455  36  Heyes, C. M. 1993 Anecdotes, training, trapping and triangulating: do animals attribute

456      mental states? *Anim. Behav.* **46**, 177-188.

457  37  Heyes, C. M. 1998 Theory of mind in nonhuman primates. *Behav. Brain Sci.* **21**, 101-134.

458  38  Thornton, A. & Lukas, D. 2012 Individual variation in cognitive performance:

459      developmental and evolutionary perspectives. *Phil. Trans. R. Soc. B* **This issue**.

460　39　Chappell, J. & Hawes, N. 2012 Biological and artificial cognition: what can we learn

461　　about mechanisms by modelling physical cognition problems? *Phil. Trans. R. Soc. B* **This**

462　　**issue**.

463　40　Darwin, C. 1859 *On the Origin of the Species by means of Natural Selection*. London:

464　　Murray.

465　41　Dukas, R. 2004 Evolutionary Biology of Animal Cognition. *Annu. Rev. Ecol. Evol. Syst.*

466　　**35**, 347-374. (doi:10.1146/annurev.ecolsys.35.112202.130152)

467　42　Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy,

468　　D. 2009 Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.*

469　　**19**, 213-217. (doi:10.1016/j.cub.2008.11.064)

470　43　Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P. & Kelley, L. A. 2009 Explanations for

471　　variation in cognitive ability: Behavioural ecology meets comparative cognition. *Behav.*

472　　*Proc.* **80**, 288-294. (doi:10.1016/j.beproc.2008.10.002)

473　44　Cheney, D. L. & Seyfarth, R. M. 2007 *Baboon metaphysics: the evolution of a social*

474　　*mind*. Chicago: University of Chicago Press.

475　45　Proops, L., McComb, K. & Reby, D. 2009 Cross-modal individual recognition in

476　　domestic horses (*Equus caballus*). *Proc. Natl. Acad. Sci. USA* **106**, 947-51.

477　　(doi:10.1073/pnas.0809127105)

478　46　Hoppitt, W. J. E., Samson, J., Laland, K. N. & Thornton, A. In press. Identification of

479　　learning mechanisms in a wild meerkat population.

480   47   Mery, F. & Kawecki, T. J. 2003 A fitness cost of learning ability in *Drosophila*

481       *melanogaster*. *Proc. R. Soc. B* **270**, 2465-2469. (doi:10.1098/rspb.2003.2548)

482   48   Sih, A. & Del Giudice, M. 2012 Linking behavioural syndromes and cognition: a

483       behavioural ecology perspective. *Phil. Trans. R. Soc. B* **This issue**.

484   49   Healy, S. D., de Kort, S. R. & Clayton, N. S. 2005 The hippocampus, spatial memory and

485       food hoarding: a puzzle revisited. *Trends. Ecol. Evol.* **20**, 17-22.

486       (doi:10.1016/j.tree.2004.10.006)

487   50   Dwyer, D. M. & Clayton, N. S. 2002 A reply to the defenders of the faith. *Trends Cog.*

488       *Sci.* **6**, 109-111.

489   51   Bolhuis, J. J. & Macphail, E. M. 2001 A critique of the neuroecology of learning and

490       memory. *Trends Cog. Sci.* **5**, 426-433.

491   52   Herrmann, E. & Call, J. 2012 Are there geniuses among the apes? *Phil. Trans. R. Soc. B*

492       **This issue**.

493   53   McNamara, J. M. & Houston, A. I. 2009 Integrating function and mechanism. *Trends*

494       *Ecol. Evol.* **24**, 670-675. (doi:10.1016/j.tree.2009.05.011)

495   54   Lotem, A. & Halpern, J. Y. 2012 Co-evolution of learning and data acquisition

496       mechanisms: a model for cognitive evolution. *Phil. Trans. R. Soc. B* **This issue**.

497   55   Lotem, A. & Halpern, J. Y. 2008 A data-acquisition model for learning and cognitive

498         development and its implications for autism. *Cornell computing and Information science*

499         *technical reports,* http://hdl.handle.net/1813/10178


500   56   Goldstein, M. H., Waterfall, H. R., Lotem, A., Halpern, J. Y., Schwade, J. a, Onnis, L. &

501         Edelman, S. 2010 General cognitive principles for learning structure in time and space.

502         *Trends Cog. Sci.* **14**, 249-258. (doi:10.1016/j.tics.2010.02.004)


503   57   Shettleworth, S. J. 2012 Modularity, comparative cognition, and human uniqueness. *Phil.*

504         *Trans. R. Soc. B* **This issue**.


505   58   Penn, D. C., Holyoak, K. J. & Povinelli, D. J. 2008 Darwin's mistake: explaining the

506         discontinuity between human and nonhuman minds. *Behav. Brain Sci.* **31**, 109-30.

507         (doi:10.1017/S0140525X08003543)


508   59   Suddendorf, T. & Corballis, M. C. 2007 The evolution of foresight: What is mental time

509         travel, and is it unique to humans? *Behav. Brain Sci.* **30**, 299-313.

510         (doi:10.1017/S0140525X07001975)


511   60   Cosmides, L., Barrett, H. C. & Tooby, J. 2010 Adaptive specializations, social exchange,

512         and the evolution of human intelligence. *Proc. Natl. Acad. Sci. USA* **107**, 9007-9014.

513         (doi:10.1073/pnas.0914623107)


514   61   Boesch, C. 2007 What makes us human (*Homo sapiens*)? The challenge of cognitive

515         cross-species comparison. *J. Comp. Psychol.* **121**, 227-240. (doi:10.1037/0735-

516         7036.121.3.227)

517    62    Carroll, S. B. 2005 *Endless forms most beautiful*. New York: WW Norton & C.

518    63    Tomasello, M. 2009 *Why we cooperate*. Cambridge, MA: MIT Press.

519    64    Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005 Understanding and

520          sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675-91.

521          (doi:10.1017/S0140525X05000129)

522    65    Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B. & Tomasello, M. 2007

523          Humans have evolved specialized skills of social cognition: the cultural intelligence

524          hypothesis. *Science* **317**, 1360-1366. (doi:10.1126/science.1146282)

525