Individual differences in cognitive performance as a consequence of natural selection, constraints and trade-offs

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Abstract. The causes and consequences of individual differences in cognitive performances of non-human animals have attracted little attention. This ignorance precludes taking an individual-level, Darwinian, perspective on how natural selection sifts the fitness outcomes of inter-individual variation. Consequently, we do not fully understand the evolutionary trajectory of cognitive performance. Cognition is unusual amongst traits such as morphology or particular behaviours in that it is still commonly considered that more extreme examples are 'better', with a focus on 'genius' taxa or individuals. In this paper, I review what is known about the fitness consequences of individual variation in cognitive performance and explore the constraints and trade-offs that operate. These constraining factors include the costs of producing and maintaining costly neural tissue, the allocation of such tissue to particular cognitive domains, the effect that domain-general or domain-specific cognitive abilities may have on individual's performance, and the role of the environment (physical, ecological and social). Understanding these factors can help appreciate why particular individuals or species exhibit apparently less extreme examples of cognitive performance. For AI researchers, an understanding of such constraints and trade-offs faced in animal cognition may provide novel examples to stimulate solutions in which an optimality approach is taken rather than simply increased exaggeration.

1 INTRODUCTION

The study of cognition in animals has traditionally taken one of three (non-exclusive) forms. First, particular model species (e.g. pigeons or rats) have been used to investigate the mechanisms underpinning specific cognitive processes. This has typically utilized laboratory paradigms involving prolonged training of batches of individuals whose learning, memory or executive control are tested with tasks often adopted from tests of human cognition. Individual animals who fail to participate, complete extended runs of trials or learn the affordances of the tasks are commonly discarded. Second, a comparative approach is taken in which species, or populations of the same species, are tested with the same, or purportedly similar, tasks in order to understand when particular cognitive processes may have emerged and what ecological or social conditions may provoke or facilitate these processes. This has involved both laboratory and field studies, and typically the performances of a sample of individuals within a population or species are pooled and considered representative of the species or population as a whole. Finally, within a species, the performances of particular, often highly enculturated, 'genius' individuals are explored in great detail, and inferences drawn about the adaptive benefits of possessing such cognitive abilities for the species, based on its ecology and social behavior. These three approaches commonly ignore inter and intra-individual variation in cognitive performance. This precludes a Darwinian approach to understanding how natural selection may sift individual differences and their attendant fitness consequences, leading to optimal expression of cognitive performance.

Different types of cognitive processes are expected to have different effects on individual fitness. For example, the ability to acquire an association between a cue and a reward could provide a selective advantage to individuals if it enhances their foraging or reproductive success [1, 2]. The speed with which individuals learn may also confer associated fitness advantages [3, 4]. Alternatively, the ability to inhibit previously learned responses when they become no longer rewarded, may also influence an individual's fitness [5] with more behaviourally flexible individuals having improved invasion success [6] or a better ability to track fluctuating social groups [7].

A Darwinian perspective on understanding how cognitive processes and performances have evolved may be instructive for the development of AI. Such a perspective acknowledges that ever more extreme examples of cognitive performance may not always be optimal, but rather optimality is the product of trade-offs. Extreme examples of performance may include improvements in memory retention to the point when information is never forgotten or degraded; improvements in learning speed to the point that affordances are updated and decisions established following a single rewarded experience; or improvements in executive control to the point that decisions are only made when a lifetime's accumulated information has been weighed and considered. While all these examples may provide benefits under certain circumstances, they likely also impose costs on the individual. Perfect retention of information may require increased physical/neural storage capacity, it may slow subsequent recall of any one piece of information, or obsolete information may continue to exert influence on decision making. Rapid learning may be susceptible to natural fluctuations in reward probabilities and lead to long-term misattribution of cue reliability. The demand for perfect information to inform a controlled decision may slow the execution of an action with potentially fatal consequences. An optimal solution may depend on the cognitive performance of others in the population such that optimality is frequency dependent. Therefore, the expression of cognitive performance in each domain is likely the result of resolving these trade-offs in response to the pressure of natural selection. The acknowledgement of trade-offs in cognitive

performance in naturally evolved populations, and indeed the active search for their occurrence and resolution, may provide novel and counter-intuitive instances that AI developers could benefit from. This paper will describe what is known about how individual differences in cognitive performance in non-human animals may be subjected to natural selection and critically, how optimal performance may arise because of constraints imposed by intra-individual physiological or cognitive factors, fluctuating external environmental factors, inter-individual interactions and competition, or the cognitive performance of peers.

2 HOW IS NATURAL SELECTION ON COGNITIVE PERFORMANCE USUALLY STUDIED?

Few studies have explored how individual differences in cognitive performance relate to fitness differences. One approach, arising from the field of behavioural ecology, measures the cognitive performance of individuals in a particular domain, and then explores how their performance correlates with a (proxy) fitness measure (reviewed by [8, 9]). This is achieved by deploying explicit psychometric tasks targeting specific, defined cognitive processes [10, 11]. The majority of such studies have reported positive relationships with individuals who exhibit faster or more accurate learning, better memory, or stronger executive control also having greater (proxy) measures of fitness, although the causal effect has not been demonstrated, so the relationships are inferred. Ants *Lasus niger* that were fast at route learning had higher colony level foraging success [12]; male African striped mice *Rhabdomys pumilio* that rapidly learned to escape from a Barnes maze had improved survival to the breeding season [13]; male guppies *Poecilia reticulata* that quickly learned a simple maze were preferred by females [14]; male bitterling *Rhodeus amarus* that exhibited better spatial memory had higher reproductive success [15]; male starlings *Sturnus vulgaris* with better spatial learning had longer song bouts [16]; male song sparrows *Melospiza melodia* that were faster at acquisition and reversal learning tasks and better at a detour reach task had larger song repertoires [17]. Positive relationships are not ubiquitous. No relationships were found between performance in discrimination, reversal or spatial memory tasks and male mating success in spotted bowerbirds *Ptilonorhynchus maculatus* [18]. There was a negative relationship between the speed of spatial learning and the size of a male's song repertoire in song sparrows [19]. Several other studies have adopted a problem-solving or innovation paradigm in which cognitive performance is inferred from the speed by which an individual typically extracts food (or may access other resources such as offspring or decorative objects) from a puzzle apparatus. Such an approach relies on the assumption that performance in such tasks reveals some unspecified facet of cognition such as learning speed, generalization, flexibility or insight. However, an individual's performance may also be strongly influenced by non-cognitive factors such as age, prior experience, strength, persistence or luck [20]. Therefore, I concentrate on studies that deploy psychometric tasks that target specific cognitive domains.

A second, even rarer approach, grounded in evolutionary ecology, uses artificial selection experiments in which cognitive performance is selected for. In two cases, such selection for improved learning appears to have negative fitness consequences for individuals. Selection for learning ability in fruit flies *Drosophila melanogaster* resulted in shorter life span and lower competitive ability in larvae [21, 22], while cabbage white butterflies *Pieris rapae* with higher learning ability suffered from a delay in reproduction [23]. In a third case, the fitness consequences were more equivocal. Male worms *Caenorhabiditis remanei* from lines selected for improved olfactory learning performance were less active and survived for less time than those from lines selected for low learning performance, but they did sire more offspring [24].

Therefore, in general, a behavioural ecological approach typically executed under field conditions in which an individual's performance in a cognitive task is correlated with their (proxy) fitness suggests that increasingly extreme cognitive performance is favoured by natural selection. In contrast, an artificial selection approach typically executed in the laboratory suggests that selection for high performance in a cognitive task usually results in fitness costs in reproductive success and/or lifespan. Few, if any, studies consider the costs of, or constraints on, the exaggeration of cognitive performance and thus fail to consider the trade-offs necessary to determine what an optimal level might be for performance in any particular cognitive domain or more generally across cognitive domains. I suggest that accounting for costs of expressing extreme levels of cognitive performance and understanding the mechanisms by which these constraints may operate, and hence the details of the trade-offs that must be resolved, is profitable for our understanding of the evolution and exaggeration of cognitive performance both in natural populations and, by extension, in AI situations.

3 PHYSIOLOGICAL CONSTRAINTS

Cognitive performance in humans is positively, albeit somewhat weakly ($r = 0.40$), related to whole brain size [25]. This relationship is assumed in non-human animals, but is not well established [26] and is likely confounded by additional social and ecological factors. Female guppies from lines selected for large brain size outperformed females from lines selected for small brains in a numerical ability task [27]. Males from the same selection lines for large brains were faster at learning to find a female in a maze [28]. There is stronger evidence that cognitive performance is related to the size of particular regions of the brain.

This positive relationship between brain (region) size and cognition imposes costs on the individual if they are subjected to selection for enhanced cognitive performance. First, the brain itself is an energetically expensive organ and thus its production and maintenance must be traded off against other organs within an individual. In humans, there is likely a relationship with the size of the digestive system and the diet of the individual [29]. In male bats, brain size is negatively related to testes size, another energetically expensive tissue [30]. When guppies were artificially selected for large brain size, males developed smaller guts and produced fewer offspring [27]. Second, there is a metabolic cost of encoding and transmitting information [31], so cognitive improvement that relies on simply

utilizing more information, rather than processing it more effectively, is likely to incur increased energetic costs.

These costs may be mediated by plasticity in brain (region) size, with large, expensive tissue only being produced when necessary and allowed to degenerate when not needed. In brood-parasitic cowbirds, the volume of the hippocampus, involved in spatial memory, is enlarged relative to the telencephalon during the breeding season, but declines when the season is over [32]. Likewise, in food-hoarding black capped chickadees *Poecile atricapillus* the hippocampus is enlarged relative to other brain regions [33] and shows increased neurogenesis specifically during the caching period [34].

4 COMPETITION BETWEEN COGNITIVE DOMAINS

Once the resolution to the trade-off between an individual's investment in neural and other tissue has been resolved, the question of how much of the limited brain tissue should be allocated to particular processes. Different cognitive processes appear to utilize different neuronal mechanisms or circuits and brain regions [e.g. 35, 36]. This may explain why increased performance in one domain may be matched by decreased performance in a second, different domain. Individuals that rapidly learn to discriminate cues are usually correspondingly slow to inhibit their responses when previously rewarded contingencies are no longer rewarded. Such inverse relationships are seen between acquisition and reversal learning performances in birds, such as Florida scrub-jays *Aphelocoma coerulescens* [37], Indian mynas *Sturnus tristis* [3] and black-capped chickadees [38]. However, this negative relationship is not inevitable. Acquisition and reversal learning performances correlate positively in song sparrows and bumblebees [17, 39]. A negative relationship was also seen in Carib grackles *Quiscalus lugubris* where individuals that were fast at solving novel extractive foraging problems also made more errors in a colour discrimination task [40].

A second broad trade-off in cognitive performance that may be required is that between the speed and accuracy of making a decision. Individuals may be selected to continue to collect further information, or spend longer assessing and weighing information already in their possession before making a final, more accurate, decision rather than relying on simple heuristics. However, such deferrals impose a cost in both time and energy to collect and process information and costs of indecision. In extreme cases, one could imagine an individual becoming a 'rational fool'; continually deferring a decision in the quest for perfect information but dying of starvation or predation because of their inactivity. More usually, there is a trade-off between the speed and accuracy of an animal's decision making (reviewed by [41]). For example, in zebrafish, *Danio rerio*, some individuals consistently made 'careful', slow but accurate decisions in colour discrimination tasks, while others made swift but less accurate choices [42].

5 GENERALITY OR SPECIFICITY?

It may be that there is much less of a trade-off between performance in different cognitive domains than we might expect, especially if individuals exhibit a general intelligence which governs their performance across a range of domains. In humans, this is referred to as *g* and typically explains around 40% of variation in an individual's performance across a battery of psychometric tasks [43]. A few studies have started to explore whether non-human animals also possess a broader domain-general ability where an individual's performance in one domain is related to their performance in other, unrelated domain even when the tests used to probe the domains appear to have little in common with one another in what cognitive processes/mechanisms they may reveal [44]. A *g* factor has been reported in mammals: non-human primates [45-47], mice, *Mus musculus* [48-53] and dogs [54]. It has also been reported in some studies of birds [18, 55]. As for humans, these studies tend to find that a single factor, construed as being equivalent to *g*, accounts for ~40% of an individual's variation in task performance. Only a single study [18] has tested whether a single factor derived from performance in a battery of psychometric tasks relates to a (proxy) fitness measure. However, the mating rate of male bowerbirds was not predicted by their single factor score.

It may be that although the cognitive performance of animals can be summarized by a single measure, that measure does not reflect the same processes as inferred in humans [56]. In humans, *g* is considered synonymous with intelligence [44]; knowing how to behave in a novel situation, based on previous experiences and information acquired elsewhere. In animals, *g* may instead indicate overarching performance in basal cognitive processes that operate in multiple different domains. One candidate basal cognitive process is associative learning. Therefore, in animals, a unifying factor may better reflect learning than knowing [56].

If there is a general cognitive ability, whether based on learning or knowing, that governs performance across a range of specific domains then this could constrain the optimal performance in any one of them. For example, if a number of different cognitive domains such as predator recognition and food item search image were governed by a single overarching learning ability then mechanisms of learning in one domain that bring benefits may be detrimental in a different domain. While highly precise, inflexible learning of predator's identity may be beneficial if the cues for the predator remain constant, the same highly precise, inflexible learning of an ephemeral food item may incur costs of misplaced search effort and reduced foraging success when that food item becomes rare. It remains unclear to what extent such general cognitive abilities exist outside humans [44].

6 EFFECTS OF THE ENVIRONMENT

Optimal cognitive performance is likely to depend on the environment in which it is exhibited. Therefore the relationship between fitness and cognitive performance is likely to differ when tested in different environments. The physical environment may differ in stability/changeability, predictability or physical complexity. Sticklebacks *Gasterosteus aculeatus* from ponds relied more heavily on visual landmarks as cues in spatial learning tasks than did fish from rivers where flow and turbulence render such cues less informative [57]. Cichlids *Simochromis pleurospilus* that were reared with an unpredictable food supply outperformed fish reared under constant food conditions when tested later in life in a learning task [58]. Pheasants *Phasianus colchicus* [59] and zebrafish *Danio rerio* [60] expressed better spatial memory or faster spatial learning if they had been reared in spatially complex as opposed to spatially simple environments. This may be because the early rearing environment affects brain size, with salmon *Oncorhynchus mykiss* reared in complex environments growing larger brain (regions) than those reared in simple environments [61].

The environment may also differ in its ecological composition, with variation in resource density or distribution, or the prevalence of predators. For example, chickadees that experience greater climatic extremes also possess enhanced cognitive adaptations for spatial memory, compared to individuals that reside in milder environments, possibly because they are more dependent on locating externally stored food items [62, 63]. The relationship between an ant's route-learning performance and their foraging success was only seen in artificially rich environments and that the relationship was lost when ants were tested in a nutritionally poor environment [12]. Fish *Brachyraphis episcopi* from high- and low-predation pressure streams differed in how rapidly they learned to detect foraging patches using spatial cues, with fish from low-predation pressure streams having shorter foraging latencies, entering fewer compartments before discovering the reward patch and navigating more actively within the maze [64]. In a second study, guppies from high-predation pressure streams tended to take longer to make the decision about which maze chamber to enter than low-predation guppies which were more willing to make quick and potentially inaccurate decisions [65]. These 'hasty' guppies from low-predation pressure streams also tended to have smaller telencephalons, the brain region most responsible for spatial memory [65].

The environment may change over the lifetime of an individual either because of ecological or climatic processes, anthropogenic effects or because the individual moves from one environment to another. Cognitive performance that has been developed and selected under one set of environmental conditions may prove to be sub-optimal when faced with a novel set of environmental conditions. For example, Indian mynas that were fast innovators and able to access food rapidly were slower to change their behavior when the significance of food cues changes compared to individuals who initially learned slowly, but could be flexible and so cope with a changing environment [3].

7 FREQUENCY DEPENDENCE

The resolution of optimal solutions within populations of individuals which interact can be achieved by using a game theory approach in which the best individual solution depends on the behaviour of others in the population [66]. While there has been work looking at optimal decision-making for individuals within interacting populations and even at the neural mechanisms underpinning such decision making [67], I am not aware of research that has explored how individuals should exhibit differential cognitive performance such as levels of memory, learning speed or executive control depending on the behavior of others. Individual variation in response to the cognitive performance of others may be expected. For example, in an environment where resources are patchy, ephemeral and unpredictable, an individual has to decide whether to rapidly learn that a location where they have received one reward are likely to provide a reward on a later occasion, or whether it is better to be cognitively flexible and 'forget' or fail to learn any single location and rather roam randomly in the hope of encountering a new site each time. If the majority of individuals 'chose' not to learn locations but rather roam randomly then a mutant population fragment may benefit from learning reward locations and returning to them. If too high a proportion of the population adopted this learning strategy then the rewarded locations would be rapidly depleted and learning would become a cost with individuals expending time and energy returning to locations with low probabilities of obtaining rewards. Although individual differences in cognitive performance are frequently reported in non-human animals [68], these have not been explained as results of frequency dependent selection with different optima depending on the population composition. This would appear to be a fruitful area for further research utilizing both empirical and modelling approaches.

8 CONCLUSION AND IMPLICTIONS FOR COLLABORATION BETWEEN AI AND ANIMAL COGNITION RESEARCHERS

A Darwinian approach to the evolution of all aspects of life, including cognitive performance, provides both a powerful explanatory framework for why exaggerated variants of particular morphological, behavioural and now cognitive features are seen in some species or populations and not others. Crucially, it also helps explain why intuitively beneficial features may not be exaggerated because selection acts on net fitness gains and some apparent benefits may incur unexpected costs. In non-human animals, continued exaggeration of cognitive performance may be constrained by physiological costs of growing and maintaining energetically expensive neural tissue; or constrained by the need to execute a range of different cognitive processes within a limited mass of neural tissue. Exaggeration of performance in specific cognitive domains may also be constrained if there exist overarching domain-general cognitive processes which regulate them and the direction of exaggeration in the different domains differs. Alternatively, if exaggeration is favoured in the same direction across a range of specific domains then exaggeration of the overarching domain-general performance may be increased further. The optimal cognitive performance of an individual is dependent on their

physical, ecological and social environment, with optimal performances differing as the environment changes or the behaviour of conspecifics alters. Such constraints and tradeoffs help explain why the cognitive performances of some species remain 'worse' that is, with slower learning, more limited in memory or less flexibility than others. Cognitive performance still seems to be viewed differently from other morphological or behavioural traits, with efforts to construct a *scala naturae* placing humans at one extreme, followed by a hotly contested suite of other species, in a way that would be ridiculous if applied to, say, body size or speed of motion. An understanding that more extreme is not always better, and that the cognitive performance of a species is the result of natural selection necessitating trade-offs under a series of constraints, allows us to look at animal cognition in a different light. This somewhat novel perspective may also benefit developers of AI, prompting them to search for optimal solutions within a given set of constraints. Examples of natural resolutions of trade-offs, such as flexible brain (region) sizes in times of greatest cognitive demand, or the expression of particular cognitive performances only under specific environmental conditions may provide novel solutions to AI problems. Pitting individual AI agents against one another may also reveal frequency dependent optimal solutions. Conversely, synthetic agent-based models in which agents with different cognitive performance levels or mixes of cognitive processes compete within a population, or where agents experience various environmental conditions, may help animal cognition researchers identify circumstances that allow, or drive, variation in individual performances to persist.

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