Why are we intelligent? A comparison of the ecological and social theories on the evolution of large brains in primates, birds, and cetaceans

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Abstract

Primates, parrots, corvids, and cetaceans are amongst the most intelligent animals. However, intelligence is an energetically costly trait and researchers are yet to agree on what selection pressures have driven its convergent evolution across these phylogenetically distant taxa. Two overarching theories have traditionally been proposed for the evolution of intelligence in primates: ecological and social. Ecological theories suggest how cognitive mapping and extractive foraging techniques used by primates to find high-quality foods demanded increased cognitive capacity. Social theories, in contrast, suggest how forced cooperation between conspecifics and resulting social hierarchies encouraged an arms race of Machiavellian strategies to compete for mates and food. This paper attempts to find a theory consistent with the characteristics and behaviours of primates, parrots, corvids, and cetaceans. Cognitive mapping is only exhibited by some primate and corvid species, so is an unsuitable candidate. Extractive foraging is exhibited by species within all present taxa. Social behaviours like cooperation, alliances, and complex mating patterns were found in primates and cetaceans but much less so amongst bird species. Social learning, however, was found amongst all taxa. A mixture of extractive foraging and social learning, sometimes described as the socioecological model, is, therefore, proposed as the most likely explanation for the convergent evolution of intelligence across these taxa.

Keywords

evolution, intelligence, primates, ecology, behaviour

Introduction

The profound intelligence of primates is one of their most characterising and evolutionary unusual adaptations. Alongside cetaceans and certain bird taxa, primates are one of the only animal groups to have evolved large brains. Why these groups have evolved such large brains relative to their body size, however, remains contested. Most research has so far concentrated only on primate species, ignoring the evolutionary implications of similar intelligence in corvids (Corvidae), parrots (Psittaciformes) and cetaceans. This article will compare the behaviours and characteristics of these groups in an effort to find a consistent theory which explains the convergent evolution of intelligence across all these taxa. The paper will discuss the evolutionary implications of large brains, as well as tease out the links between brain size and architecture and cognitive functionality. It will then summarise and provide evidence for the various theories that have been proposed to explain the evolution of intelligence; classified as ecological and social theories. Finally, the paper will draw on this evidence and make comparisons among the ecology and cognitive abilities of primates, birds, and cetaceans to determine which hypothesis best explains selection for relatively large brains.

Do big brains matter?

Intelligence has been variously defined as the ability to learn, innovate, and solve new or complex problems (van Schaik and Burkart 2011). Specific cognitive functions typically associated with intelligence include abilities to form social relationships, respond flexibly to new situations and problems, recognise oneself, use advanced communication, and to memorise and form mental maps (Gallup 1998; Vorhees and Williams 2006; Pinker 2010; van Schaik and Burkart 2011). Despite being an energetically-costly trait—with the human brain using up to 20–25 per cent of the body's available energy—large brains, relative to their body size, have been selected for in several endothermic vertebrate taxa (Dunbar 1992). This suggests that larger brains must, sometimes, provide a significant fitness benefit (Dunbar 1992). Despite this, few animal groups—aside from birds and mammals—have evolved large brains relative to their body size (Yu et al. 2014). The fact that a clear majority of animals have not evolved large brains implies that the fitness benefits of intelligence are not normally worth the energetic cost (Dunbar 1998). This begs the question: what type of selection pressures could have caused big brains in these groups, particularly primates?

Absolute brain size is not an especially accurate measure of intelligence, especially when comparing different taxa; birds, primates, and cetaceans all differ greatly in body size. For example, corvids and parrots are considered among the most intelligent of birds, and compared with other birds have relatively larger brains (Iwaniuk et al. 2005; Kabadayi et al. 2016). When compared with great apes, however, despite having considerably smaller brains in absolute terms, corvids have been found to perform equally well or better on some intelligence tests (Kabadayi et al. 2016). This can be explained by the fact that, at least to a certain extent, brain size is also dependant on body size (Yu et al. 2014). Absolute brain size alone, therefore, cannot be regarded as a precise indicator of intelligence and must be considered in relation to body size. Corvids compare similarly to primates in terms of relative brain-to-body size, with the brain usually accounting for between 1–2 per cent of overall body mass (Iwaniuk and Nelson 2002; Isler et al. 2008).

Intelligence is a broad and nuanced concept which relative brain size alone cannot fully explain. Research surrounding primate intelligence has traditionally assumed a causal link between relative brain size and cognitive function, a notion not demonstrated until 2002 by Reader and Laland. Relative brain size, however, is just one of the many attributes and measures that have been used to qualify intelligence (Shultz and Dunbar 2009). Another indicator of cognitive function in primates is specific brain architecture, with hippocampus size and relative neocortex size also being correlated with intelligence (Shultz and Dunbar 2009). Intelligent birds have also been shown to have relatively larger hippocampi, although they lack a neocortex almost entirely (Gould et al. 2013; Veit and Nieder 2013). Cetaceans, in contrast, have been shown to have comparatively small hippocampi and neocortices (Stefan 2008; Patzke et al. 2015). These discrepancies may reflect the likelihood that there are different types of intelligence which potentially evolved due to separate selection pressures, with different effects on the brain (Reader et al. 2011). Primates have been hypothesised to have the widest array of ecological and social pressures working for their intelligence; comparatively, birds lack advanced social interactions, and cetaceans evolved in drastically different aquatic ecosystems. Due to the different requirements of these selection pressures, *between* group comparisons of relative brain size and architecture are not appropriate. Nevertheless, *within* each of these groups, brain size and architecture correlate well enough with intelligence to allow for fair comparisons.

Ecological theories

Broadly speaking, ecological pressures are hypothesised to have favoured increased cognition as primates exerted energy foraging for, and extracting, challenging or seasonal foods (Reader et al. 2011; Melin et al. 2014). The extractive foraging hypothesis suggests that primates evolved higher cognition and intelligent tool use to enable them to obtain these otherwise inaccessible, hidden, or protected foods (Parker and Gibson 1977; Melin et al. 2014; Parker 2015). These advanced extractive methods include fishing, dipping, and cracking open or excavating (Parker and Gibson 1977). A good example of this is the yellow-breasted capuchin monkeys' (*Cebus xanthosternos*) use of stones as hammers and anvils to open nuts (Canale et al. 2009). Other primates to engage in this extractive foraging behaviour include aye-ayes (*Daubentonia madagascariensis*), chimpanzees (*Pan troglodytes)*, and other capuchins (*Cebus)* (Parker 2015). This theory suggests that as primates began to rely on these methods to obtain more nutritious food, they developed more conceptual kinds of intelligence including concepts of topography, enclosure, and penetration (Parker 2015). The ability to manipulate objects may also select for increased cognitive abilities and the associated problem-solving and spatial-awareness skills (Melin et al. 2014). Extractive behaviour has been strongly linked with sensorimotor intelligence and increased size of the cerebral cortex in white-face capuchins (*Cebus capucinus*) and most of the above-listed extractive foragers have large relative brain sizes (Melin et al. 2014; Parker 2015).

The widespread and seasonal nature of many primate diets, particularly frugivores, further requires that they remember where the food is, which has been theorised to have led to ‘cognitive mapping’ (Tomasello 2000). This theory proposes that primates form highly-detailed mental maps which outline the spatial and temporal availability of food and allows for more efficient navigation (Whiten and Byrne 1997). This is can be particularly challenging as, although somewhat predictable, the distribution of such food is often based on nonannual cycles (Whiten and Byrne 1997). The advanced memory and geographic awareness needed to map such environmental complexity is presumed to have been selected for in primates who are able to be more successful at obtaining high-quality, seasonal foods (Clutton-Brock and Harvey 1980). This may be particularly true of heavier frugivorous primates like some great apes—which expend more energy whilst foraging and are fussier eaters, often only eating fruit when ripe (Whiten and Byrne 1997). For these species, efficiency and accurate timing of arrival at a food source are even more important, and their improved cognitive abilities may have evolved to accommodate this need. DeCasien et al. (2017) have shown, using a large sample size and controlling for body size, that frugivores—like spider monkeys (*Ateles)*—generally have far larger brains than folivorous and closely related primates—such as howler monkeys (*Alouatta)*—providing renewed credence to this theory.

The ecological intelligence model may, in some respects, also help explain the evolution of intelligence in birds and cetaceans. Corvids—which have large brains relative-to-body-size compared to other bird groups—have been shown to use extractive foraging techniques similar to primates—including using sticks to catch insects hiding in crevices—and display comparable motor-regulation abilities to primates (Roffman et al. 2015; Kayabayi et al. 2016). Similarly, large-brained parrot species including keas (*Nestor notabilis*) and Senegal parrots (*Poicephalus senegalus*) have also been shown to exhibit advanced exploration and extraction techniques (Huber and Gajdon 2006; Demery et al. 2011). Cetaceans likewise have been observed using innovative foraging and extractive techniques, including tool use. Bottlenose dolphins (*Tursiops*) exhibit particularly advanced techniques, including hydroplaning across extremely shallow water and probing the seabed with sponges to catch difficult-to-reach fish. They also have the largest relative brain sizes amongst cetaceans (Krützen et al. 2005; Connor 2007; Sargeant and Mann 2009). There is extremely limited research on the ability of nonprimates to form cognitive maps, although some corvid species have been observed ‘scatter-hoarding’ certain foods by burying them in the ground at specific locations to eat later (Clary and Kelly 2011; Pesendorfer et al. 2017). This behaviour would likely necessitate some ability to form cognitive maps; however, the extent and success of these abilities requires further study to determine how advanced such mental mapping is.

Social theories

Dunbar (1992, 1995, 1998) first developed the social brain hypothesis, which posits that primates developed large brains to survive and compete in their remarkably complex social groups. Dunbar (1992, 1995) showed that neocortex size was strongly associated with group size. Other social hypotheses have since been developed, generally concluding that conspecifics forced to live together in groups constantly compete with one another for limited resources and so continually develop higher intelligence through a form of a cognitive arms race (Barrett and Henzi 2005; Byrne and Bates 2010). This basic premise—commonly termed ‘Machiavellian intelligence’—relies on the notion that most primates are unwilling collaborators, forced to live in groups to minimise the risks of predation and infanticide from conspecifics (van Schaik and Kappeler 1997; Barrett and Henzi 2005). This group living requires the adoption of behaviours such as grooming and negotiation to allow individuals to coexist peacefully and productively, and to more easily find potential mates (Barrett and Henzi 2005). Competition for food and, especially, mates, however, remains and simultaneously drives adaptations for manipulation, deceit, and alliances. Maintaining group cohesion whilst improving individual reproductive success is thus at the heart of social intelligence hypotheses.

The need for group cohesion necessitates selection for efficient cooperative interactions, especially in conjunction with concepts of kin selection. New research has modelled how selection for efficient decision-making in cooperative dilemmas leads to an increase in cognitive abilities (McNally et al. 2012). This mechanism relies largely on the idea of reciprocal altruism, where individuals help others with the expectation that aid will be returned (Barrett and Henzi 2005). This concept demands that individuals keep track of what they owe others, what others do for them, and whether other individuals treat others fairly. These cognitive abilities to remember past interactions help avoid conflict and quickly resolve cooperative dilemmas, reducing stress and violence (McNally et al. 2012). Selection for such functions probably began as altruism associated with kin selection, which relies on genetic relatedness to function. The concept likely expanded beyond familial limitations as primate groups grew larger, putting increased cognitive demands on memory and manipulation (Dunbar 1998; Allen-Arave et al. 2008; McNally et al. 2012). Reciprocal altruism thus maintains group cohesion and selects for higher cognitive function.

Primates living together peacefully can also expect increased reproductive success, as reciprocal cooperation and cohesiveness can help reduce the negative effects of competition and aggression; this notion is at the core of further elements of social intelligence (Barrett and Henzi 2005). Primate groups are often highly structured and hierarchical, especially in species with high sexual dimorphism and polygynous relationships – where more dominant males in the hierarchy often attempt to monopolise females through aggressive mate guarding, leading to the emergence of underhanded tactics by lower-ranked males to gain mating opportunities (Pawlowski et al. 1998). Less dominant males may engage in male-female friendships and build all-male alliances to distract or overpower dominant males to gain mating opportunities. These subtle strategies demand, and may select for, increased information-processing capacity (Pawlowski et al. 1998). Supporting this, there is evidence that primates living in large groups with complex dominance hierarchies—like chimpanzees and baboons (*Papio)*, which are especially known to engage in subtle mating strategies—have larger brains and neocortices compared with smaller-grouped species, like macaques *(Macaca)* (Pawlowski et al. 1998). Somewhat conversely, however, it has also been theorised that monogamous mating systems in small-grouped primates—such as gibbons (family Hylobatidae)—also require great social acuity to effectively maintain what are often intense and intricate relationships (Schillaci 2008). Schillaci (2008) found that monogamous species like humans and gibbons have the largest neocortices amongst primates, although he did not include chimpanzees or baboons in his study.

Intimate social environments also permit the sharing of skills and abilities through cultural transmission. Primates are highly exploratory and inquisitive animals which often observe and attempt to emulate the abilities of their peers (van Schaik and Burkart 2011; Coelho et al. 2015). This is often an essential process, as primates acquire new skills faster and gain a greater repertoire through social learning than they would individually (van Schaik and Burkart 2011). This amounts to more than simple copying, as primates preferentially rely on social learning over individual exploration. Many actively choose to learn from more proficient individuals within the group rather than those who are physically closest, indicating they have advanced recognition and social skills (Coelho et al. 2015). This transmission, in a sense, makes some forms of intelligent behaviours heritable and, by co-opting these behaviours, further increases an individual’s capacity to learn asocially (van Schaik and Burkart 2011). Furthermore, if a species becomes reliant on these learning opportunities, selection for individual learning capacity and behavioural flexibility may be increased, and therefore improve cognitive function and increases brain size (Reader and Laland 2002; van Schaik and Burkart 2011).

Birds and cetacean taxa have also been shown to exhibit many of these characteristics and behaviours. That said, birds (even when living in extremely large groups) are very socially flexible and rarely display any advanced behaviours associated with dominance or cooperation, and their relative brain sizes are not correlated with group size or cooperativeness (Clayton et al. 2007; Emery et al. 2007). Both corvids and parrots, however, have been shown to cooperate to solve problems, but not to the degree nor with the social ramifications of cooperation in primates (Seed et al. 2008; Péron et al. 2011). Nonetheless some birds do display elements of complex social cognition when confronted with food competition. Corvids can seemingly infer the mental states of conspecifics whilst scatter-foraging and will wait until potential food thieves are distracted or obscured before burying food (Emery and Clayton

2004; Clayton et al. 2007). Monogamous, life-bonding birds tend to have larger relative brains, which Emery et al. (2007) attribute to reciprocal behaviours like food sharing and alliances. Some social-living corvids have also exhibited social learning, and other bird species, including starlings (Sturnidae) and parrots—which likewise have relatively large brains—have also been shown to copy the behaviours of conspecifics to spread social information faster (Templeton et al. 1999; Iwaniuk et al. 2005; Butler et al. 2016). Cetaceans have also been shown to pass on skills and behaviours via cultural transmission (Sargeant and Mann 2009; Visser et al. 2014). There is also tentative evidence to suggest that cetacean group size is positively correlated with brain size (Lori 2002). Moreover, dolphins have been observed engaging in alliances, potentially reciprocal altruism, and caregiving behaviour (Kuczaj et al. 2015). Genetic studies have further suggested that the evolution of their large brains is tied to social complexity, as genes tied with the evolution of brain complexity are also correlated strongly with larger group sizes (Connor 2007; Xu et al. 2017).

Which theory is stronger?

It is important to note that virtually all hypotheses for the evolution of intelligence have been based on primates, however, the intelligence of birds and cetaceans has, in more recent years, been considered by some as convergent and based on the same evolutionary principles (Emery and Clayton 2004; Clayton et al. 2007). If so, comparisons between these taxa and identifying consistent traits and patterns can help clarify which theory or combination of theories is most compelling in explaining the evolution of intelligence.

Early evidence for the evolution of primate intelligence focussed on proving ecological hypotheses. Frugivorous primates had both larger brains and larger home ranges when compared with folivorous primates, suggesting cognitive mapping required for finding fruit increases brain size (Clutton-Brock and Harvey 1980; MacLean et al. 2009). Similar mapping in corvids further suggest this pressure could increase intelligence, although there is little to no evidence of its occurrence in cetaceans. A common criticism of this theory in primates is that it does not explain how folivorous primates—which still have large brains compared with other animals—could have also evolved intellectual complexity (Whiten and Byrne 1997). Ken (2013) goes someway to explaining this in demonstrating how folivorous langurs have great behavioural flexibility, engage in food competition, and have home range sizes that rival frugivores. The dynamic behaviours and social flexibility of primates, however, generally makes such comparisons difficult. It has also been shown that many primates, birds, and cetaceans with larger brains relative-to-body-size engage in extractive foraging and advanced dextrous manipulations (Parker 2015; Heldstab et al. 2016).

In his landmark paper, Dunbar (1992) criticised the evidence for ecological models, suggesting it was too exclusive of other possibilities and only measured overall brain size. Dunbar instead focussed on the size of the neocortex, which he argued was the ‘thinking’ part of the brain, and he showed processing capacity was correlated strongly with an increase in group size (Dunbar 1992, 1995). This association is not, however, universal, especially among strepsirrhine primates or among birds, although may hold true among cetaceans (Maclean et al. 2009). Nonetheless, primates with bigger neocortices employ more advanced mate-gaining strategies (Pawlowski et al. 1998; Allen-Arave et al. 2008). Polygyny does not, however, guarantee greater intelligence, with many monogamous birds and primates possessing relatively large brains (Emery et al. 2007; Schillaci 2008).

Considering that intelligent birds are monogamous and utilise social mapping, and both intelligent birds and cetaceans engage in extractive foraging, social intelligence theories do not seem especially more convincing than ecological theories. Indeed, that some birds appear to infer state of mind without engaging in complex social interactions suggests that ecological theories may be a more probable explanation. Additionally, Dunbar’s (1992) assertion that neocortex size is the best indicator of intelligence is not supported by recent research (Stefan 2008; Gould et al. 2013; Veit and Nieder 2013; Patzke et al. 2015). One notion not widely explored in this debate is the possibility that more than one of these models could simultaneously drive selection for intelligence. This seems a particularly important possibility to consider given the widespread contradictions in the evidence. The extractive foraging hypothesis in particular commonly includes elements of cultural transmission, and so can be termed a socioecological model (Parker 2015). This mixture of theories seems increasingly likely considering that all three [primate, bird, and cetacean] groups have been regularly observed using extractive foraging and passing on these behaviours through social learning.

Conclusion

Primates, corvids, parrots, and cetaceans all have relatively large brains, the cognitive advantages of which allows them increased behavioural flexibility and the ability to adapt and exploit a wider variety of niches. Nonetheless, large brains are energetically demanding, a problem which has sparked animated debate regarding their evolutionary origins. Ecological models theorise that the acquisition and extraction of energy-rich foods selected for increased spatial and sensorimotor intelligence alongside memory. Social intelligence instead posits that conspecifics forced to live together developed intelligence as a method of managing group cohesion and profitability whilst subtly gaining competitive advantages. The evidence for these hypotheses is plentiful, although contradictions are common. The evidence for the 'cognitive mapping' ecological model is probably weakest, as only circumstantial and contested evidence links frugivory to increased brain size and home range in primates, and only corvids appear to use it amongst birds. Additionally, no other animal taxa have been shown to have evolved larger brains due to such pressures, and the most intelligent frugivorous primates are also usually social (Reader et al. 2011). The body of evidence for the social brain theory is far broader and more widely accepted. Many aspects of the social intelligence model can also be applied to cetacean intelligence. Nonetheless, exceptions exist to Dunbar's (1992, 1995) oft-cited findings, and socialisation does not appear to have played a significant role in the evolution of intelligence in larger-brained birds like parrots and corvids. The notion that elements of both these hypotheses could be acting together is surprisingly unexplored in the scientific literature, especially given the often contradictory nature of the evidence. The socioecological hypothesis of extractive foraging, combined with cultural transmission, is particularly convincing given that parrots, corvids, starlings, cetaceans, and primates all appear to engage, at least to some extent, in such behaviours. Given this is the only hypothesis that links all these big-brained groups, it is fair to characterise it as the most convincing theory. Nonetheless, evolution and intelligence remain difficult to study as evidence is often circumstantial or based on correlation. Until more empirical studies can be devised, we should remain openminded concerning the evolutionary origins of intelligence.

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