Cognitive innovations and the evolutionary biology of expertise

Reuven Dukas

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Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, Ontario, L8S 4K1, Canada

Email: dukas@mcmaster.ca

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Abstract. Animal life can be perceived as the selective use of information for maximizing survival and reproduction. All organisms including bacteria and protists rely on genetic networks to build and modulate sophisticated structures and biochemical mechanisms for perceiving information and responding to environmental changes. Animals, however, have gone through a series of innovations that dramatically increased their capacity to acquire, retain and act upon information. Multicellularity was associated with the evolution of the nervous system, which took over many tasks of internal communication and coordination. This paved the way for the evolution of learning, initially based on individual experience and later also via social interactions. The increased importance of social learning also led to the evolution of language in a single lineage. Individuals' ability to dramatically increase performance via learning may have led to an evolutionary cycle of increased lifespan and greater investment in cognitive abilities, as well as in the time necessary for the development and refinement of expertise. We still know little, however, about the evolutionary biology, genetics and neurobiological mechanisms that underlie such expertise and its development.

38
1. Introduction: the major cognitive innovations
As they interact with their surroundings, animals rely on their cognitive system to make decisions that ultimately determine their survival and reproductive success. Broadly defined, the cognitive system comprises the structures and processes concerned with the acquisition, retention and use of information (Dukas, 2004). Animal cognition can be divided into a few interrelated components. The first essential stage is perception, which involves capturing information from the external environment and translating it into internal representations retained by neurons. Information acquisition is carried out by receptors specialized to capture distinct cue attributes including visual, auditory, olfactory, flavour and physical contact. Some types of receptors are typically located in dedicated organs positioned and structured to enhance information capture. Newly perceived information may either fade quickly, remain for a short duration necessary to perform a given task, or consolidate into long lasting internal representations that can persist anywhere between days to decades. The process of adding new representations to the internal storage is termed learning, and the information retained is referred to as memory. The sole utility of information acquisition and retention is to maximize survival and reproduction. To this end, individuals have to constantly determine their subsequent action given the known states of relevant environmental features and their experience. Once individuals make a decision, they have to execute the sequence of behaviours constituting a given action (Dukas, 2004; Rolls, 2014; Anderson, 2015).

While single cell organisms such as bacteria and protists already possess remarkable information processing abilities, a few major innovations have dramatically increased animals' capacities to selectively use information for maximizing fitness. This review focuses on these innovations, which include the nervous system, learning, social learning and language. I will begin with an analysis of information processing by genetic networks because they occur in all organisms and constitute the most fundamental organic system for the acquisition and use of information. I will then discuss in turn the added features enabled by each successive innovation as well as its ecological and evolutionary impacts. I will argue that the major cognitive innovations have fueled an evolutionary cycle of greater investment per individual, which in turn selected for a larger allocation of resources and time for the development of enhanced cognitive abilities. This in turn empowered individuals to devote long time periods for acquiring complex skills. The evolutionary trend of increased individual expertise opened up novel niches requiring and selecting for greater animal intelligence.

Most categorizations have an arbitrary element, meaning that one can argue that there is room for including additional innovations or perhaps excluding ones that I have included. Such feasible future modifications are of course appropriate, especially if the focus remains on enhancing our

fundamental knowledge of the evolutionary biology of animal cognition. Similarly, one can debate the very meaning of 'innovation'. Most notably, there is perhaps an expectation of innovation being a single abrupt modification with dramatic consequences. Such expectation, however, is not consistent with our knowledge of the intricate mechanisms enabling gradual evolutionary change (Futuyma and Kirkpatrick, 2017). Hence biological innovation most likely summarizes a long and complex evolutionary process. Similarly, while we often perceive innovation in modern humans as a sudden event typically attributed to a single person, extensive research indicates that it is most often a long process involving many individuals and spanning many years or even decades (Johnson, 2010; Bessen, 2015). Finally, space limitation compels me to focus on conceptual essentials while leaving out many details to the enlightening key sources I cite.

2. Information processing by genetic networks

There are two primary means by which genetic networks control cognition. First, during development and throughout life, they assemble and maintain all the structures that handle information. Second, the modulation of gene action can lead to changes in the way organisms perceive, process and respond to information. Through these mechanisms, unicellular organisms such as bacteria continuously monitor the environment and adaptively respond by altering behaviour, physiology, development and virulence. Here I will briefly review information processing by genetic networks. My goal is to establish a clear baseline that helps us understand the significance of subsequent cognitive innovations.

In the extensively studied bacterium, *Escherichia coli*, genetic networks orchestrate information reception and processing, and subsequent action through production of the complex molecular machinery of the cell membrane, cytoplasm and flagella. Bacteria can gain from moving towards higher food concentration and away from harmful substances. While receptors at the cell surface can detect several relevant molecules, simultaneous comparison of gradients is impossible owing to the small bacterium size. Instead, the bacterium relies on a sequential comparison. For example, when the glucose concentration increases over time, the time-averaged occupancy of the binding site of the glucose receptors increases and they send a signal to the flagella. This causes the flagella to raise their rotational bias in a counter-clockwise direction, which results in directional movement towards higher glucose concentration (Koshland, 1980; Segall et al., 1986; Eisenbach and Lengeler, 2004; Hazelbauer et al., 2008). Furthermore, genetic modulation allows *E. coli* to switch diet. When glucose, *E. coli*'s preferred sugar, is not available but lactose is present, lactose detectors turn on alternative genes that enable lactose metabolisms (Beckwith and Zipser, 1970, Jacob and Monod, 1961).

125   At the other end of organismal complexity, genetic networks orchestrate
126   the adaptive immune system in vertebrates. Two remarkable features of this
127   system are that it can detect novel pathogens and retain a memory of the
128   microbes it has encountered (Tonegawa, 1983; Rajewsky, 1996; Abbas et al.,
129   2016). The immunological memory allows an individual's immune system to
130   respond more rapidly and more effectively to a pathogen that it has
131   encountered previously (Weng et al., 2012).
132   The above examples illustrate that, through the construction of a
133   complex cellular machinery and alterations in gene expression, genetic
134   networks enable fast and effective responses to a multitude of environmental
135   challenges and changes. The examples, however, implicitly demonstrate what
136   genetic networks may not readily achieve. To respond to a certain nutrient, a
137   bacterium must possess the receptor for that specific nutrient. To adjust to
138   change in the availability of that nutrient, the bacterium has to have the built
139   in genes and mechanism for their adaptive activation. Even in the exceptional
140   case of the vertebrate adaptive immunity, the system can handle a very
141   narrow range of targets and responses. In contrast, the evolution of the
142   nervous system discussed next has allowed many animals to exploit and
143   respond to limitless resources and environmental features. While very simple
144   nervous systems are primarily determined by genetic networks, more complex
145   ones increasingly rely on experience and thus generate individuals with
146   somewhat unique cognitive abilities and even expertise. I will elaborate on
147   these issues in sections 4-6.
148
149   **3. The first innovation: the nervous system**
150   The evolution of the nervous system is such a significant innovation because
151   it has led to the establishment of the only other major biological information
152   system beside genetic networks. Initially, nervous systems took over the tasks
153   of communication, coordination and modulation already present in unicellular
154   organisms. Further evolution, however, has allowed the basic neuronal
155   architecture to evolve the unique abilities for the acquisition and long-term
156   retention of vast amounts of information (figure 1). These capacities will be
157   discussed in section 4. In the subsections below, I will assess the new features
158   facilitated by neurons as a specialized novel system for the transmission,
159   coordination and modulation of information.
160
161   *(a) Communication*
162   The evolution of multicellularity opened up ample opportunities for cell
163   specialization. This allowed the division of the three fundamental cognitive
164   tasks of information acquisition, signal transmission and action among
165   dedicated cells. Neurons, which took over the task of transmitting information
166   from receptors to effectors, coopted many of the genes and mechanisms used
167   by single cell organisms for communication (Mackie, 1970; Anderson, 1989;
168   Ryan and Grant, 2009). There were two major advantages for neurons

169 mediating between sensors to effectors such as cilia and muscles. First, when
170 each cell contains both sensor and effector, the system efficiency is low given
171 the 1 to 1 ratio of sensor to effector. This can limit the number of costly sensor
172 types. When neurons mediate between sensors to effectors, one sensor can
173 communicate with many effectors. The high efficiency of such a system can
174 lead to the evolution of many specialized receptors (Jekely et al., 2008;
175 Jekely, 2011). The other advantage of neuronal communication between
176 sensors and effectors is that each cell type can be positioned optimally without
177 constraining the placement of the other type. That is, each sensor type can
178 be placed optimally in the body region where it is most likely to detect specific
179 cues, while effector location can be optimized based on biomechanical
180 principles.
181
182 ### *(b) Coordination*
183 In addition to an increased need for inter-cell communication, the evolution of
184 multicellularity also posed novel challenges of integration and coordination
185 among cells. Given their initial role in communication, neurons were naturally
186 preadapted for coordinating action among cells. Such coordination of complex
187 behaviour can already be seen in cnidarians such as hydras and jellyfishes,
188 which possess relatively simple, diffused neural nets. Moving can be risky to
189 an individual hydra because it can be swept away by the water current. A
190 hydra solves this challenge by performing an elaborate summersault, which
191 involves bending its body so its tentacles can reach and attach to the bottom,
192 releasing its foot, swinging its body in the desired direction, reattaching the
193 foot and then releasing the tentacles to regain its typical erect position (see
194 lower right panel of Fig. 2 in Bosch et al., 2017). The exact neuronal
195 mechanisms orchestrating this summersaulting are still unknown.
196 Early in the evolution of animals, nervous systems already showed clear
197 centralization, termed central nervous system or brain (Arendt et al., 2008).
198 In addition to coordinating behaviour based on the integration of sensory
199 information from the periphery, brains carry out multiple organizational tasks
200 including the control of growth and development, and a variety of physiological
201 features such as circadian activity, digestion, metabolism and excretion
202 (Jékely et al., 2015).
203
204 ### *(c) Modulation*
205 The output from neural networks can be modulated via the action of a variety
206 of substances including neurotransmitters, neuropeptides and hormones.
207 Such neuromodulators act through two major mechanisms. First,
208 neuromodulators can modify the type, number, or kinetic properties of the ion
209 channels in neurons' membranes. This can lead to changes in the excitability
210 of neurons and their response properties. Second, neuromodulators can alter
211 either the amount of transmitters released from presynaptic terminals or the
212 postsynaptic responsiveness (Harris-Warrick and Marder, 1991; Marder,

213 2012). A single neuromodulator can affect multiple neurons and the activity
214 of multiple ion channels. Furthermore, a single neuron can respond to multiple
215 modulators. Consequently, neuromodulators can generate enormously
216 complex dynamics by changing the configuration and output of neural
217 networks (Bargmann, 2012; Bargmann and Marder, 2013). For example,
218 foraging animals typically alternate between exploration for and exploitation
219 of resources, characterized by movement through the environment in the
220 former and a relatively stationary state in the latter. In the nematode,
221 *Caenorhabditis elegans*, long-lasting exploration and exploitation states are
222 modulated by two opposing neuromodulators, the neuropeptide pigment
223 dispersing factor (PDF) and serotonin. PDF promotes roaming through PDF
224 receptors whereas serotonin induces dwelling states through serotonin-gated
225 chloride channels (Flavell et al., 2013). Neuromodulation is essential for the
226 retention of information in neural networks discussed next.
227
228 **4. The second innovation: learning and memory**
229 The evolution of learning and associated long-term memory is probably the
230 most important cognitive innovation throughout the evolution of organismal
231 life because it opened up numerous novel ecological and evolutionary
232 opportunities. In the ecological domain, learning allows animals to exploit
233 abundant environmental features that are unique to certain times and places.
234 For example, an individual can learn the spatial features unique to its shelter
235 location. This means that it can invest more in this shelter because it can
236 return to the shelter after exploring for and exploiting resources such as food,
237 and thus occupy the shelter throughout its life. This also means that spatial
238 learning and memory can improve parental care because parents can invest
239 more time and resources in a nest and keep using it while providing their
240 offspring with shelter and food. Furthermore, provisioners such as bees can
241 learn unique features including the spatial location, odour and colour of their
242 preferred flowers, and learn new motor patterns for optimizing the handling
243 of these flowers. Finally, in many animal species, individual recognition allows
244 one to identify parents, neighbours, competitors, potential mates and
245 offspring (Dukas, 1998; Dukas, 2008a).
246   In the evolutionary arena, learning increases the value of the individual.
247 This is because experience can lead to older individuals having much higher
248 reproductive success relative to that of young novices. Strong positive effects
249 of experience on performance or reproductive success have indeed been
250 documented in a broad range of species including honey bees (*Apis mellifera*)
251 (Dukas and Visscher, 1994; Dukas, 2008c), a large variety of birds (e.g.
252 Wooler et al., 1990; Leach and Sedinger, 2016), and both human hunter
253 gatherers (Walker et al., 2002) and people in developed countries (Ericsson
254 et al., 2006; Bessen, 2015). Increased individual value due to experience may
255 have led to an evolutionary cycle of enhanced learning and memory selecting
256 for life histories characterized by longer life spans. In turn, longer life spans

257 may have increased the value of further investment in structures that improve
258 learning and memory as well as other cognitive abilities, and so forth.
259 Moreover, the increased value of longer lived individuals has probably selected
260 for tilting the trade off between offspring quantity and quality towards the
261 quality end. With greater investment in fewer offspring, parents could allocate
262 more resources and parental care time per offspring. Consequently, young
263 could allocate more physical resources to cognitive structures and more
264 protected time for developing and refining based on experience the cognitive
265 mechanisms handling the acquisition, retention and use of information (figure
266 2). Some of that experience could come via social learning discussed in section
267 5.
268   From a mechanistic point, learning and memory rely on the basic
269 organismal tools already well used by bacteria and protists for altering
270 behaviour based on experience. These tools consist of biochemical chains and
271 changes in gene expression. The use of these processes in neurons, however,
272 opened up novel opportunities. Briefly, long term memory is the culmination
273 of multiple, interactive, dynamic processes that start with the neuronal
274 encoding of new information via the modulation of synaptic properties by
275 neurotransmitters. The initial chemical modulation is followed by a molecular
276 cascade leading to gene expression activated by the cAMP-response element
277 binding protein (CREB). The products of these genes cause structural and
278 functional changes in selected synapses as well as changes in the intrinsic
279 properties of certain neurons, which affect their subsequent activity (Benito
280 and Barco, 2010; Kandel et al., 2014).
281   Basic learning abilities already exist in animals with simple nervous
282 systems including the nematode *C. elegans*, which possesses only about 302
283 neurons. *C. elegans* shows associative learning, which allows it to acquire and
284 exploit an association between some novel stimulus and an environmental
285 state affecting its fitness. For example, in an experiment with *C. elegans*,
286 individuals experienced their favorite food, a suspension of *E. coli* bacteria
287 with either sodium or chloride ions, and the alternate ions with no food. In the
288 subsequent test, worms showed a strong preference for the ions previously
289 associated with food. Worms in the control groups, which were naïve or had
290 experienced either food with no ions or ions with no food, showed no ion
291 preference (Wen et al., 1997).
292   Learning and long-term memory abilities have been documented in
293 most bilateral animals that have been closely examined (Dukas, 2009). The
294 full power of learning, however, is best expressed in long lived animals.
295 Individuals in such species can acquire complex learned skills over years of
296 practice, ultimately achieving performance dramatically superior over that of
297 inexperienced individuals. Learning improves all stages of information
298 processing within the heavily practiced tasks, including selective perceptual
299 improvements, greater abilities to learn new information and retrieve old one
300 from memory, superior decision making, and refined motor skills. While the

most detailed data on the development of expertise exist for humans (Ericsson and Lehmann, 1996; Ericsson et al., 2006), it is well known in other species as noted earlier in this section. A general definition of expertise applicable to all species can thus be 'the characteristics, skills and knowledge allowing individuals with extensive experience to perform significantly better than novices on a given complex task'. For example, in shearwaters (*Puffinus tenuirostris*), birds with a single year of breeding experience produce an average of 0.4 young. The birds' reproductive success gradually increases over subsequent breeding seasons, peaking at a yearly average of about 0.7 young after 6 years of experience (Wooler et al., 1990) (figure 3).

Factors other than expertise can explain some of the increase in the performance with individual age. These factors include higher survival rates of individuals of higher quality, an increase in effort with age, and physical and physiological improvements. Nevertheless, studies that either considered all the variables that can enhance performance with experience or addressed specific features such as foraging performance or antipredatory behaviour, have convincingly shown a dominant role for expertise. For example, the effects of differential survival rates were eliminated in studies that compared the same individuals over time (e.g. Desrochers, 1992b; Dukas and Visscher, 1994; Sergio et al., 2014). Effort had a negligible effect on increased performance with age in studies that measured it directly (e.g. Reid, 1988; Desrochers, 1992a; Dukas, 2008b). And at least one study that carefully measured physiological factors documented peak physiological performance much earlier than the peak in foraging success (Schippers et al., 2006). Similarly, many studies have documented that young birds require very long periods of time for acquiring complex foraging skills and for reducing mortality rates due to starvation and predation (e.g. Sullivan, 1989; Weathers and Sullivan, 1989; Desrochers, 1992b; Daunt et al., 2007).

Learning can contribute to large improvements in performance even in short-lived species such as honey bees (Dukas and Visscher, 1994; Dukas, 2008c). Expertise in short lived individuals, however, is severely limited by the short time, typically several days, available for the development of cognitive abilities that depend on extensive learning and practice. Intriguingly, two whole genome duplication events early in the evolution of vertebrates (Putnam et al., 2008) opened up ample opportunities for evolutionary innovations that expanded neuronal complexity and cognitive abilities in that lineage (Van de Peer et al., 2009). On the gross anatomical scale, vertebrate innovations include complex brains, neural crest and placodes. Complex brains have specialized forebrain, midbrain and hindbrain regions. The neural crest contributes to a few structures including the sensory ganglia. Sensory placodes contribute to the eye, ear, lateral line and olfactory organs, while neurogenic placodes contribute sensory neurons to cranial ganglia (Shimeld and Holland, 2000).

344　　　　At the molecular level, the two whole genome duplications in vertebrates
345　led to gene expansion in many synaptic gene families. Consequently, many
346　fruit fly (*Drosophila melanogaster*) synaptic genes have up to four orthologues
347　in mice (*Mus musculus*) (Ryan and Grant, 2009; Emes and Grant, 2012). At
348　least two innovative experimental studies have attempted to link synaptic
349　gene expansion and its associated increased complexity in synapse signalling
350　mechanisms to cognition and behaviour in mice (Nithianantharajah et al.,
351　2013; Ryan et al., 2013). Given the enormous complexity of the synapse
352　proteome, which consists of over 2000 proteins in mice (Ryan and Grant,
353　2009), further experimental work is needed in order to assess the exact
354　contribution of the massive synaptic gene expansion to vertebrate cognition
355　in general and to expertise development in particular.
356　　　　Another evolutionary consequence of advanced learning and associated
357　cognitive abilities is that they open up opportunities for individuals to adopt
358　novel behaviours. First, learning often involves an early exploratory phase.
359　When numerous individuals of each generation explore, the combined
360　outcome is a massive search, which can lead to the discovery and adoption of
361　novel, fitness-enhancing behaviours. Second, some types of learning lead to
362　each individual changing its behaviour based on its specific experience at a
363　certain place and time. Thus, if a given task (e.g. locating food) has a new
364　optimum in a new environment (e.g. settings with novel foods), an individual
365　may find that optimum via learning. That is, learning is a mechanism that can
366　naturally lead to individuals adopting novel behaviours (Dukas, 2013). If such
367　novel behaviours disappear when individual innovators die, they would
368　probably have negligible evolutionary impact. This is because the novel
369　behaviours are not associated with heritable genetic variation that natural
370　selection can act upon. Novel behaviours, however, can be transmitted across
371　individuals and generations in species with social learning discussed next.
372
373　**5. The third innovation: social learning**
374　Social learning, defined as the acquisition of novel information from other
375　individuals (Heyes and Galef, 1996; Hoppitt and Laland, 2013), deserves its
376　place on the cognitive innovations list owing to two unique effects it has had
377　on animal evolution. First, as noted in section 4, the evolution of learning
378　probably led to an evolutionary cycle of increased individual value leading to
379　selection on further improvement in learning, memory and other cognitive
380　abilities that contribute to enhanced information capture and utilization. The
381　trouble with individual expertise is that it is lost when that individual dies.
382　Social learning resolves this organic constraint by allowing other individuals
383　and, most importantly, members of subsequent generations, to acquire
384　relevant knowledge from experts. Second, the evolutionary cycle of increased
385　individual value has likely also led to the evolution of parental care. Parental
386　care can merely mean providing food and protection. Such care alone can
387　dramatically increase a young individual's probability of reaching adulthood.

388 With social learning, however, parental care enables young novices to acquire
389 successful skills from their experienced parents. This opens up novel ecological
390 niches that require the use of extensive knowledge and complex abilities that
391 are acquired through prolonged practice. Such niches may even further
392 promote the evolution of cognitive features that enable the development of
393 expertise. Examples include carnivores (e.g. cheetahs, *Acinonyx jubatus*) and
394 raptors (e.g. sparrowhawks, *Accipiter nisus*) that feed on highly evasive or
395 large prey (Newton, 1986; Caro, 1994).
396   We do not know the number of independent evolutionary origins of
397 social learning but it likely has had multiple beginnings as it is well established
398 in a few classes of vertebrates and at least two insect orders (Heyes and Galef,
399 1996; Dukas, 2010; Hoppitt and Laland, 2013). There is currently too little
400 information for generalizing about the biological mechanisms that enabled the
401 evolution of social learning (but see Olsson and Phelps, 2007; Zeigler and
402 Marler, 2008; Munger et al., 2010; Kavaliers and Choleris, 2013). It is
403 feasible, however, that reliance on social cues for learning is attainable by
404 many animals with some threshold cognitive machinery. The ecological
405 context for the evolution of social learning was most likely the tendency of
406 individuals in many species to join others. For naïve individuals, the presence
407 of conspecifics at a given site might indicate the availability of good resources
408 and safety. Joining others can also enhance feeding and predatory avoidance
409 (Allee, 1931; Danchin and Wagner, 1997; Prokopy and Roitberg, 2001). An
410 individual's tendency to associate with others can readily lead to that
411 individual biasing its resource preference to that chosen by the other group
412 members. A tendency to aggregate opens up further opportunities for taking
413 advantage of the social setting, including the acquisition of relevant
414 information from others.
415   A basic tendency to socially bias food selection has been documented in
416 fruit flies (*D. melanogaster*). In addition to their natural attraction to odours
417 of yeast and fermenting fruit (Becher et al., 2012), which constitute the larval
418 and adult food, fruit flies show long distance attraction to the pheromone cis-
419 vaccenyl acetate (cVA), which is produced by males and transferred to females
420 during copulation (Bartelt et al., 1985). Consequently, fruit flies typically occur
421 in aggregations in the field and show modest social behaviours (Ramdya et
422 al., 2017). In controlled experiments, we (Sarin and Dukas, 2009) found that
423 focal females that experienced novel food together with mated females, who
424 had laid eggs on that food, subsequently showed a stronger preference for
425 laying eggs on that food over another novel food compared with focal females
426 that experienced the food alone. We observed no social learning, however,
427 when observers experienced food with more ambiguous social information
428 provided by the presence of either virgin models or the aggregation
429 pheromone, cVA, alone.
430   At the other extreme of the social learning spectrum, many vertebrates
431 with extensive parental care provide opportunities for their offspring to learn

10

432 complex skills. For example, parents in a variety of carnivores and raptors
433 provide wounded prey for young, who can then practice killing the animal
434 (Caro and Hauser, 1992). Similarly, adult helpers in meerkats (*Suricata*
435 *suricatta*) provide young with live scorpions without their stingers. The young
436 can then safely practice handling that dangerous food (Thornton and
437 McAuliffe, 2006). Another type of advanced social learning with a limited
438 taxonomic distribution is imitation, defined as the copying of an action
439 performed by another individual. With a few exceptions, most notably, vocal
440 imitation in birds (Catchpole and Slater, 1995; Beecher and Brenowitz, 2005),
441 imitation may have had significant effects on behaviour only in great apes
442 (family Hominidae) (Whiten, 2011). By far, the most significant case of
443 imitation is language acquisition in human infants.
444
6. The fourth innovation: language
446 Language has evolved only once in a single lineage and set its possessors
447 apart from all other animals. Language is acquired via vocal imitation, which
448 is rare among animals in general and absent even in humans' closest extant
449 relatives (Tomasello, 2002; Jarvis, 2006). The evolution of language most
450 likely furthered the evolutionary cycle of enhanced cognitive abilities enabling
451 greater expertise, with the latter selecting for improved cognition. Specifically,
452 improved social learning and memory abilities allowed the evolution of
453 language. In turn, improved language expertise probably selected for better
454 cognitive abilities for better language acquisition and optimal handling of the
455 larger volume of information acquired through language. Most notably,
456 language could dramatically advance human social behaviour and the
457 transmission of cultural information (Dunbar, 2003; Herrmann et al., 2007).
458 Language acquisition is highly cognitively demanding. Each newly born
459 human infant initiates a long process of acquiring language expertise
460 culminating in a vocabulary of 50,000-100,000 words and complex grammar
461 in adulthood (Clark, 2009). Infants rely heavily on social learning from their
462 parents, who talk to them in infant-directed speech (motherese) characterized
463 by slower speech with simplified sentence structure, repetition, longer pauses,
464 a higher fundamental frequency and greater pitch variation than in adult-
465 directed speech (Ferguson, 1964; Thiessen et al., 2005). Language learning
466 involves sophisticated social understanding, detection of statistical
467 regularities, perception across modalities (e.g. connecting face to speech,
468 sight with sound and symbol with object), and extensive memory (Kuhl, 2004;
469 Hollich, 2012).
470 We cannot reconstruct the evolutionary dynamics among enhanced
471 cognition, cultural changes and language in early hominid evolution (see
472 Henrich, 2016). It is commonly agreed, however, that language capacity has
473 existed for at least 100,000 years (Johansson, 2005). It is also widely
474 recognized that language precipitated a range of unique abilities that have
475 allowed humans to successfully spread to all continents except Antarctica.

476 These abilities include enhanced tool technologies such as composite tools
477 with handles, use of novel tool materials including bones and antlers, long-
478 distance exchange of raw materials, hunting of large, dangerous animals,
479 structured use of domestic space, use of pigments and self ornaments, and
480 rituals (McBrearty and Brooks, 2000; Klein, 2009). The strong reliance on rich
481 language for social learning in increasingly larger social groups and the rapid
482 accumulation of culture led to the evolution of human agriculture, writing,
483 and, more recently, to the industrial and technological revolutions. A
484 consequence of the large increase in social groups, social organization and
485 rapid accumulation of cultural knowledge in the past few thousands years has
486 been increased specialization among individual humans. In addition to general
487 expertise in language and social skills shared by all individuals, some humans
488 spend many years, even decades, honing their highly specialized narrow
489 expertise. Well studied examples include expertise in specific fields of science,
490 medicine and arts, and in competitive games such as chess (Chase and Simon,
491 1973; Stephan and Levin, 1992; Ericsson et al., 2006).
492
493 **7. The evolutionary biology of expertise: conclusions and prospects**
494 An individual's life can be perceived as acquiring and relying on information to
495 make decisions that maximize fitness. Key innovations throughout animal
496 evolution have led to some lineages expanding resource allocation to cognitive
497 structures handling information and time necessary both for their
498 development and for the acquisition of complex skills, or expertise. The
499 evolution of the nervous system was a natural consequence of the increased
500 complexity associated with multicellularity. Such complexity allows for greater
501 efficiency and regulation of specialized cells, and provides more opportunities
502 for further refinement, improvement and innovation (Maynard Smith and
503 Szathmary, 1997; Sterling and Laughlin, 2015). While neurons' initial role was
504 internal communication and coordination, the associated neuromodulation
505 opened up mechanistic opportunities leading to information acquisition and
506 retention. Learning, initially via individual experience and later also through
507 social interactions, likely stimulated an evolutionary cycle of increased
508 investment in and reliance on cognitive skills culminating in the evolution of
509 language and modern human civilization.
510   With a few exceptions (Dukas and Visscher, 1994; Dukas, 2008b;
511 Helton, 2008), expertise has been subjected to research only in the field of
512 human psychology (Ericsson and Lehmann, 1996; Ericsson et al., 2006). While
513 we know little about the genetics and neurobiology of complex skill acquisition,
514 it is likely that humans share similar mechanisms with non-humans. It is
515 possible, however, that a major axis of evolutionary change within vertebrates
516 has been associated with cognitive improvements leading to increased
517 capacities for storing and effectively using vast amounts of knowledge and
518 experience. The two whole gene duplications early in vertebrate evolution and
519 further events of gene duplication in primates and humans (Dorus et al., 2004;

520 Putnam et al., 2008; Van de Peer et al., 2009; Somel et al., 2013) have indeed
521 vastly increased brain complexity and likely enhanced complex skill
522 acquisition. The exact genetic, neurobiological and physiological mechanisms,
523 as well as the evolutionary biology of expertise and expert performance,
524 deserve rigorous examination.
525   On the mechanistic side, we have to test whether there are unique
526 mechanisms underlying expertise acquisition in certain species. In humans, a
527 remarkable aspect of expertise is that experts can handle more information
528 more rapidly and execute better decisions within their expertise than can
529 novices. Moreover, tasks that are initially very challenging and attention
530 demanding become "automated" with extensive practice, meaning that they
531 are performed easily with little attention. Familiar examples include reading
532 and driving (Feltovich et al., 2006). If there are universal mechanisms that
533 underlie complex skill acquisition, they can most readily be examined in
534 classical animal model systems such as fruit flies and mice. Alternatively,
535 documenting variation among taxa in the mechanisms underlying expertise
536 will open up a search for the genetic and neurobiological mechanisms
537 generating such probable differences.
538   On the evolutionary side, we ought to quantify genetic variation in the
539 rate of expertise acquisition and peak expert performance, and their
540 association with fitness. We know, for example, that young in a variety of
541 species that rely on complex foraging skills face high mortality rates while in
542 the process of attaining their expertise (e.g. Sullivan, 1989; Daunt et al.,
543 2007). But we know little about the evolutionary biology of such and other
544 cases of slow and costly expertise development, which is likely followed by
545 large benefits to the surviving experts. The functional and mechanistic
546 properties of expertise constitute an exciting central topic for future research.
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Figure legends

Figure 1. (a) All organisms including bacteria and protists rely on genetic networks to orchestrate reception and processing of information and responses to environmental changes. (b) The first major cognitive innovation involved the evolution of nervous system. This set the stage for the subsequent major cognitive innovations: learning and memory, social learning, and language. In animals possessing more of these innovations, individuals have greater abilities to acquire expertise over long periods of practice.

Figure 2. Learning increases individual value over time because cumulative experience increases reproductive rate. In some lineages, this may have led to an evolutionary cycle of selection for life histories characterized by longer life spans, greater resource and time investment in enhanced cognitive abilities, and the evolution of parental care and social learning.

Figure 3. The gradual development of expertise leads to a corresponding increase in performance in a long-lived bird: the average (± SE) proportion of eggs that developed into free-flying young as a function of the breeding experience of their short-tailed shearwater mother. Data from Wooler et al. (Wooler et al., 1990).
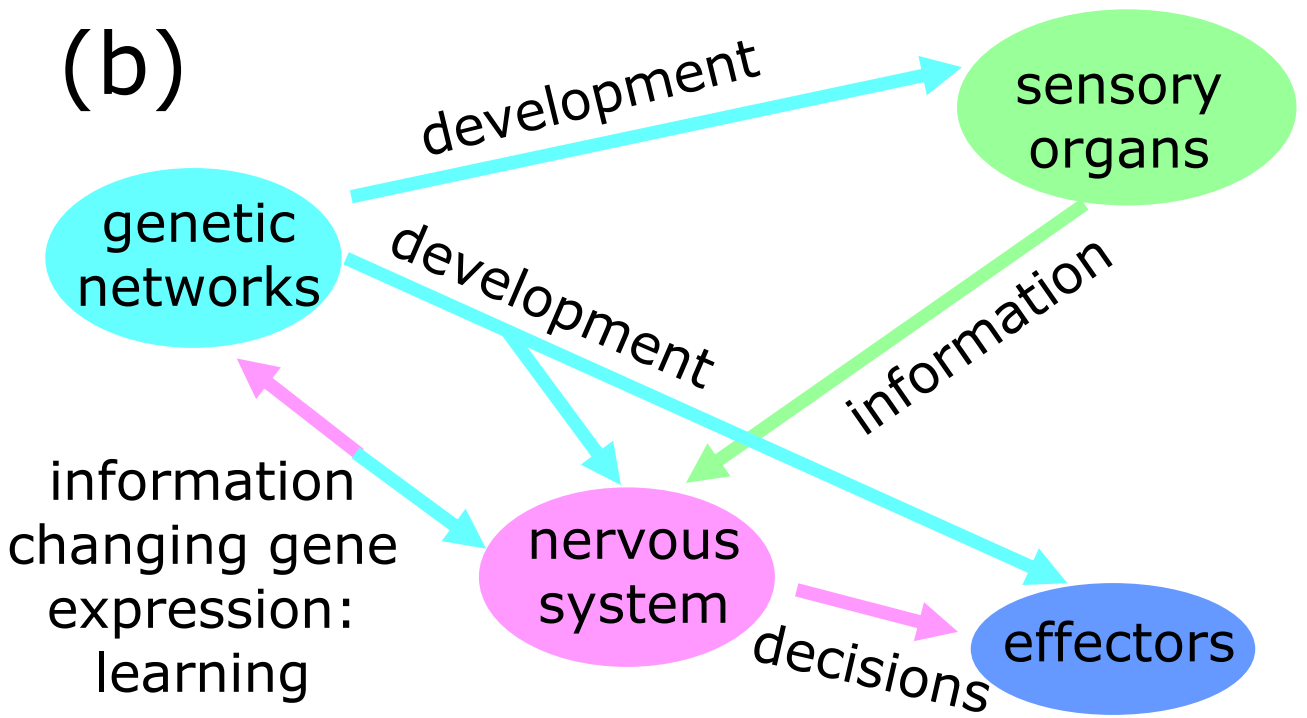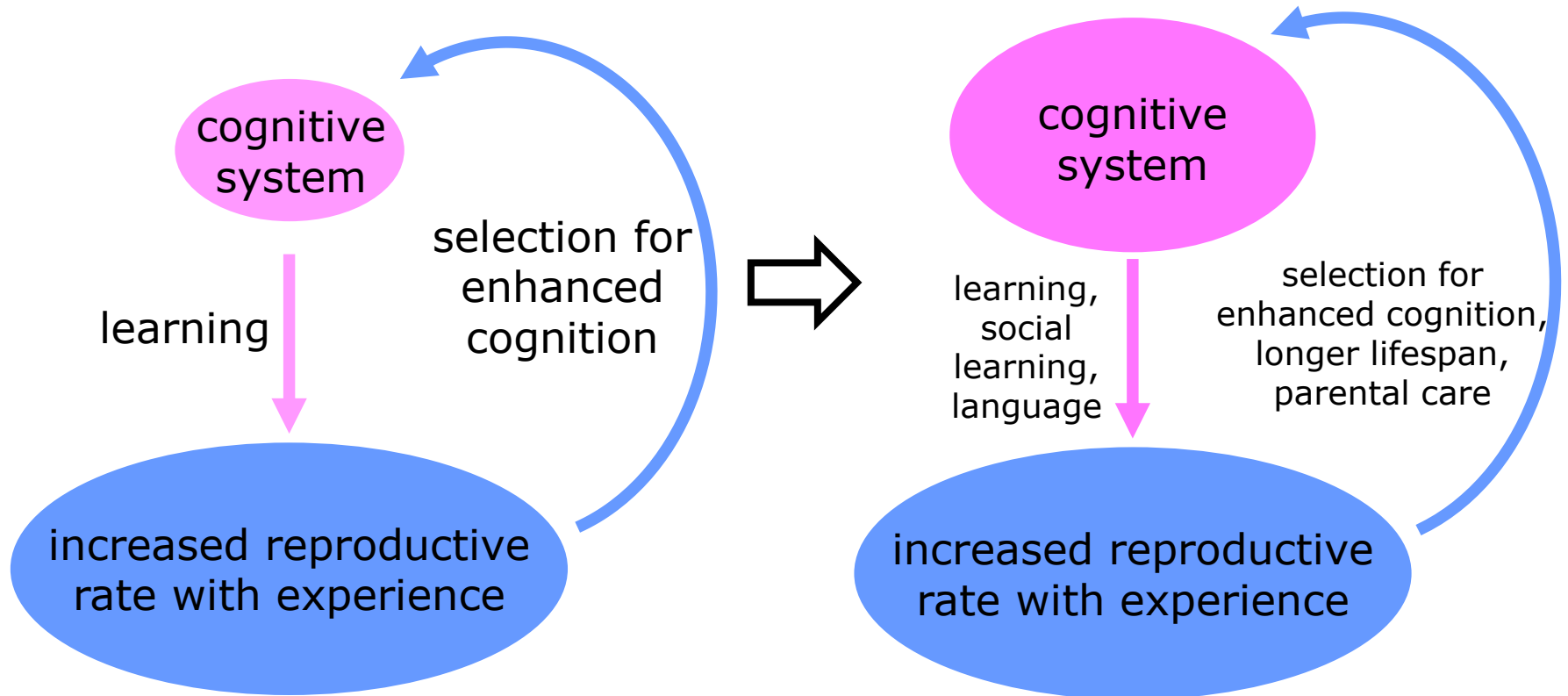
Fig. 1

Fig. 2

Fig. 3