

Evolution of primate intelligence

© Copyright Bruce Owen 2010

- Primates are relatively intelligent compared to other animals
 - As we saw earlier, primates tend to have large brains relative to their body size
 - humans are an extreme case, even among primates
- So why are primates, and especially humans, so smart?
- First, what do we mean by intelligence?
 - this is a slippery issue, as any psychology student will tell you
 - it is more than just complex behavior
 - many complex behaviors among animals do not impress us as particularly intelligent
 - for example, we don't think that homing pigeons are particularly smart, in spite of their ability to find their way home from distant, unknown places
 - presumably, intelligence involves *flexible* behavior, the ability to solve novel problems
- Intelligence presumably increased in many steps
 - Changing with each evolutionary split that eventually led to us
 - we shouldn't expect a single explanation for human intelligence
 - instead, we should expect that different processes may have been involved at different stages
 - each relevant to the particular kind of creature involved in that evolutionary change
 - 1. a non-primate mammal species became the first, strepsirrhine-like primate species
 - this change happened in small, rodent-like, nocturnal animals
 - why would intelligence have improved their reproductive success more than it does for squirrels, opossums, or other similar animals?
 - 2. a strepsirrhine-like primate species became an haplorrhine species
 - this change happened in larger, smarter, arboreal, diurnal animals... why?
 - 3. an haplorrhine species became a hominine (a great ape)
 - this change happened in still larger, still smarter animals... why?
 - This "step" actually lumps quite a few potentially separate steps
 - 4. a hominine species became a hominin (us)
 - we'll leave this change for later
 - again: each step in intelligence could have been for a different reason
- This only looks like a continuous increase in intelligence because we are looking backwards from our endpoint
 - At each branch, one side increased intelligence, and the other not so much, or not at all
 - Naturally, if you pick the more-intelligent side of each split, you get to the most intelligent of the many living species
 - But all the others have been evolving for just as long
 - There is no goal of increasing intelligence; we are just the result of a bunch of increases
 - that happened for probably various reasons
 - at various times
 - among different kinds of animals

- Let's look at a bunch of processes that probably contributed to increasing intelligence in primates at one point or another
 - all have some evidence to support them for some kinds of primates, or some points in the evolution of our ancestors
 - and all probably did NOT apply to some other points in the evolution of our ancestors
- One process: selection acting on life history strategies
 - **Life history theory**: theory about tradeoffs and selection in overall strategy of lifespan and reproduction
 - **life history strategy** refers to
 - the general plan of an organism's life, including its rate of maturation, body size, lifespan, effort spent on reproducing vs. parenting vs. surviving, etc
 - viewed in terms of how this plan affects the organism's reproductive success
 - animals vary roughly along a single scale of life history strategies
 - from the **short/fast** extreme
 - have lots of offspring as quickly as possible
 - but have high mortality (lots of offspring die young) and short lifespans
 - to the **long/slow** extreme
 - have few offspring and take a long time for each
 - but have low mortality (fewer offspring die young) and long lifespans
 - The short/fast life history strategy
 - life history factors that promote having lots of offspring quickly include:
 - having a small body
 - because small bodies permit short gestation (a mother can produce offspring quickly)
 - because small bodies mature quickly, so they can reproduce sooner after being born
 - large litters
 - produce lots of offspring quickly
 - small brains relative to body size
 - larger brains take longer to develop
 - larger brains require lots of energy to grow and operate; this energy could be used for mating and producing offspring
 - short lifespan
 - quick-maturing bodies tend to be less durable
 - more energy is expended on reproducing, and less on maintenance
 - The short/fast strategy might work well for animals that face a high risk of predation
 - breed as soon as you can (before you get eaten)
 - mature quickly
 - don't waste time or energy growing a large, durable body
 - produce lots of offspring as quickly as possible
 - don't invest much in any given one, since most will get eaten anyway
 - this maximizes the number of surviving offspring the individual produces before a predator kills it
 - the long/slow life history strategy
 - features that aid in having a few offspring that are more certain to survive:

- larger bodies
 - less subject to predation once full grown
 - can eat more varied, lower quality, more available foods
 - requires longer gestation and longer juvenile development
- smaller litters
 - more energy is available to develop a few or just one offspring
- larger brains relative to body size
 - larger brains may improve survival and/or reproductive success
 - higher survivorship is necessary for the large investment in offspring to pay off
- longer lifespan
 - slow-maturing bodies can be more durable
 - slowly growing a large brain and body only pays off if you then have a long lifespan during which to reap the reproductive success benefits of them
- the long/slow strategy might work well...
 - if large size is beneficial
 - as when predation is rare, but size helps when it threatens
 - as when size helps in competition for food or mates
 - if large brains are beneficial
 - for reasons we will get to shortly
 - the benefit of having a large brain must be great, because brains require a lot of energy to grow and maintain
 - but if selection favors them, the rest of the long/slow life history strategy has to evolve in order to support them
 - there is no other way to grow large brains and have the large investment in time and energy pay off in reproductive success
- Primates tend towards the long/slow end of the life history strategy spectrum
 - Probably due to selection for large brains
 - So, why did natural selection favor large brains in primates?
- In order to test some hypotheses about primate intelligence, let's define a rough measure of intelligence for animals
 - Intelligence is hard to measure, but we can use the relative size of the brain's neocortex as an approximate guide
 - the **neocortex** is the convoluted outer surface of the forebrain (the major part of the "cerebral cortex")
 - brain studies indicate that this is the part of the brain involved in problem solving and novel behavior – what we associate with intelligence
 - the neocortex is greatly expanded in primates, and especially in haplorrhines, and most especially in humans
 - since we consider haplorrhines and humans to be unusually intelligent, it makes sense to use the brain feature that is most exaggerated in them as a measure of intelligence
 - **neocortex ratio** is the fraction of the brain that is neocortex
 - a higher neocortex ratio means that relatively more of the brain is neocortex, which should mean that the brain is "smarter"

- this measure of the “smartness” of the brain is not affected by the brain’s size, but rather by which portions are more emphasized within it
- So, why might selection favor larger (or “smarter”) brains? Three general hypotheses
 - 1. **Ecological intelligence hypothesis:**
 - greater intelligence was favored because it helped individuals better exploit their ecological circumstances, especially regarding getting food
 - “**resource patchiness**” variant of the ecological intelligence hypothesis:
 - intelligence was favored among animals that had to find resources that were distributed in patches that changed seasonally
 - especially fruit, available at the same tree every year, but only for a limited time
 - individuals with
 - better memory
 - greater ability to learn about their environment
 - more ability to plan ahead
 - might be more efficient at finding food
 - wasting less time on travel to barren trees or random, fruitless foraging
 - “**resource extraction**” variant of the ecological intelligence hypothesis:
 - intelligence was favored among animals that benefited from performing complex tasks to extract their food
 - as in recognizing where to dig up roots
 - breaking open hard-shelled nuts or fruits
 - finding insects under tree bark
 - “fishing” for termites, as chimps do, etc.
 - Evidence that supports the ecological intelligence hypothesis
 - The average neocortex ratio is indeed greater for species that
 - have larger home ranges
 - As predicted, since larger home ranges should offer a bigger payoff for having better memory and strategizing abilities in searching for food
 - eat more fruit
 - As predicted, because fruit has is distributed in patches that vary over time, so again, having good memory and strategizing should pay off more
 - Hominines (Great apes) are presumably the smartest of primates, and they tend to use complex sequences of actions to process food
 - gorillas break and peel stalks of wild celery, then pick out the edible bits inside
 - chimpanzees and orangutans use sticks to fish for insects and break into fruits
 - chimpanzees break open hard nuts using hammers and anvils of stone or large branches and roots
 - all the great apes are able to use tools in captivity
 - so maybe greater intelligence helped with resource extraction
 - Evidence against the ecological intelligence hypothesis
 - Neocortex ratio does NOT correlate well with complex resource extraction behavior
 - Other animals depend on patchy resources like fruit, but have not evolved exceptional intelligence

- Many fruit-eating birds, bats, rodents, etc.
- Other animals use complex resource extraction methods, but have not evolved exceptional intelligence
 - Sea otters that break sea urchins open by banging them on flat, smooth rocks balanced on their chests while they float on their backs...
- **2. Social intelligence hypothesis:**
 - greater intelligence was favored because it helped individuals better take advantage of the more complex social interactions of larger social groups
 - the larger the group, the more relationships to track and manage
 - like establishing and keeping track of dominance relations at minimum cost
 - without losing more resources than necessary to less dominant individuals
 - or getting injured by more dominant ones
 - forming coalitions that successfully benefit the individual without costing too much
 - keeping track of who is more and less related, so that the individual performs altruistic acts only for kin
 - keeping track of reciprocated altruistic acts, in order to ensure getting “paid back” for altruistic acts
 - individuals who handled these problems better might have higher reproductive success (or rather, higher inclusive fitness)
 - Evidence that supports the social intelligence hypothesis
 - The average neocortex ratio is indeed greater for species that
 - Live in larger groups
 - As predicted, because the larger the group, the more frequent and complex the social interactions
 - chimpanzees and bonobos seem to be very smart, and they do live in large, very socially complex groups
 - better ability to solve complex social problems (mating strategies, dominance hierarchies, etc.) would improve their reproductive success and/or inclusive fitness
 - Evidence against the social intelligence hypothesis
 - Some hominines with very high neocortex ratios do NOT live in large groups
 - Orangutans are solitary
 - Gorillas live in small groups
 - So how would better ability to solve complex social problems help their reproductive success?
 - Other mammals live in large groups but have not evolved particularly complex social behavior or notable intelligence
- **3. Flexible behavior hypothesis:**
 - Greater intelligence helped individuals solve novel problems, invent new behaviors, and learn from each other (social learning)
 - This could help in both ecological and social matters
 - Especially if the circumstances were unstable and changing
 - This is essentially a broader hypothesis that includes the ideas of both the ecological intelligence hypothesis and the social intelligence hypothesis
 - but emphasizes flexibility more than complexity of behavior

- Evidence that supports the flexible behavior hypothesis
 - Executive brain ratio (another rough measure of brain tissue associated with intelligence, similar to neocortex ratio) is indeed greater for species that
 - have had more reports of observed cases of innovative behavior (inventing novel behaviors)
 - have more reports of observed cases of social learning (learning from others, as opposed to figuring something out by oneself)
 - have more reports of tool use
- Bottom line: all of these processes were probably involved in some stages, and not others, of the evolution of greater intelligence among some primates
- Another approach to testing the social intelligence hypothesis
 - if the social intelligence hypothesis were correct, then primates should be unusually good at handling complex social problems
 - it is hard to compare abilities for solving different social problems in different species
 - but we can at least show that many primates are very good at solving social problems
 - which supports the idea that primate intelligence developed specifically to handle these kinds of problems
 - for example, many primates “know” a lot about the kin relationships in their social groups
 - they “know” who their own relatives are
 - usually only on their mother’s side, from growing up with them
 - this is not too surprising, since kin selection would favor individuals who can most effectively direct their altruistic behavior towards close kin
 - but many *also* know how *other* individuals are related to each other
 - these are **third party relationships**: between two other individuals, not directly involving the individual who knows about them
 - there is no obvious kin selection explanation for this
 - primates don’t know who is related to who automatically; they have to learn it
 - in many primates, all group members study new infants, apparently learning to recognize them and associating them with their mothers
 - this requires a lot of learning, and a lot of memory
 - the effort they spend to learn and remember this information (maintaining the necessary large brains) suggests that this knowledge must serve an important purpose
 - which could only be social
 - the fact that they can do this suggests that natural selection for these social abilities must have been strong
 - how can we tell what monkeys “know”?
 - Dorothy Cheney and Robert Seyfarth played tape recorded calls of a specific infant to a group of vervet monkeys
 - not surprisingly, the mother looked toward the call longer than the other monkeys did
 - she obviously recognized her own infant’s call
 - what was interesting was that the other monkeys tended to look not at the source of the call, but at the mother
 - that is, they not only recognized the infant

- but they also knew who its mother was!
- and that she was likely to do something worth seeing
- so these monkeys don't just know their own kin, they know kin relationships between others who are not their own close relatives
 - that presumably takes some intelligence to learn and keep track of
 - more than I have at some family gatherings!
- another experiment showing similarly complex understanding of kin relationships among other individuals, by Verena Dasser with captive macaques
 - she showed one macaque photos of pairs of certain macaques from her group
 - she rewarded the macaque when she picked out pairs that were mother and offspring
 - once the macaque was trained, she showed the macaque photos of pairs of different individuals from the same group
 - the macaque still picked out mother-offspring pairs, even though she had not been trained on these particular individuals
 - this implies that the macaque understood the *reason* that the pairs in the first phase got her a reward
 - it wasn't those particular pairs, it was the fact that they were mother-offspring pairs
 - otherwise, when presented with new individuals, she would not have known which to pick
 - this shows that macaques know the mother-offspring relationships of most or all their group members!
- further evidence that primates know relationships of others, this time from observations in the field
 - Cheney and Seyfarth documented **redirected aggression**
 - vervet A (for aggressor) threatens vervet V (for victim)
 - Later, vervet V threatens not vervet A (its opponent), but a *relative* of vervet A
 - non-relatives are rarely the target
 - so they must know the relationships of others
 - and not just mother-offspring, but longer chains of relationships
 - in addition, the relative is generally a relative through the mother
 - recall that primates learn kin relationships by observing mother-infant relationships
 - so they probably don't know who the father was
 - so they must learn mother-offspring relationships, and chain them together into more distant relationships
 - so if they have a conflict with one individual, they know which others are related to it, and can pick a less threatening relative to take out their aggression on
- baboons know about dominance hierarchy (rank) relationships among third parties
 - Cheney and Seyfarth played back recordings of dominant grunts and submissive barks by different individuals
 - when they played a higher-ranking baboon's dominance grunt, followed by a lower-ranking baboon's submission bark
 - other baboons did not react much
 - this was a normal, expected situation

- when they played a lower-ranking baboon's dominance grunt, followed by a higher-ranking baboon's submission bark
 - other baboons responded strongly
 - they recognized that this was a reversal of the relationship
 - which means that they know the relative ranks of other individuals
- hominines may know something about other individual's minds, but this is not certain
 - chimps know to follow another chimp's or human's gaze to see what the other is looking at
 - but do chimps go from this to understanding what the other individual knows about?
 - evidence that they do not
 - a chimp will beg from a human in exactly the same way, whether the human is looking at the chimp or not
 - suggesting that the chimp does not have an understanding of what is in the mind of the other
 - evidence that they do
 - experiment in which a low-ranking chimp can see two pieces of food, and can see that a higher-ranking chimp can only see one of them
 - the low-ranking chimp almost always goes to the food that is hidden from the higher-ranking chimp
 - suggesting that it does, in fact, understand what the other chimp knows and does not know
 - all of these studies have problems, though, so whether or not chimps understand what others know is still undecided
- Another indicator that primates are particularly good at handling complex social problems: Many primates manipulate social relationships in complicated ways
 - such as forming coalitions
 - deciding who to support against who involves a complex calculation about
 - the benefit to the one supported
 - the cost to the one being repelled
 - the cost to the supporter
 - all depending on the relatedness of the individuals and their dominance rank, if not also other factors
 - also on recent history of who has supported who, who has groomed who, etc.
 - bonnet macaques and capuchin monkeys consistently make appropriate choices of which individuals to support or to solicit support from
 - macaques tend to intervene in a dispute only when they outrank both of the participants
 - so they can expect to win
 - and they solicit support mainly from individuals who outrank both themselves and the other participant
 - that is, they solicit support not from just anyone present, but specifically from others who are likely to intervene, and likely to win
 - capuchins tend to support individuals who have recently associated with them, typically in grooming

- and disputants “know” not to solicit support from recent associates of their opponent
 - there are several observed cases of chimps trying to prevent lower-ranking individuals from forming coalitions that might later be able to challenge them
 - suggesting a considerable grasp of politics
 - some primates deceive each other in complex ways
 - a chimp who was shown where food was hidden would lead the others off in the wrong direction, then rush back and get the food himself
 - a baboon in the wild in a conflict suddenly looked off at the horizon when supporters of his opponent arrived
 - the outnumbered baboon is about to lose the conflict
 - because of his behavior, the others assumed he has sighted a predator, and were distracted from the conflict
 - a male chimp who was being challenged sat with his back to the challenger trying to control his submissive grin, even pushing his lips together with his fingers three times, before turning to face him!
 - the point is that primates have surprisingly great abilities to solve social problems
 - primates know a lot about social relationships, including ones between third parties
 - they are remarkably good at handling complex social situations
 - coalitions, reciprocity, altruism towards kin, dominance relations, deception
 - so maybe these are the skills that were favored by selection
 - which led to generally greater intelligence
 - that is, at least part of the “reason” for greater intelligence was that it improved the primates’ abilities to handle social problems
- The point of today’s discussion (and the previous several weeks’)
 - Humans are notable among all animals for being unusually
 - social: living in groups with very complex social interactions
 - smart: having very complex, flexible behavior
 - living non-human primates suggest how our ancestors might have evolved those characteristics
 - sociality might be due to selection for better abilities in
 - resource defense
 - mate defense
 - protection from predators
 - complex social behavior might be due to
 - sexual selection for complex mating strategies, coalitions, etc.
 - kin selection
 - selection for abilities needed to benefit from reciprocal altruism
 - intelligence might be due to selection for
 - abilities to solve ecological problems
 - like locating patchy resources
 - or devising and carrying out complex routines to extract resources
 - abilities to better take advantage of complex social interactions