

Animal Consciousness: A Synthetic Approach

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Abstract

Despite anecdotal evidence suggesting conscious states in a variety of non-human animals, no systematic neuroscientific investigation of animal consciousness has yet been undertaken. We set forth a framework for such an investigation that incorporates integration of data from neuroanatomy, neurophysiology, and behavioral studies, uses evidence from humans as a benchmark, and recognizes the critical role of explicit verbal report of conscious experiences in human studies. We illustrate our framework with reference to two subphyla: one relatively near to mammals—birds—and one quite far—cephalopod molluscs. Consistent with the possibility of conscious states, both subphyla exhibit complex behavior and possess sophisticated nervous systems. Their further investigation may reveal common phyletic conditions and neural substrates underlying the emergence of animal consciousness.

(terms in **bold** appear in the glossary)

26 **A synthetic framework for studying animal consciousness.**

27

28 Although Darwin proposed that animal and human minds alike are the products of
29 natural selection ¹, questions of animal consciousness were largely neglected throughout
30 the 20th century (but see Griffin²; note the term ‘animal’ is used here to mean ‘non-human
31 animal’). This neglect may have arisen in part because, seemingly, only humans are
32 capable of accurately describing their phenomenal experience. However, there is now
33 abundant and increasing behavioral and neurophysiological evidence consistent with, and
34 even suggestive of, conscious states in some animals. We will use humans as a
35 benchmark for the development of new empirical criteria for further investigation. Here,
36 we apply this approach to birds and cephalopod molluscs, subphyla that exhibit complex
37 cognitive faculties and behaviors and have strikingly elaborate brains. These two
38 subphyla are examples of highly distinct lineages, and their study provides an excellent
39 opportunity to examine how conscious states might be instantiated in very different
40 nervous systems. While we do not resolve this issue here, we propose that its
41 examination lies within the reach of contemporary neuroscience.

42

43 ***Humans as a benchmark.*** The notion that consciousness can be engendered in
44 different nervous systems by a variety of underlying mechanisms suggests a need to
45 examine constraints, and therefore to synthesize behavioral, neurophysiological, and
46 neuroanatomical evidence. Human studies involving the correlation of **accurate report**
47 with neural correlates can provide a valuable benchmark for assessing evidence from
48 studies of animal behavior and neurophysiology. A constraint on this strategy is that the
49 capacity for accurate report of conscious contents implies the presence of **higher-order**
50 **consciousness**, which in advanced forms may require linguistically-based narrative
51 capability. This is in contrast to **primary consciousness**, which entails the ability to
52 create a scene in the ‘remembered present’³ in the absence of language. Primary
53 consciousness may be a basic biological process in both humans and animals lacking true
54 language.

55 Various properties of human consciousness can be identified at neural, behavioral,
56 and phenomenal levels ⁴. Neural correlates of human consciousness include the presence

57 of thalamocortical signaling, fast, irregular, low-amplitude electroencephalographic
58 (EEG) signals, and widespread cortical activity correlated with conscious contents⁵⁻⁷. At
59 the behavioral level, consciousness has been associated with behavioral flexibility⁸,
60 rational action⁹, and certain forms of conditioning¹⁰. These can be related to cognitive
61 properties involving widespread access and associativity⁸, multiple discriminations¹¹,
62 and the capacity for accurate report⁵. These properties can be mapped to a variety of
63 functions related to consciousness¹². At the phenomenal level, human consciousness
64 involves the presence of a sensorimotor scene, the existence of a first-person perspective,
65 the experience of emotions, moods, and a sense of agency^{13 14}.

66 Using humans as a benchmark, behavioral, cognitive, and neural properties can be
67 employed as empirical criteria informing the ascription of conscious states to animals
68 (Figure 1). The application of this approach requires that: (i) at least some of these
69 properties reliably occur in both humans and animals; (ii) human brain areas responsible
70 for consciousness can be seen to be integrated with those areas responsible for accurate
71 report of phenomenal experience; and (iii) neural evidence that can be correlated with
72 phenomenal properties of consciousness must in addition *account for* those properties.
73

74 In humans, explicit verbal, or linguistic, report of a conscious experience is
75 sometimes taken as a ‘gold standard’ in the sense that it guarantees the presence of
76 consciousness. However, many creatures, including infants, most animals, and aphasic
77 human adults, are constitutively unable to produce linguistic reports. The production of
78 such reports is therefore too limiting a criterion for ascription of consciousness in general.
79 Importantly, accurate report may exploit behavioral channels other than language, for
80 example lever presses or eye blinks (Box 1). However the ability to provide such report
81 nonetheless implies the presence of higher-order (metacognitive) access to primary
82 conscious contents, which may not be constitutively required for primary consciousness.
83 Our approach therefore recognizes that the mechanisms responsible for primary
84 consciousness may be distinct from those mechanisms enabling its report.

85

86 The extent to which neural evidence can account for phenomenal properties is
87 particularly important with respect to those properties that are common to most or all
88 conscious experiences. For example, in humans, every conscious scene is both integrated
89 (i.e., ‘all of a piece’) and differentiated (i.e., composed of many different parts) ¹¹.
90 Therefore, finding neural processes that themselves exhibit simultaneous integration and
91 differentiation would help to *explain*, and not merely correlate with, the corresponding
92 phenomenal property. Such neural processes can therefore be considered to be
93 ‘**explanatory correlates of consciousness**’ ¹⁴, and because they are explanatory, their
94 identification in animals is more suggestive of the presence of corresponding phenomenal
95 properties than is the identification of neural correlates *per se*. In this view, conscious
96 states are neither identical to neural states nor are they computational or functional
97 accompaniments to such states; rather, conscious states are entailed by neural states in
98 much the same way that the spectroscopic response of hemoglobin is entailed by its
99 molecular structure ⁶.

100

101 The presence of voluntary behavioral responses is another candidate ‘gold
102 standard’ for the ascription of consciousness. However, the absence of such responses in
103 humans does not necessarily imply absence of phenomenal experience. For example, in a
104 recent study of a patient in a behaviorally unresponsive vegetative state, brain activity
105 related to volition was taken as persuasive evidence of residual consciousness ¹⁵.
106 Conversely, behavior that appears to be volitional could be attributed widely among
107 animals on the basis of spontaneous and adaptive behavioral responses. Therefore,
108 apparent voluntary behavior at best provides a weak criterion for the ascription of
109 consciousness. In addition, conditions such as the vegetative state underscore the point
110 that consciousness should not be confused with arousal or inferred directly from the
111 existence of distinct sleep/wake cycles. States resembling deep sleep have been
112 observed in many animals, including *Drosophila melanogaster* ¹⁶ and *Caenorhabditis*
113 *elegans* ¹⁷; conversely, female killer whales and dolphins and their newborn calves may
114 not sleep for periods of four to six weeks *postpartum* ¹⁸.

115

116 ***Mammalian consciousness: Extending the benchmark.*** Mammals, particularly
117 primates, share with humans many neurophysiological and behavioral characteristics
118 relevant to consciousness, and therefore represent a relatively uncontroversial case for the
119 ascription of at least primary consciousness⁵. In a classical example, Logothetis *et al.*
120 trained rhesus macaque monkeys to press a lever to report perceived stimuli in a
121 **binocular rivalry** paradigm¹⁹ (Box 1). Neurons in macaque inferior temporal (IT)
122 cortex showed activity correlated with the reported percept, whereas neurons in the visual
123 area V1, instead responded to the visual signal. This suggests a critical role for IT in
124 visual consciousness. These observations are consistent with evidence from humans
125 subjected to binocular rivalry while being examined via magnetoencephalography
126 (MEG). The results from these studies suggest that consciousness of an object involves
127 widespread coherent synchronous cortical activity²⁰. This correspondence between
128 monkeys and humans provides an example of how benchmark comparisons across
129 humans and animal species can be made. With this in mind, we now explore the
130 application of benchmark comparisons to two widely divergent animal subphyla: birds
131 and cephalopod molluscs. We are aware of the pitfalls of making facile comparisons and
132 implying that homologies exist in the absence of strong evolutionary evidence. In each
133 case, we will present behavioral evidence first, and then present evidence based on neural
134 architecture and dynamics.

135

136 **Building a Case for Avian Consciousness**

137

138 ***Avian cognition and behavioral capabilities.*** Feats of avian memory^{21,22}, tool use and
139 manufacture²³, deception²⁴, and vocal learning and performance^{25,26}, the capacity of
140 some species to employ lexical terms in meaningful ways²⁷, and evidence for higher
141 order discriminations in some birds^{27,28} collectively support the functioning of nervous
142 systems as sophisticated as those of most mammals.

143

144 Episodic and working memory capabilities are implied by the sophisticated food
145 caching behaviors of corvids (e.g., jays, jackdaws, magpies, rooks, crows, and ravens)²³
146 and by laboratory-based demonstrations of **transitive inference** and delayed-match-to-

147 sample in pigeons and great tits²⁹. African grey parrots, magpies, and ring doves have
148 shown the ability to track periodically hidden and displaced objects; such object
149 constancy certainly requires working memory³⁰. In addition, spatial learning, though
150 obviously implied by navigation during flight, has been shown explicitly by hooded
151 crows learning to negotiate a radial maze³¹.

152

153 Studies of avian tool use and manufacture imply not only elaborate memory and
154 learning substrates, but also the ability to make sophisticated discriminations and to plan
155 behaviors before executing them. For example, New Caledonian crows have been
156 observed to fashion hooked-wire tools to retrieve food from a glass cylinder, sometimes
157 flying to a distant perch to bend the wire before returning to the cylinder²³. Similarly,
158 wild crows are known to fabricate tools from twigs and leaves in order to extract insects
159 from holes in trees²³. In addition, a variety of avian species, including Japanese quails³²
160 and European starlings³³, may be capable of social or observational learning (but see
161 Zentall³⁴ and Heyes³⁵). Perhaps most notable are instances in which scrub jays re-
162 cached food in private after their initial caching was witnessed by conspecifics³⁰, and
163 observations of ravens challenging conspecifics that witnessed caching activities while
164 ignoring 'naïve' birds³⁶. These behaviors suggest that some birds may be capable of
165 theory of mind.

166

167 ***The avian vocal channel.*** While the foregoing cognitive capabilities are suggestive of
168 conscious states, the most promising avenue for investigating avian consciousness may
169 involve the study of species capable of vocal learning, which enables a highly flexible
170 form of accurate report. The capacity for some form of vocal learning is shared by at
171 least six animal groups, including cetaceans, bats, parrots, songbirds, hummingbirds,
172 elephants, and possibly even mice and some other rodents³⁷. In birds, vocal learning
173 enables sophisticated song learning and production, mimicry of sounds, and, in the
174 psittacines (parrots), word production, comprehension, and naming²⁷. For example,
175 African grey parrots were able to name objects, having acquired vocabularies roughly
176 equivalent to those of some language-trained chimpanzees (albeit after years of training
177 and reinforcement)³⁸. Indeed, by naming objects in categorization paradigms, these

178 animals appeared to produce accurate reports of sophisticated discriminations they were
179 making. ‘Alex,’ a principal subject of many of these experiments, when presented with
180 an altered array of objects, seemed able to make a judgment to the effect that, “I know
181 that something in this perceptual scene has changed, and here is what has changed.”
182 This finding suggests the ability to make discriminations about putative primary
183 conscious states that appears to resemble some form of higher order consciousness^{27 28}.

184

185

186 *Avian neural structures and processes homologous to those of mammals suggest*
187 *possible neural substrates for both consciousness and its report.*

188

189 On what structural bases might avian vocal behavior be related to structures
190 underlying human verbal accurate report? Supporting evidence could come from shared
191 neural mechanisms. One example may be the neural substrate for motor learning in
192 mammals and that for song learning in some birds. Much of the neural basis for song
193 learning in oscines (songbirds) and psittacines resides in an anterior forebrain pathway
194 involving the basal ganglia, in particular, a striatal nucleus called Area X³⁹ (see Figure
195 2). The anatomical and physiological properties of neurons in Area X closely resemble
196 those of neurons in the mammalian striatum. Specifically, the four neuronal phenotypes
197 found in mammalian striatum are also present in Area X. A notable difference is the
198 presence of a fifth neural phenotype in Area X—but not in mammalian striatum—that is
199 similar to cells found in the mammalian globus pallidus. Area X may therefore comprise
200 a novel mixture of striatal and pallidal anatomies, but it is nonetheless recognizably
201 homologous to the direct striatopallidothalamic pathway of the mammalian basal ganglia
202³⁹. A similar circuit has been reported in the anterior forebrain of the budgerigar, a parrot
203⁴⁰. Together, these findings strongly suggest common functional circuitry underlying the
204 organization and sequencing of motor behaviors related to vocalization in birds and
205 mammals capable of vocal learning. However, whether in some birds this circuitry is
206 embedded within a broader network homologous to that underlying human verbal report
207 remains to be determined.

208

209 Another avenue for exploring non-mammalian consciousness is to identify
210 structural and functional homologs to mammalian thalamocortical systems. Vertebrate
211 nervous systems follow a highly conserved body plan that emerged with the first
212 chordates more than 500 million years ago. Consequently, many vertebrate neural
213 structures can be traced to common origins in specific embryological tissues. Avian
214 homologs of subcortical structures, such as the hypothalamus and pre-optic area, are
215 relatively easy to recognize. Although the identity of the avian neural homolog of
216 mammalian isocortex remains controversial^{41, 42}, comparative embryological studies
217 suggest that the basic underlying neuronal composition and circuitry of the mammalian
218 cortex were established within clustered arrangements of nuclei long before the
219 appearance of the distinct six-layered mammalian cortex⁴³. In particular, the nuclei
220 comprising the dorsal ventricular ridge (DVR) of the developing avian brain contain
221 neuronal populations homologous to those present in different layers of the mammalian
222 neocortex. These include neurons receiving thalamic input, as well as cells projecting to
223 brainstem and spinal cord neurons. The neurons of the avian DVR and mammalian
224 cortex are nearly identical in both their morphology and constituent physiological
225 properties⁴⁴.

226

227 Structural homologies can also be identified using molecular and
228 immunohistological techniques. In particular, neurotransmitters, neuropeptides, and
229 receptors specific to particular neuronal populations within mammalian brain regions
230 have been localized to homologous avian brain regions. For example, both AMPA
231 receptor subunits and the pallidal neuron/striatal interneuron marker Lys8-Asn9-
232 neurotensin8-13 (LANT6) are found in the neurons of both mammalian and avian basal
233 ganglia^{45, 46}. Finally, gene expression patterns similar to those of mammals have been
234 identified in the avian brain. For example, a comparison of homeotic genes involved in
235 early brain development in chick and mouse embryos has revealed robust structural
236 homologies between parts of the avian telencephalon and mammalian cortex⁴⁷.

237

238 Deep avian-mammalian homologies have also been revealed by examining
239 functional properties of neuronal populations within particular brain regions. The avian

240 anterior forebrain pathway may be functionally analogous to the mammalian corticobasal
241 ganglia–thalamocortical loop. This is suggested by the presence of both inhibitory and
242 excitatory pathways in the medial nucleus of the avian dorsolateral thalamus (DLM), as
243 well as by functional similarities between neurons in the DLM and mammalian
244 thalamocortical neurons. Similarities have also been found among the excitatory and
245 inhibitory circuitry of birds and mammals, particularly in the serotonergic, GABAergic,
246 and dopaminergic systems ⁴⁸.

247

248 In addition to neuroanatomy, electrophysiological studies are critical in
249 establishing functional homologies between avian and mammalian nervous systems.
250 Currently, however, common properties of mammalian thalamocortical neurons, such as
251 low-threshold calcium (Ca²⁺) spikes and slow oscillations, have not yet been found in
252 birds ⁴⁹. Nonetheless, similarities between the waking EEG patterns of birds and
253 mammals, as well as slow wave electrical activity recorded during avian sleep ⁵⁰, are
254 suggestive of neural dynamics that might support conscious states in birds.

255

256 The existence in birds of structural and functional homologies to mammalian
257 thalamocortical systems is certainly consistent with the presence of higher cognitive
258 faculties and perhaps consciousness ^{30, 51}. Nevertheless, a compelling case for avian
259 consciousness cannot be made solely on the strength of relevant neuroanatomical and
260 neurophysiological resemblances. Nor are descriptions of avian behaviors that imply
261 sophisticated cognitive capabilities sufficient to make such a case. New experimental
262 strategies are needed for evaluating possible conscious discriminations in awake,
263 behaving birds. The findings obtained from studies of Alex the African grey parrot
264 encourage the development of such strategies. Even more challenging though are
265 approaches to investigating conscious behavior in invertebrates.

266

267 **Searching for Consciousness in Invertebrates: The Cephalopod Case**

268

269 *The richness of cephalopod behavioral repertoires.* In addition to possessing large
270 brains, cephalopod molluscs have extremely flexible behavior and highly developed

271 attentional and memory capacities that may be suggestive of conscious states ⁵². The
272 performance of some cephalopods (particularly *Octopus vulgaris*) in several learning and
273 memory paradigms (e.g., flexibility, persistence of memory traces, contextual learning)⁵³
274 is formidable, and comparable in sophistication to that of some vertebrates. Octopuses
275 can make discriminations between different objects based on size, shape, and intensity ⁵⁴,
276 ⁵⁵, classifying differently shaped objects in the same manner as vertebrates ranging from
277 goldfish to rats ⁵⁵. Octopuses are also capable of finding the correct path to a reward in a
278 plexiglas maze and can retrieve objects from a clear bottle sealed with a plug ^{56,57}. In
279 another striking study, ‘naïve,’ or ‘observer,’ octopuses watched conditioned animals
280 (‘demonstrators’) choose between two simultaneously presented objects that differed in
281 contrast only; the observer octopuses later made the same contrast choices in isolation
282 and without any explicit conditioning ⁵⁸. Although controversial ⁵⁹⁻⁶², this finding
283 suggests that octopuses are capable of observational learning, a faculty previously
284 thought to be unique to highly social animals.

285

286 Finally, distinct capacities for short- and long-term memory have been shown in
287 both the octopus and the cuttlefish ^{53,63}. In a maze containing obstacles that were
288 changed *ad libitum*; octopuses could remember these changes and adjust their movements
289 accordingly. Interestingly, the octopuses in this study appeared to pause and deliberate
290 about the layout of the maze before proceeding ⁶⁴.

291

292 ***Cephalopod brains: complex nervous systems distant from the vertebrate line.*** The
293 organization of invertebrate nervous systems diverges so greatly from those of
294 vertebrates such as birds and mammals that, until recently, sophisticated cognitive
295 capabilities had rarely been ascribed to invertebrate species (see Figure 2). Bees ^{65,66},
296 spiders ^{67,68}, and the cephalopod molluscs ⁵² are notable exceptions.

297

298 Of all cephalopod molluscs, the octopus has the largest population of sensory
299 receptors. These receptors communicate with a nervous system that, in adults, may
300 contain between 170 million and 500 million cells, most of which are neurons ^{69,70}. In
301 the brain of one genus of squid, *Loligo*, at least 30 distinct nucleus-like lobes have been

302 identified⁷¹. The optic lobe, the largest of the fused central ganglia, contains as many as
303 65 million neurons. In addition to processing visual input, the optic lobe plays a critical
304 role in higher motor control and the establishment of memory⁶⁹. A number of other
305 lobes may be functionally equivalent to vertebrate forebrain structures⁶⁹, though their
306 organization bears little resemblance to the laminar sheets of mammalian cortex. In
307 particular, the vertical, superior frontal, and inferior frontal lobes of octopus, squid, and
308 cuttlefish are involved in memory consolidation^{63, 72, 73}. In experiments in which the
309 vertical lobe of *Octopus vulgaris* was lesioned, the ability to learn visual discriminations
310 was severely impaired, but long-term memory consolidation remained intact⁶³. Removal
311 of the median inferior frontal lobe caused memory deficits that compromised learning^{54,}
312 ⁷⁴. Taken together, these studies suggest that some regions of the octopus frontal and
313 vertical lobes are functionally comparable to regions of mammalian cortex (see Young⁷⁵
314 for a review).

315

316 Radical differences between cephalopod nervous systems and those of vertebrates
317 are exemplified by the parallel, distributed architecture of the octopus locomotor system.
318 The number of neurons in the tentacles of the octopus collectively exceeds the total
319 number in the central fused ganglia of the brain itself⁷⁰. A detached octopus arm will
320 flail in a realistic manner when stimulated with short electrical pulses⁷⁶, suggesting
321 pseudoautonomous control of some locomotor behavior patterns and hinting at a
322 sophistication of sensorimotor coordination rivaling that of many vertebrates. This
323 elaborate bodily representation in the service of sensorimotor coordination for adaptive
324 behavior (e.g., locomotion, camouflage, mimicry) might support a ‘core selfhood’⁷⁷ (see
325 Box 2), a tantalizing concept as applied to cephalopods.

326

327 With regard to neuropharmacological and physiological properties, the
328 cephalopod nervous system contains many of the major neurotransmitters that are found
329 in mammalian brains^{69, 78}. In particular, the presence of dopamine (DA), noradrenaline
330 (NA), and serotonin (5-HT) receptor subtypes that resemble those found in vertebrates
331 may reflect the presence of circuitry similar to vertebrate excitatory and inhibitory
332 pathways. As is the case with functional avian neuroanatomy, application of

333 immunohistochemical and genetic techniques may help determine cephalopod functional
334 analogs to neural regions in mammals that show correlated activity during conscious
335 behavior. An encouraging indication is the recent identification of a cephalopod ortholog
336 to the FoxP2 gene, which in birds and humans has been implicated in motor function
337 related to song and language production, respectively. Notably, FoxP2 expression has
338 been observed in the adult octopus chromatophore lobes⁷⁹.

339

340 What can be said of neurodynamics in cephalopod brains? Examination of
341 octopus vertical lobe slices has identified long-term potentiation (LTP) of glutamatergic
342 synaptic field potentials similar to those found in vertebrates⁸⁰. More directly related to
343 possible conscious states, electrophysiological studies have identified EEG patterns,
344 including event related potentials, which resemble those of awake vertebrates, and at the
345 same time are distinct from those recorded in other invertebrates.^{81,82} Identifying
346 cephalopod EEG patterns that reflect low amplitude fast irregular activity similar to that
347 observed during human conscious states will require determination of suitable recording
348 sites. Optic, vertical, and superior lobes of the octopus brain—all of which are critical to
349 learning and memory—are relevant candidates.

350

351 The similarities discussed above by no means confirm the existence of conscious
352 states in cephalopod molluscs, but neither do they exclude them. An intermediate effort
353 to clarify the situation might be the pursuit of psychophysics in cephalopods, an approach
354 not yet represented in the literature (see Box 1).

355

356 **Concluding remarks.** Approaches to animal consciousness require both clear theoretical
357 frameworks and relevant experimental evidence. We have suggested that a useful
358 approach is to synthesize neuroanatomical, neurophysiological, and behavioral evidence,
359 using humans as a benchmark. We recognize that a distinction between primary and
360 higher-order consciousness implies that mechanisms underlying putative primary
361 conscious states might be distinct from, though possibly overlapping with, mechanisms
362 allowing its accurate report, such that absence of evidence need not be evidence of
363 absence in regard to animal consciousness.

364

365 Within this framework, we find that birds exhibit rich cognitive and behavioral
366 capabilities consistent with conscious states, including working memory, social learning,
367 planning, and possibly even insight during problem solving. These capabilities are
368 complemented by substantial anatomical homologies and functional similarities with
369 mammals in the thalamocortical systems that are associated with consciousness. The
370 case for cephalopod molluscs is currently much less clear. However, abundant evidence
371 of sophisticated learning and memory faculties and rich behaviors, as well as early
372 indications from studies of cephalopod neurophysiology, suggest at least the possibility
373 of conscious states.

374

375 Given profound gaps that remain in the neuroanatomical characterization of both
376 subphyla, many basic questions remain concerning the existence, form, and prevalence of
377 non-mammalian consciousness (see Outstanding Questions). Future progress in
378 addressing these questions will require elaboration of behavioral paradigms designed to
379 assess complex discriminatory behavior associated with consciousness. Vocal learning in
380 birds provides a particularly promising avenue for achieving this objective (Box 1). In all
381 cases, theoretical developments are necessary to facilitate the transition from correlation
382 to causal explanation¹⁴. Such a transition will allow attribution of animal consciousness
383 to be based causally on neural properties rather than on indirect behavioral report.
384 Finally, we note that work on animal consciousness may help in assessing consciousness
385 in humans incapable of report, including infants and patients in vegetative and minimally
386 conscious states.

387

388 **Glossary**

389

390 **Accurate report** is a first-person account of what an individual is experiencing, made
391 without the attempt to mislead. Accurate report, which can be given through language or
392 related varieties of voluntary response, has been critical in the investigation of conscious
393 states in humans. In animals without the faculty of natural language, forms of behavioral
394 report acting through other motor channels might be examined to determine the possible

395 presence of high-order discriminations suggesting conscious states.

396

397 **Binocular rivalry** occurs when the two eyes are each simultaneously presented with a
398 different image. Rather than seeing both images superimposed on one another, the
399 subject sees one image first, then the other, in an alternating sequence. For example, if
400 one eye is presented with parallel vertical stripes and the other with horizontal parallel
401 stripes, rather than seeing an overlapping ‘weave’ of vertical and horizontal stripes, the
402 subject sees first one orientation of stripes, then the other ⁸³.

403

404 **Explanatory correlates of consciousness.** Conventional approaches within
405 consciousness science have emphasized the search for so-called ‘neural correlates of
406 consciousness’: neural activity having privileged status in the generation of conscious
407 experience ⁷. However, the transition from correlation to explanation requires an
408 explanation of how particular neural correlates *account for* specific properties of
409 consciousness. Searches for explanatory correlates of consciousness attempt to provide
410 this link ^{11 14}.

411

412 **Primary consciousness** refers to the experience of a multimodal scene composed of
413 basic perceptual and motor events. Primary consciousness is sometimes called perceptual
414 or phenomenal consciousness, and it may be present in animals without true language.
415 By contrast, **higher-order consciousness** involves the referral of the contents of primary
416 consciousness to interpretative semantics, including a sense of self and, in more advanced
417 forms, the ability to explicitly construct past and future narratives ³. The presence of
418 higher order consciousness or metacognition should not be assumed to be necessary for
419 the ascription of primary consciousness, though it may be constitutively required for
420 advanced forms of self-consciousness and consciousness of consciousness (Box 2).

421

422 **Transitive inference** is the ability to connect two or more separate relations, and is
423 widely regarded as a fundamental process in reasoning. Such abilities have been
424 demonstrated in certain birds. For example, in experiments involving the relative ranking
425 of objects presented in pairs, pigeons were able to determine that B>D after they had

426 separately learned that $A > B$, $B > C$, $C > D$, and $D > E$, while great tits have been observed to
427 deduce complex social dominance rankings³⁰.
428

428 **Box 1: Metacognition, blindsight, and behavioral report**

429

430 In seminal experiments by Cowey and Stoerig⁸⁴, rhesus macaques with lateralized
431 lesions to the visual area V1 were trained to touch a region of a video display where
432 stimuli appeared. These monkeys could detect and discriminate between stimuli
433 presented within their lesioned hemifields, but they could not distinguish between regions
434 with stimuli presented in these hemifields and regions containing no stimuli presented in
435 their unaffected hemifields. The absence of response in the latter case has been
436 interpreted as a ‘metacognitive comment,’ indicating lack of awareness of the difference
437 between the two hemifields. This could be compared to the responses of human
438 ‘blindsight’ patients who claim not to see stimuli to which they nonetheless successfully
439 respond. The plausibility of this comparison depends to a degree on the highly conserved
440 neuroanatomy between macaques and humans. When adapted in conjunction with an
441 improved understanding of neural analogs and homologs between mammals and other
442 subphyla, the ‘commentary key’ paradigm suggested by Cowey and Stoerig⁸⁴ provides a
443 valuable experimental platform. For example, ‘avian blindsight’ might be inducible by
444 lesioning the ectostriatum, the avian brain area analogous to mammalian V1 (Figure 2).
445 Although the optic tracts of many birds are nearly completely decussated (>99%) to
446 opposite hemispheres of the brain, precluding hemifield arrangements analogous to those
447 in monkeys and humans, and the avian brain lacks a corpus collosum, evidence of
448 interhemispheric switching⁸⁵ suggests that binocular rivalry might be achieved under
449 appropriate experimental conditions. Metacognitive comments on the presence or
450 absence of stimuli in occluded hemifields could be made through vocalizations
451 previously entrained to those stimuli.

452

453 Similar approaches can be envisioned in cephalopod molluscs if functional analogs
454 to mammalian visual cortex can be discerned (Figure 1). For example, we suggest a
455 version of the ‘attentional blink’ paradigm, a phenomenon observed when human
456 subjects are presented with a rapid sequence of co-located visual stimuli. A subject will
457 fail to observe a secondary salient target stimulus occurring within this succession if it is
458 presented between 200 and 500 ms after the first stimulus⁸³. In an octopus presented

459 with a serial stream of stimuli containing a 'blink' stimulus, the chromatophore system ⁸⁶,
460 ⁸⁷ or other components of body patterning ⁸⁸ might provide a channel for experiments to
461 explore similar effects. For example, an octopus could be presented with a serial stream
462 containing an image of an octopus displaying chromatophore patterns associated with
463 aggression in succession with patterns associated with mating display. Variation in
464 responses to the second target, if presented in close temporal proximity to the first, would
465 be suggestive of a 'blink.' Such 'psychophysical' experiments must recognize that
466 cephalopod vision is substantially different from vertebrate vision. Most cephalopod
467 molluscs are color-blind ⁸⁹, but many are known to perceive polarized light and make
468 subtle discriminations based on this capacity ^{90, 91}.

469

470

470 **Box 2: Animal selves**

471

472 Animal selfhood can be conceived at many levels. A primitive or ‘core’ self may depend
473 on self-modeling processes that use sensorimotor predictions to guide behavior leading to
474 the emergence of a ‘point-of-view’¹³. Core selfhood may arise from the complexity of
475 the sensorimotor coordination and proprioception needed to support adaptive behavior⁷⁷.
476 It may also depend on ‘feelings’ or emotional states mediated by interoceptive
477 representations of bodily states^{92,93} related to homeostatic control of low-level drives for
478 (at least) air, water, food, and pain avoidance^{94,95}.

479

480 Advanced selfhood involves the emergence of the subjective ‘I’ of higher order
481 consciousness, and, in its most elaborated form, the ability to understand the world from
482 the perspective of another. Basic requisites for a subjective ‘I’ are suggested by ‘mirror
483 self-recognition’ (MSR) experiments, in which, for example, animals spontaneously use a
484 mirror to examine an otherwise inaccessible body region⁹⁶. MSR has been demonstrated
485 in primates, including chimpanzees, orangutans, and (less conclusively) gorillas^{96,97};
486 evidence suggestive of MSR has also been elicited from Asian elephants⁹⁸, dolphins⁹⁹,
487 and magpies¹⁰⁰. Even in chimpanzees, however, the prevalence of MSR behavior is only
488 about 75%¹⁰¹.

489

490 Even though animals lacking higher order consciousness cannot construct a
491 subjective ‘I,’ taking humans as a benchmark suggests new experimental approaches.
492 For example, combining virtual reality with tactile feedback can lead to a displacement of
493 the first person perspective to a place outside the physical body, similar to spontaneous
494 ‘out-of-body’ experiences¹⁰². This displacement, possibly due to a disruption of self-
495 modeling, can be validated both by accurate report (e.g., “I see myself from behind”), and
496 by indirect behavioral evidence (e.g., subjects move in directions reflecting their
497 perceived location). Similar results obtained from animals would suggest that they, too,
498 possess a body-centered locus of experience.

499

500 Recent neuroimaging results have exposed new self-related neural processes in
501 humans that may prompt similar searches in animals. Activity in the human ‘default
502 network’ is correlated with stimulus-independent thought and self-related conscious
503 content ¹⁰³, and is anti-correlated with sensitivity to external somatosensory stimuli ¹⁰⁴.
504 The right insular cortex appears important for self-consciousness ¹⁰⁵, with anterior
505 subregions possibly supporting explicit representations of feeling states underlying
506 higher-order self-representations ⁹². Hypoactivation of insula has been reported in
507 humans with ‘depersonalization disorder,’ involving reduced subjective validity of the
508 self ¹⁰⁶. Identification of animal analogs to these processes would require demonstration
509 of very close homologies so far not achieved. Indeed, the thalamocortical pathway
510 conveying interoceptive signals to the right anterior insula appears to be unique to
511 primates ⁹², suggesting important species-specific differences as well as commonalities to
512 be kept in mind in considering animal consciousness.

513

514

515

515 **Outstanding questions**

516

- 517 • How can we distinguish the neural mechanisms underlying accurate report from
518 those underlying primary consciousness?
- 519 • Can degrees of consciousness be established among different species?
- 520 • What invertebrate neural structures and mechanisms may be analogous in
521 function to mammalian thalamocortical systems?
- 522 • What function does consciousness serve in adaptive behavior?
- 523 • When did consciousness appear in the course of evolution?
- 524 • How might a synthetic approach facilitate the study of consciousness in other
525 phyla, i.e., reptiles, amphibians, and bony and cartilaginous fish?
- 526 • What ethical implications would emerge if convincing evidence is obtained for
527 widespread animal consciousness?

528

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530

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539

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764

765

766

766 **Figure 1 Caption**

767

768 The investigation of possible conscious states in non-human species as disparate as birds
769 **(a)** and cephalopods **(b)** can be informed by searching for neural properties that have
770 been correlated with consciousness in humans, including reentrant signaling between
771 thalamus and cortex **(a, i)** or putative functional analogs **(b, i)**, fast, irregular, low-
772 amplitude EEG signals **(a and b, ii)**, and widespread electrical activity in cortex **(a, iii)** or
773 functionally analogous structures **(b, iii)**. Such processes in animals can best be related to
774 consciousness when they can be correlated with accurate reports. Relevant forms of
775 report include vocalizations in the case of African grey parrots **(a, iv)** or coloration and
776 body patterning in the case of cephalopods **(b, iv)**. In the figure, an African grey parrot
777 and a common octopus (*O. vulgaris*) respond to salient artificial stimuli presented on
778 video displays: an orange block in a discrimination task **(a, iv)** and a white ball that has
779 been previously associated with food (herring) during training **(b,iv)** (see Box 1).

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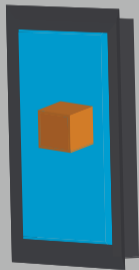
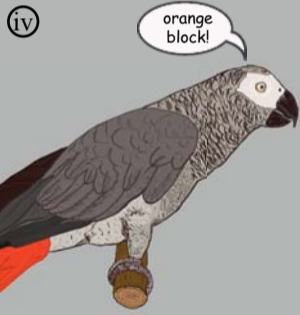
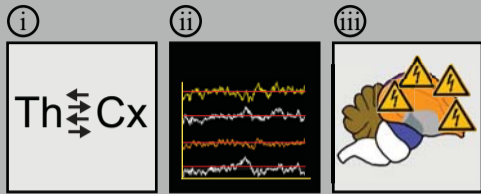
782 **Figure 2 Caption**

783

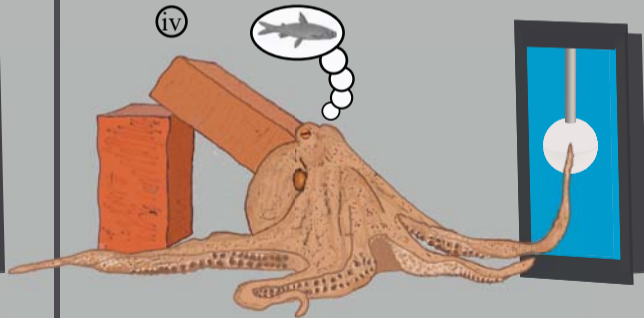
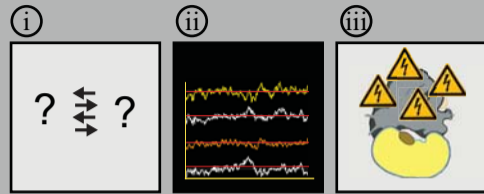
784 Avian and mammalian brains contain homologous structures and similar functional
785 circuitry; the complex nervous systems of coleoid cephalopods may exhibit some
786 functional circuitry analogous to those of higher vertebrates. **a.** Midline sagittal section
787 of a human brain showing major structures, including those involved in generating
788 conscious states (e.g., cortex, thalamus, and basal ganglia). **b.** Midline sagittal section of
789 the brain of a zebra finch, a songbird. Major neural structures are shown, including those
790 with mammalian homologs. Also shown is a greatly simplified schematic of the anterior
791 forebrain pathway for song learning (yellow arrows) involving components of the basal
792 ganglia, including the striatal nucleus Area X ('X' in filled red circle). Circular inset to
793 right of human brain shows zebra finch brain to scale for comparison. **c.** Midline section
794 of the brain of an octopus (*O. vulgaris*). Most major lobes and ganglia are shown.
795 Vertical (VL) and medial superior frontal (MSF) lobes (purple hatched lines), containing
796 circuitry critical for long-term memory, are shown in a magnified view in circular inset
797 on right. Key (bottom of figure) shows color-coding of major brain regions to indicate

798 homology or functional and/or structural analogy. Other regions of human and avian
799 brains labeled: LV: lateral ventricle; Pd: pallidum. Pallial divisions of the avian
800 cerebrum are indicated as follows: HPa: hyperpallium; MPa: mesopallium; NPa:
801 nidopallium. Components of the avian anterior forebrain pathway are indicated as
802 follows: DLM: medial nucleus of the dorsolateral thalamus; HVC: higher vocal center;
803 LMAN: lateral magnocellular nucleus of the anterior neostriatum; nxIIIts:
804 tracheosyringeal portion of hypoglossal nucleus; RA: robust nucleus of the archistriatum.
805 Major lobes and ganglia of the octopus brain are indicated as follows: AB: anterior basal
806 lobe; BrG: brachial ganglia; Es: esophagus; IF: inferior frontal lobe; MB: median basal
807 lobe; MIF: medial inferior frontal lobe; PBu: posterior buccal lobe; Pe: peduncle; PeG:
808 pedal ganglia; PB: posterior basal lobe; PvG: palliovisceral ganglia; SuV: subvertical
809 lobe; SBu: superior buccal lobe; SF: superior frontal lobe; SuF: subfrontal lobe. Scale
810 bars are shown at the bottom of each brain section.
811
812

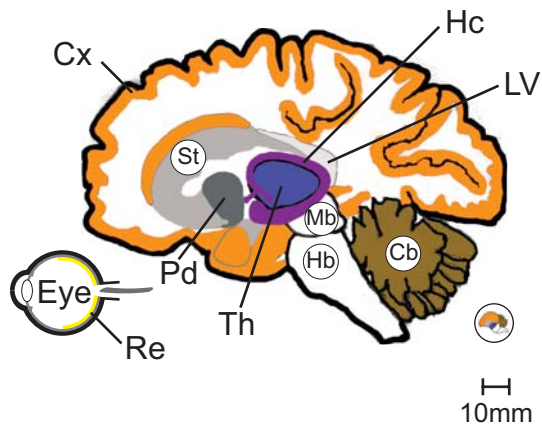
(a)



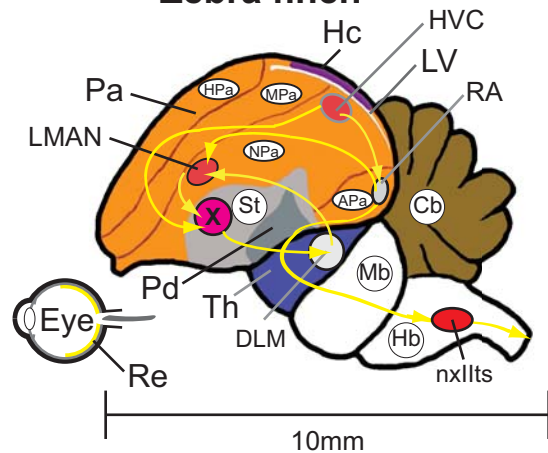
(b)



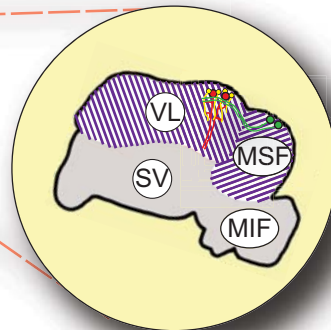
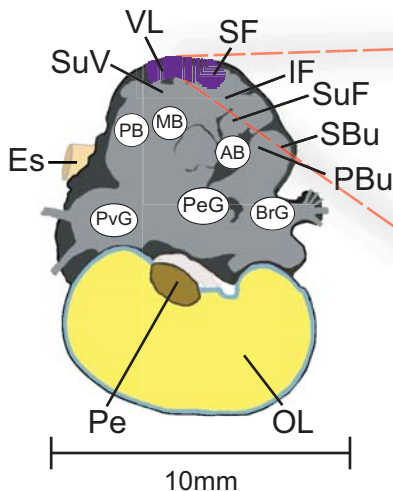
(a)

Human

(b)

Zebra finch

(c)

Octopus

Orange ~ pallial structures (mammalian cerebral cortex (Cx); avian pallium (Pa))

Blue ~ thalamus (Th)

Purple ~ hippocampus (Hc)

Vertical (VL) and median superior frontal (MSF) lobes

Grey ~ striatum (St)

White ~ midbrain (Mb) and hindbrain (Hb)

Brown ~ cerebellum (CB) and peduncle (Pe)

Yellow ~ retina and retina-like optic lobe (vertebrate Re; octopus OL)