Primate Brains

Introduction

Brains are something that we humans are rather proud of. I wouldn't be at all surprised if many people didn't think that humans had the biggest brains on the planet. We certainly think that we are the smartest animals on the planet. This lecture looks at the primate brain specialisations in terms of gross anatomical structure with only limited comment on function – after all, this is an anatomy course not a psychology one!

Size

As the saying says, "size isn't everything". However when we are dealing with gross anatomy and with fossils where soft tissues are rarely preserved size may be all we can measure. Brain size is therefore an important parameter. Humans do not have the biggest brains – elephant brains are bigger, and several large Cetacea all have bigger brains. The biggest is possessed by the sperm whale (*Physeter catadon*) which, at 9.2 kg [Nowak, 1991], is about 7 times larger than a human brain. Since we clearly feel that we are more intelligent than Proboscidea and Cetacea (although one or two New Age cults might dispute the latter assertion) there must be more to it than that. Firstly, brain size is very strongly positively correlated with body size. It seems that to keep a larger body working requires more neural circuitry which makes a certain amount of sense. Secondly, certain parts of the brain are deemed more important for the process of intelligence. Thirdly, brain complexity – in other words how highly folded the cortex is – may be just as important as overall size.

Allometry

This is a good place to introduce the concept of allometry. It has been known for a long time that changes in organisms can be brought about by processes of differential growth [Thompson, 1917] and this has become a cornerstone for morphological studies. Huxley [Huxley, 1932] produced a very simple equation that can be widely used to characterise relationships between measured parameters (whether anatomical, such as brain size; physiological, such as basal metabolic rate; ecological, such as home range size; or whatever) and body size. This is equation 1.

Equation 1.

$$y = Bx^k$$

y is the measurement that we are measuring or predicting in relation to body size. x is the body size of the animal (this is usually measured as the body mass, although body volume could probably be substituted since overall body density does not vary much). B and k are constants that are either measured empirically by fitting the equation to a set of data or produced theoretically from some model of the expected relationship.

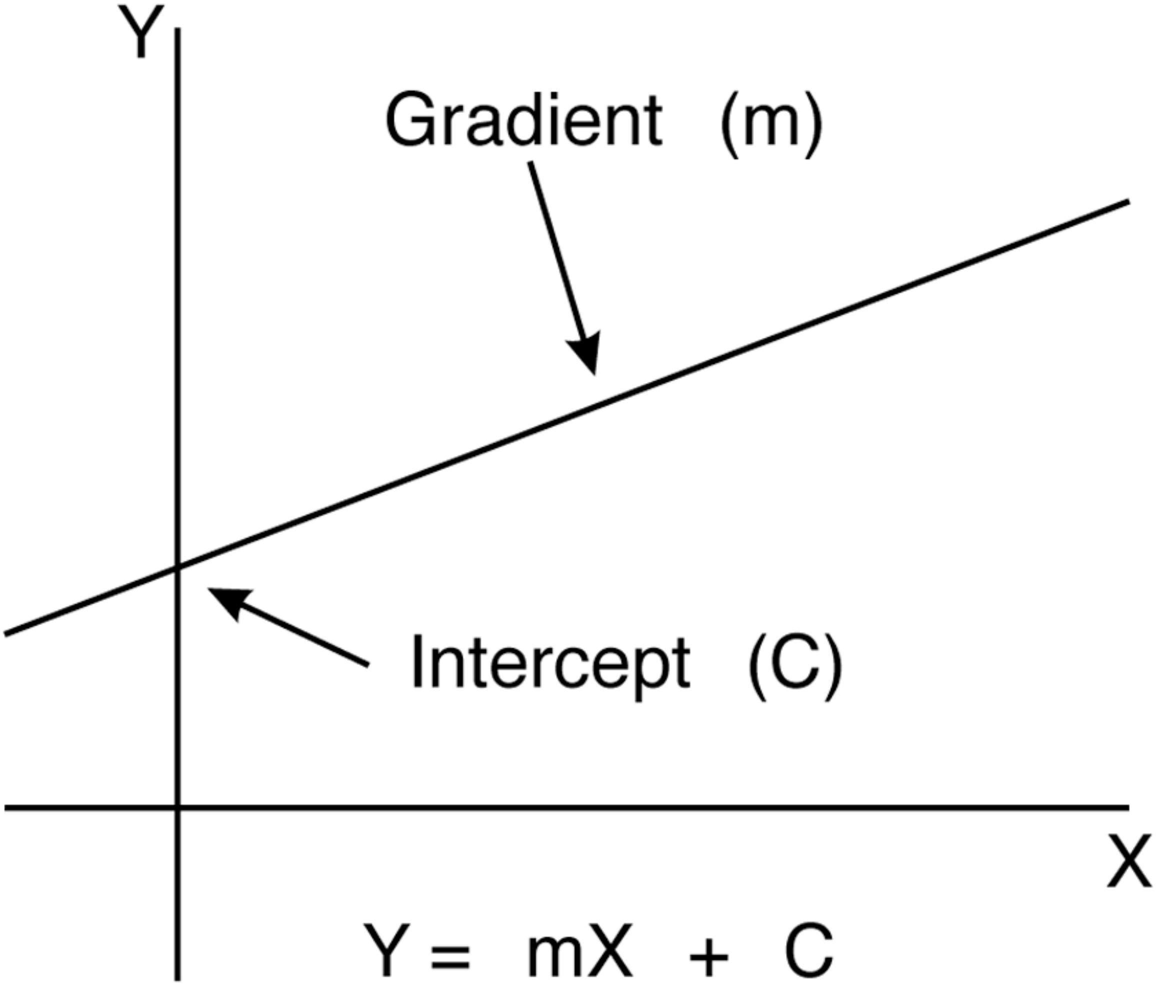
This equation has proved to be immensely useful in a wide variety of fields, especially in its alternative form, equation 2. This equation is obtained by applying the logarithm function to both sides of the equation since by definition $y = a^x \Rightarrow x = \log_a y$ and by the **law of indices** $\log x + \log y = \log xy$ and $\log x^n = n \log x$ [Norton, 1982].

Equation 2.

$$\log y = \log B + k \log x$$

The advantage of equation 2 is that by calculating the logarithm of the body mass and the measured parameter (log x and log y) we end up with a linear equation of the form $Y = mX + C$ which when we plot on a graph will produce a straight line with gradient m and intercept C. This means that finding the best fit from empirical data is relatively straightforward and the quality of the fit is very easy to interpret by eye.

Straight line graph



The value of k, the index in equation 1 often relates to the geometry of the measurements. For example if we are trying to relate a linear dimension, such as the length of the femur, to the body mass, we might expect a value of 3 for the index. This is because body mass is basically a measure of the volume of an organism, and that the volume (measured in metres^3) depends on the cube of the linear dimensions. This is illustrated in the next slide..

Illustration of the geometric effect of increasing linear dimensions (from Foley [Foley, 1987]).

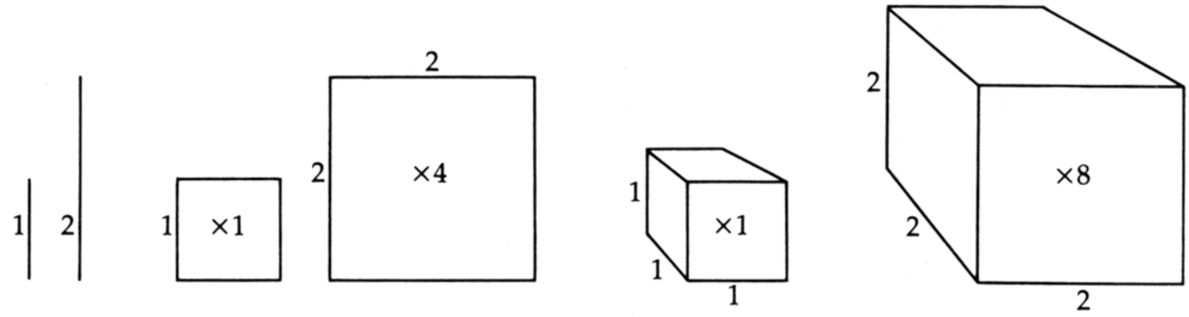
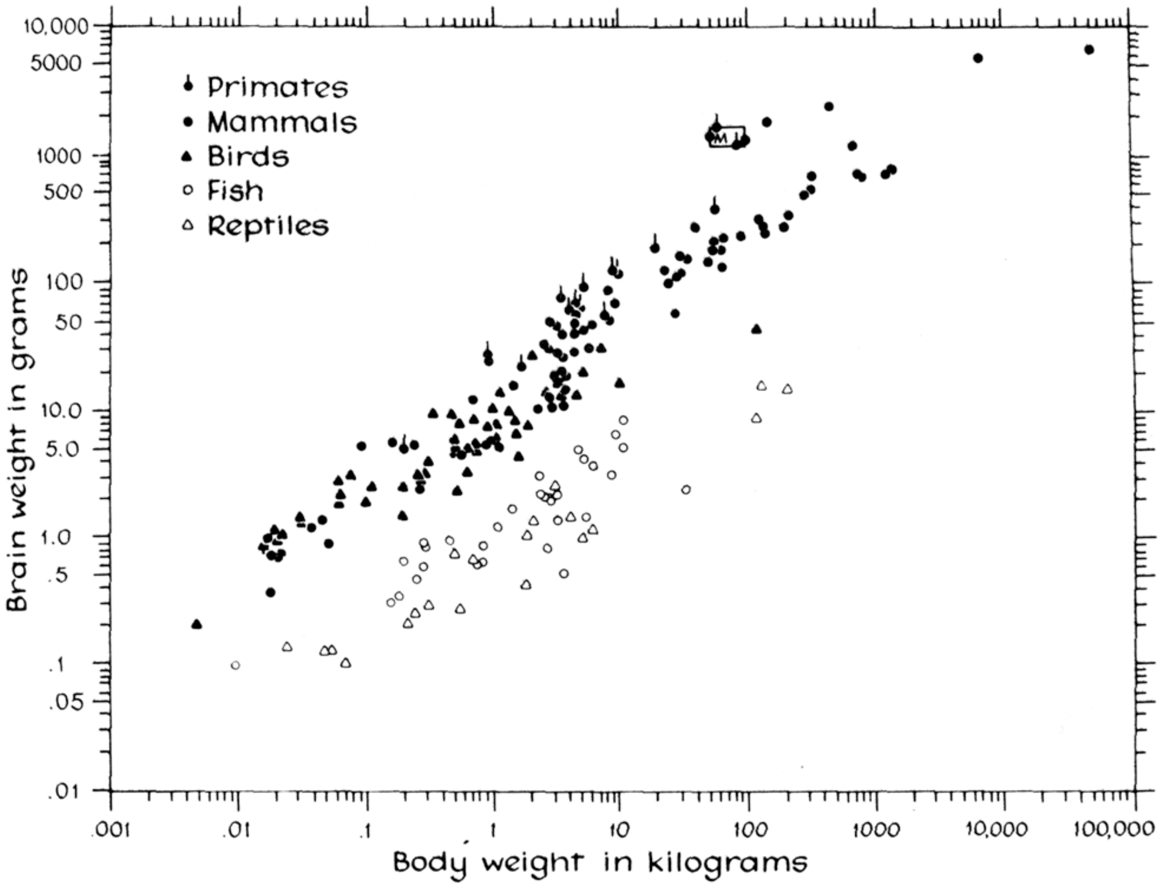


Diagram of the way in which changes in linear dimensions will result in allometric changes in two and three dimensions (surface area and volume).

Encephalisation Quotient

We can calculate the allometric equation for any group of animals we choose. It turns out that it makes sense to divide the groups at the class level – a single straight line fits mammals quite well, whereas a single line works less well if we include all vertebrates. The equation obtained empirically by Jerison [Jerison, 1973] based on raw data from Quiring [Quiring, 1950] is:

A graph showing the relationship between measure brain and body sizes for a number of vertebrates. From Jerison [Jerison, 1973].



Equation 3.

$$E_{brain} = 0.12 M_{body}^{2/3}$$

E_{brain} is the expected mass of the brain (in grams) for a mammal with a body mass M_{body} (also in grams). The **Encephalisation Quotient** is defined as the ratio of the actual mass of the brain (M_{brain}) to the expected mass of the brain given the body size. Thus:

Equation 4.

$$EQ = \frac{M_{brain}}{E_{brain}}$$

Therefore from equations 3 and 4 we can obtain the formula for EQ of:

Equation 5.

$$EQ = \frac{M_{brain}}{0.12 M_{body}^{2/3}}$$

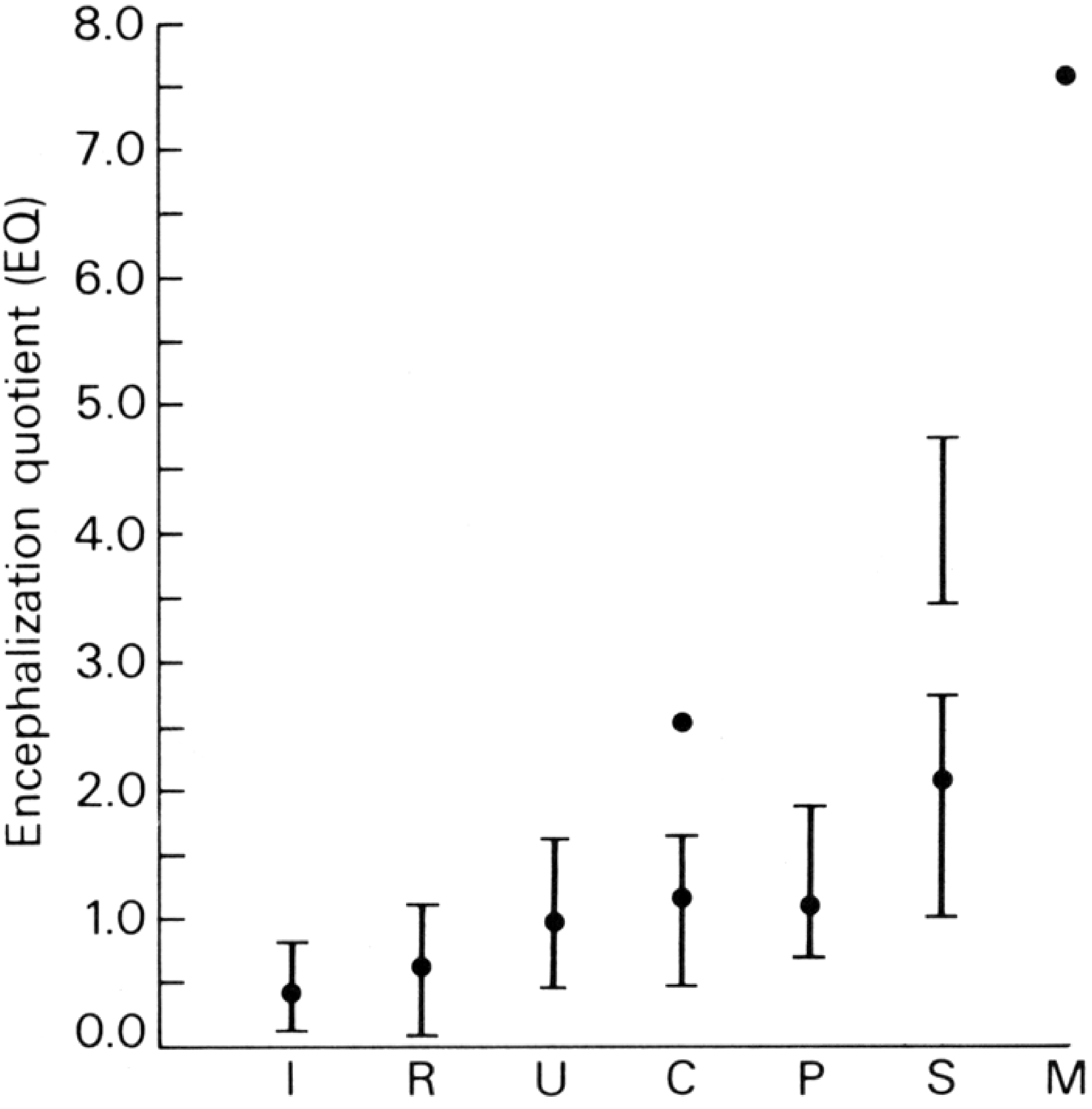
However other people have also done this calculation with different datasets and Martin for example [Aiello and Dean, 1990] came up with this empirical relationship:

Equation 6.

$$E_{brain} = 0.059M_{body}^{0.76}$$

Encephalisation quotient is a useful measure because it tells us how much bigger or smaller an animal's brain is after we have corrected for body size. This is nice for humans because it turns out that we have the largest EQ of all mammals. The next slide shows how EQ varies among a number of mammalian orders. There are a number of examples of animals that have very much higher values for EQ than the rest of their order. Humans, of course, and capuchin monkeys have very high values for primates. The high value for carnivores is the Malayan sun bear (*Ursus malayanus*). It would be nice to think of bears as fitting a very primate-like niche in temperate zones (primates are almost exclusively tropical animals), but the brown bear (*Ursus arctos*) has an EQ of 1.0 so unusually large brains is not a general feature of the family.

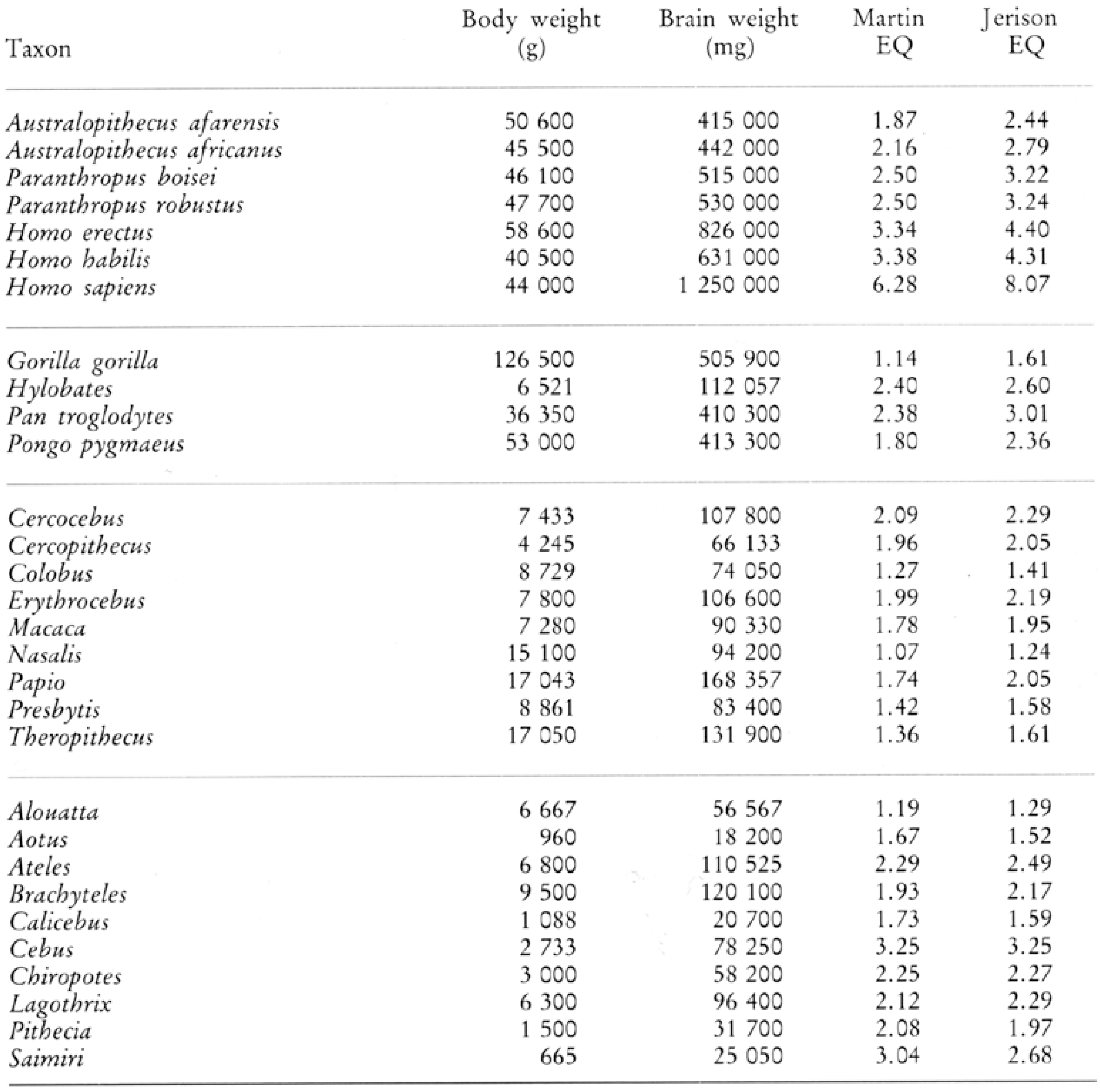
A comparison of the encephalisation quotients (EQ) in a variety of mammal groups. This figure, redrawn from Passingham [Passingham, 1982], shows the ranges of values in the different orders with a number of specific outliers indicated.



EQ is always a measure of relative brain size but you need to be careful when comparing EQ values from different sources. Although the calculation given here using the allometric equation for the mammals as a whole is probably the commonest form, people often use the allometric relationship from a much more restricted group of animals as their baseline (primates as a whole, anthropoids, catarrhines) and there are subtleties in the calculation of brain size such as whether it was calculated from a volume or from a wet weight that can effect the value.

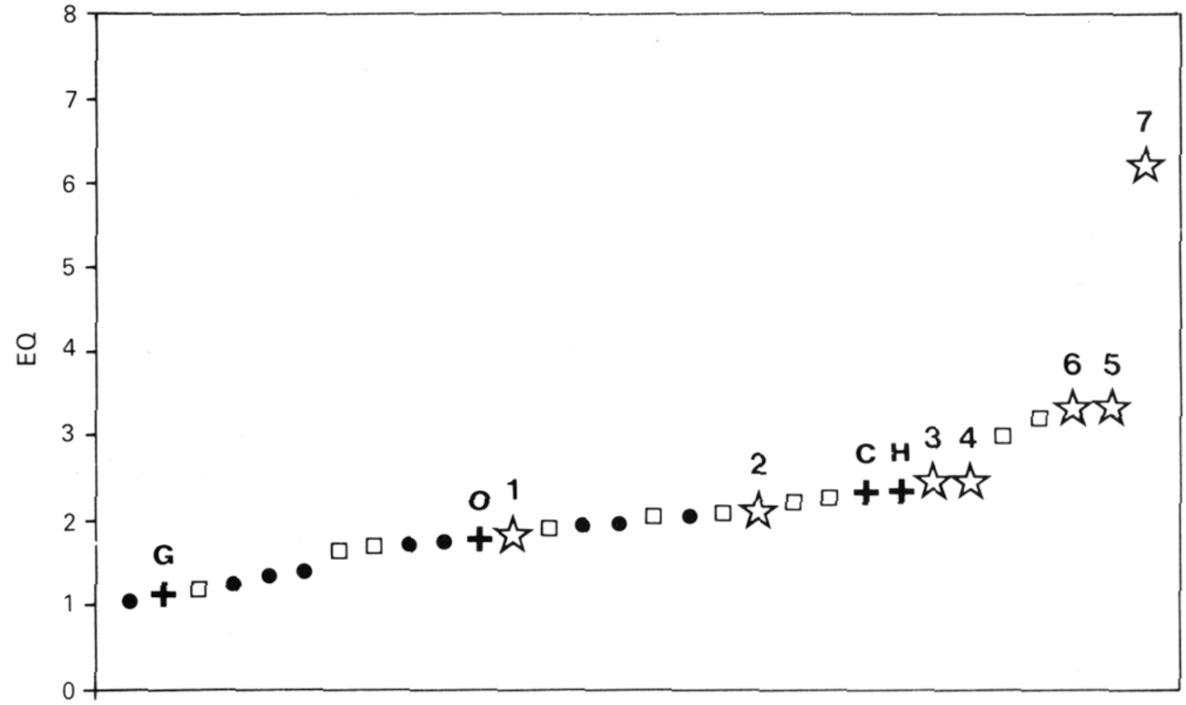
Primate Encephalisation Quotients

Table of primate EQ [Aiello & Dean 1990]



Taxon	Body weight (g)	Brain weight (mg)	Martin EQ	Jerison EQ
Australopithecus afarensis	50 600	415 000	1.87	2.44
Australopithecus africanus	45 500	442 000	2.16	2.79
Paranthropus boisei	46 100	515 000	2.50	3.22
Paranthropus robustus	47 700	530 000	2.50	3.24
Homo erectus	58 600	826 000	3.34	4.40
Homo habilis	40 500	631 000	3.38	4.31
Homo sapiens	44 000	1 250 000	6.28	8.07
Gorilla gorilla	126 500	505 900	1.14	1.61
Hylobates	6 521	112 057	2.40	2.60
Pan troglodytes	36 350	410 300	2.38	3.01
Pongo pygmaeus	53 000	413 300	1.80	2.36
Cercocebus	7 433	107 800	2.09	2.29
Cercopithecus	4 245	66 133	1.96	2.05
Colobus	8 729	74 050	1.27	1.41
Erythrocebus	7 800	106 600	1.99	2.19
Macaca	7 280	90 330	1.78	1.95
Nasalis	15 100	94 200	1.07	1.24
Papio	17 043	168 357	1.74	2.05
Presbytis	8 861	83 400	1.42	1.58
Theropithecus	17 050	131 900	1.36	1.61
Alouatta	6 667	56 567	1.19	1.29
Aotus	960	18 200	1.67	1.52
Ateles	6 800	110 525	2.29	2.49
Brachyteles	9 500	120 100	1.93	2.17
Calicebus	1 088	20 700	1.73	1.59
Cebus	2 733	78 250	3.25	3.25
Chiropotes	3 000	58 200	2.25	2.27
Lagothrix	6 300	96 400	2.12	2.29
Pithecia	1 500	31 700	2.08	1.97
Saimiri	665	25 050	3.04	2.68

Graph of primate EQ [Aiello & Dean 1990]



Closed circle = OWM; Open square = NWM; Plus = Apes; Star = Hominids
1 = afarensis; 2 = africanus; 3 = boisei; 4 = robustus; 5 = habilis; 6 = erectus; 7 = sapiens

There are several things to note about primate EQ values. Firstly, primates tend to have higher values (and hence bigger brains) than equivalent non-primates. As the slide shows, primates classified as ‘prosimian’ – in other words strepsirhines plus the tarsiers – really do not have particularly large brains with EQ values ranging about 1.0. Catarrhines and platyrrhines (anthropoids) do have appreciably higher values but it is interesting to note that apes do not have noticably larger brains than monkeys and that the prize winner for the highest EQ for non-human primates is the tufted capuchin monkey *Cebus appella*. Interestingly, capuchins are one of the few primate species that have been observed spontaneously using tools in the wild. This has caused a great deal of interest among ethologists and capuchins are widely used in experiments on animal cognition. Actually how intelligent they are is a subject of heated debate!

Encephalisation Quotient over Time

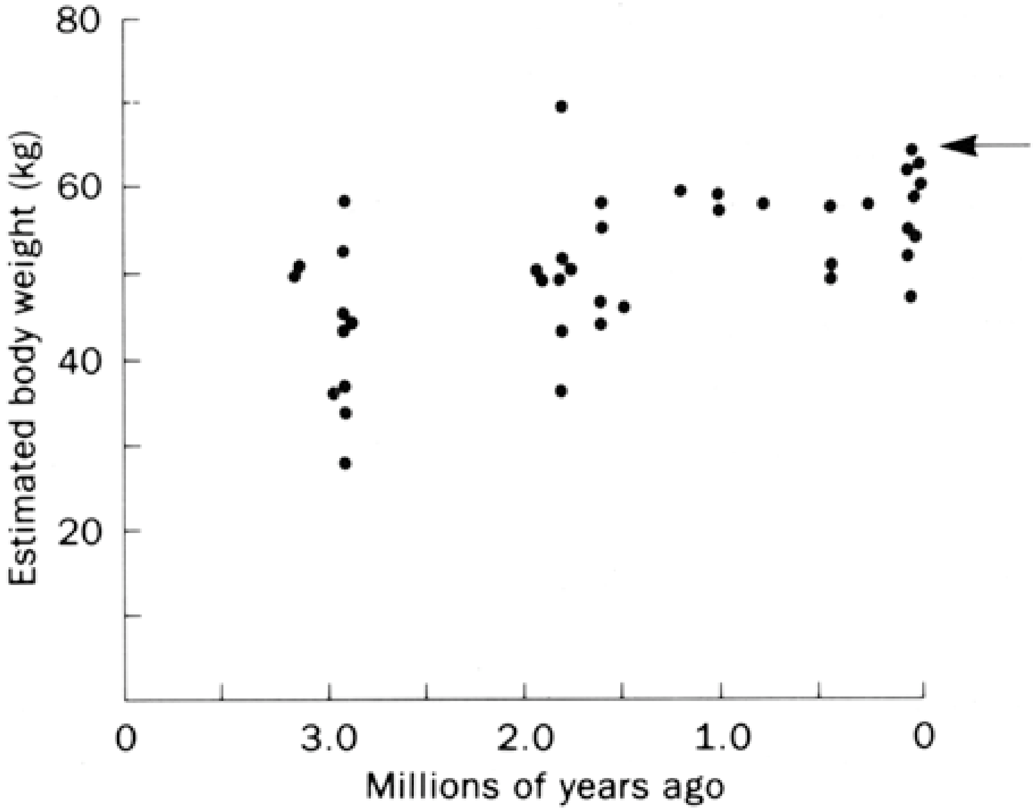
Another item of interest is the change in EQ values over time. Basically, during the course of the Cenozoic, brains have been getting bigger. In the Palaeocene, Plesiadapids have EQ values in the range 0.2 to 0.62 [Conroy, 1990] (this range could be mostly due to methods of calculation since we have very few fossil specimens since indirect means often have to be used to estimate EQ [Radinsky, 1967]). Amblypods and condylarths (early herbivores with a similar ecological niche to modern ungulates but not necessarily ancestral) have an EQ range from 0.11 to 0.37 and creodonts (early carnivores, but not necessarily ancestral to modern Carnivora) have an EQ range from 0.33 to 0.55 [Jerison, 1973]. In the Oligocene and Eocene primate EQs are in the range of 0.39 to 0.97 [Conroy, 1990] with the EQ for ungulates (Artiodactyla and Perrisodactyla) ranging from 0.19 to 0.92 and for Carnivora ranging from 0.32 to 0.92 [Jerison, 1973]. By the Miocene, the EQ, for example, of the Hominoid *Proconsul africanus* is 1.5 [Conroy, 1990] and ranges for ungulates are 0.26 to 0.98 and carnivores

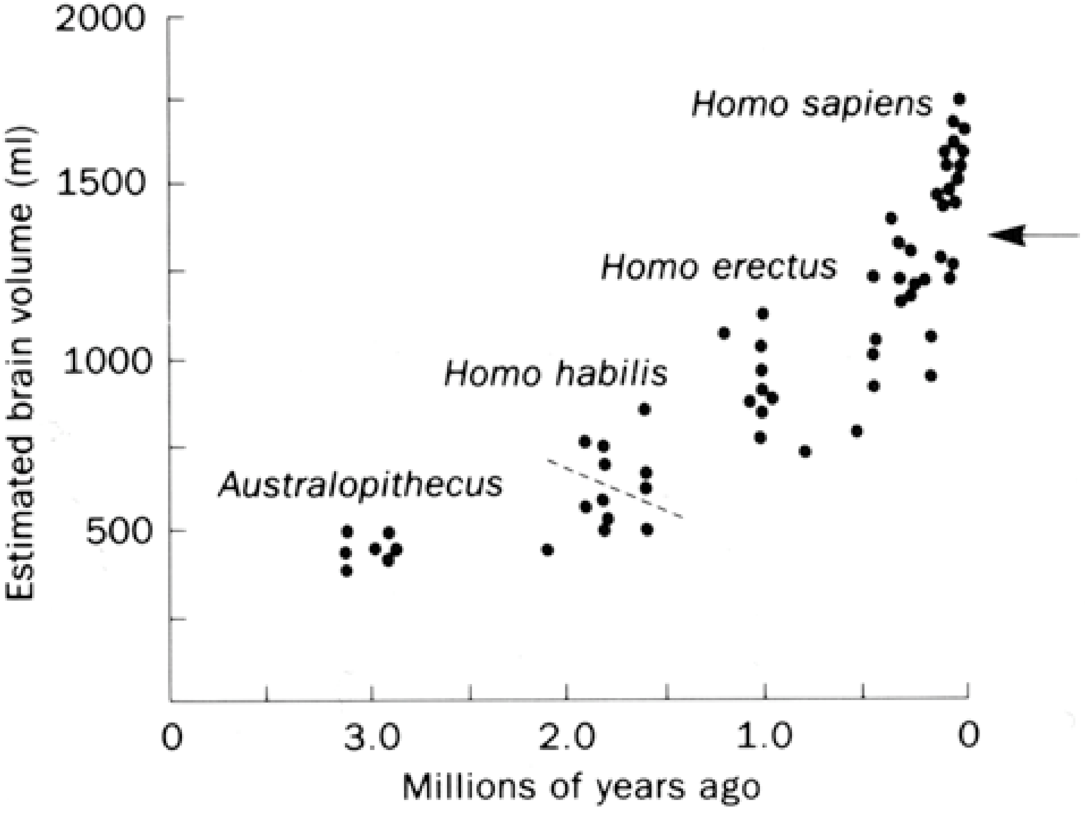
0.54 to 1.03 [Jerison, 1973]. The extreme increase in human brain size has happened in the last 5 million years and most of that has occurred in the last 2 million.

Table 1. Sample Encephalisation Quotients in the Cenozoic [Jerison 1973]

Epoch	Primate-like examples	Ungulate-like examples	Carnivore-like examples
Palaeocene	Plesiadapids 0.2-0.62	Amblypods and condylarths 0.11-0.37	Creodonts 0.33-0.55
Oligocene and Eocene	Primates 0.39-0.97	Ungulates 0.19-0.92	Carnivores 0.32-0.92
Miocene	Proconsul 1.5	Ungulates 0.26-0.98	Carnivores 0.54-1.03

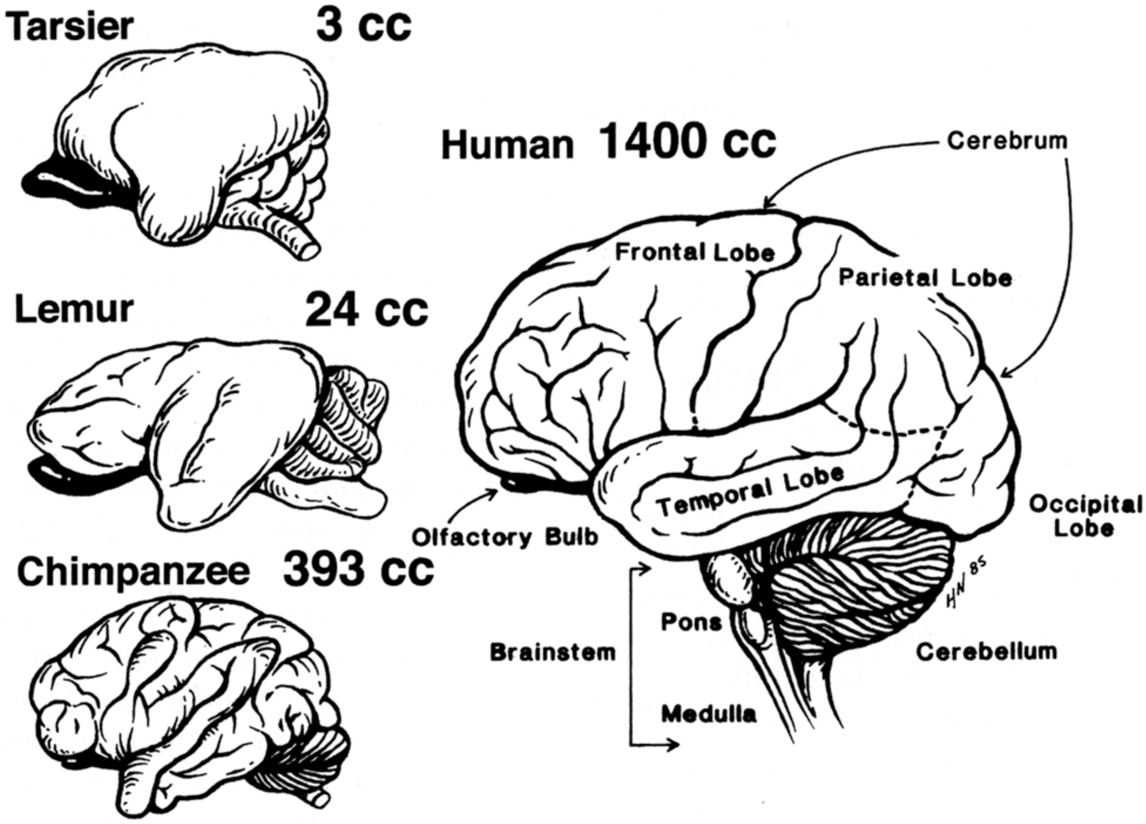
Hominid brain size [Deacon 1992]





Brain Localisation

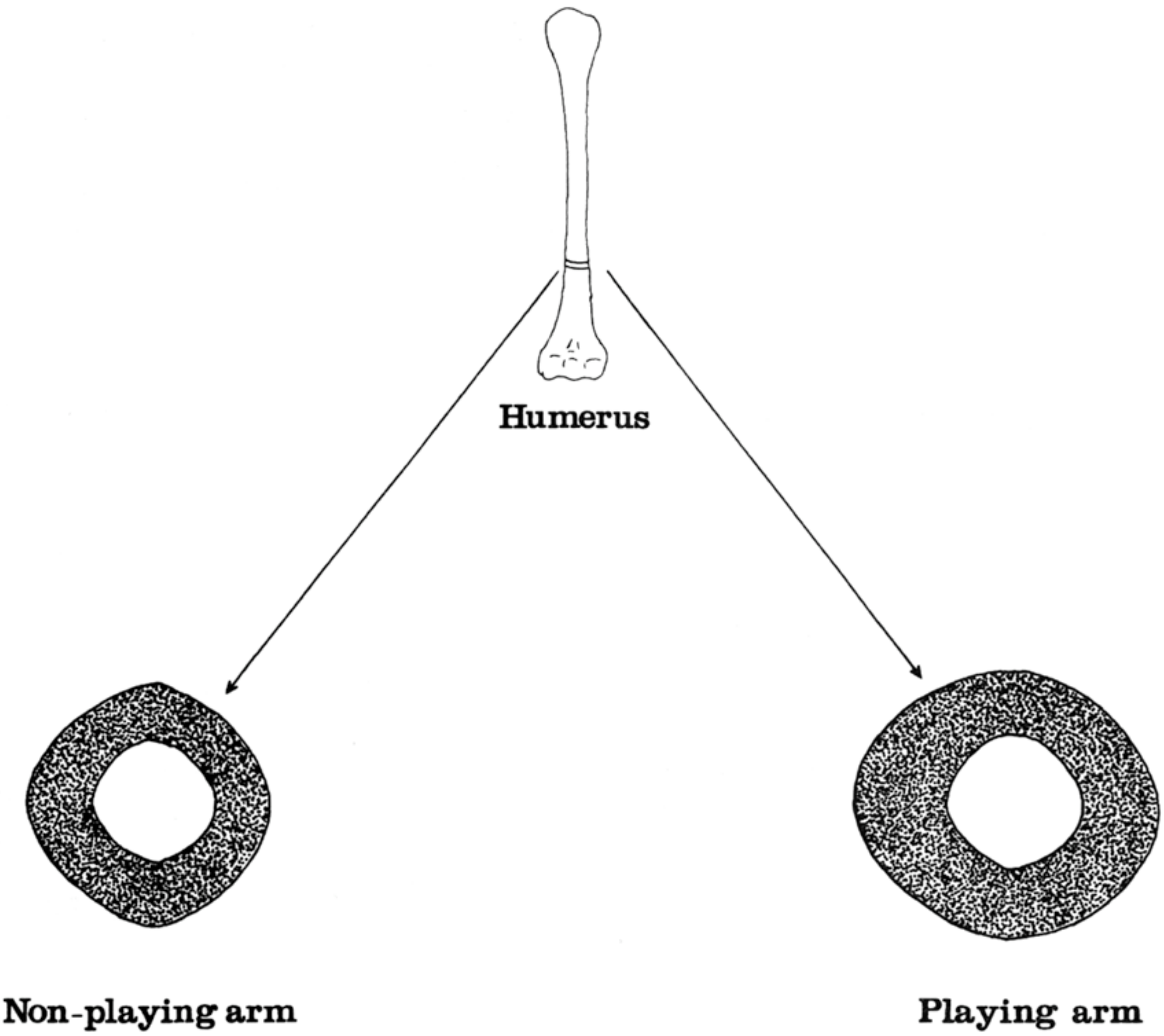
Primates brains showing relative olfactory bulb size variation [Fleagle 1999]



Raw brain size, even when corrected for body mass, is not the only brain measure that is used. Brain function is localised to certain areas of the brain and in living brains these areas can be measured and tested. Much of this work has been electrophysiological – electrical activity in areas of the brain is measured whilst particular behaviours are elicited, or the reverse where areas of the brain are stimulated and the resultant behaviour observed. This can be linked to special senses: for example the olfactory bulb of the brain is the area where smell is analysed. Relative proportions of particular parts of the brain can be used as a measure of the relative importance of that part and the information processing associated. Thus an animal with an olfactory bulb taking up an an usually large proportion of the brain is assumed to be highly scent dependent. Classically haplorhine primates are described as having relatively small olfactory lobes compared to the rest of their brains due to being less smell reliant than the nocturnal (and diurnal) prosimians and other mammals in general.

The olfactory bulb is part of the cerebral cortex. This is the part of the forebrain that processes the data received from smell, sight, taste and hearing and is the area associated with higher cognitive functions. The olfactory bulb is one of the parts of the cortex that are considered a ‘remnants of the primitive brain’ [Last, 1978], also known as the **archaepallium** or **palaeocortex**. The rest of the cortex which has become hugely enlarged in primates is called the **neopallium** or **neocortex**. The ratio of the neocortex mass to the to total brain mass (the ‘neocortex ratio’) may well be a concrete measure of the importance of higher cognitive functions (reasoning, intelligence) to an animal. Neocortex rations in most mammals are about 30 to 40%, they are between 50 to 80% in primates [Dunbar, 1996].

Tennis player humerus size illustrating extreme laterality [Mays 1998]



Also important in terms of brain specialisation is the development of lateral specialisation. Primate brains are morphological bilaterally symmetrical but in terms of function certain tasks are associated primarily with either the right of left hemisphere. Notable are functions to do with language processing. This brain lateralisation seems also to be associated with population level handedness. Thus human populations tend to be right-handed (about 90%) whereas non-human populations tend not to show a hand preference at population level. Thus a specific chimpanzee may show a preference for using a particular hand for a particular job, when a group of them are looked at there are equal numbers of individuals who are right and left handed. Now this area is very contentious. There have been lots of studies looking for population level handedness in non-human species (primates and others - parrots are popular subjects). These have involved looking at a variety of behaviours and at varying numbers of subjects. The results have been very equivocal. These are difficult experiments because the results can be influenced by the handedness of the experimenter. To further muddy the waters, careful experimentation has shown that human handedness is not as prevalent as might be supposed and is mostly concerned with complex tasks and tool-use. However as we can see by the slide, handedness can be detected in some fossils and some people claim it can also be detected in stone tools and the evolution of population level handedness may well be associated with higher cognitive ability.

Evolution of Large Brains

Since primates have larger than normal brains and humans have particularly large brains and because this size increase has happened relatively recently, a number of theories have been postulated to explain the evolutionary pressure that has driven this size increase. People are particularly interest in the special case of why humans have very large brains but the arguments are generally applicable.

The ‘why’ question can be argued on a number of levels. Tinbergen [Tinbergen, 1963] suggests 4 ‘why’s’ in biology and some nice examples are given in Krebs and Davies [Krebs and Davies, 1987]. Consider the question, “Why do starlings (*Sturnus vulgaris*) sing in the spring?”. There are 4 answers depending on the interpretation of why.

1. The answer can be given in terms of the **survival value** or **function** which in this case is that starlings sing to attract mates.

2. The answer can be in terms of **causation**. In this case in terms of physiology because increasing day length has altered hormone levels which have triggered the singing behaviour and anatomically because of air flowing through the syrinx causes membrane vibrations.

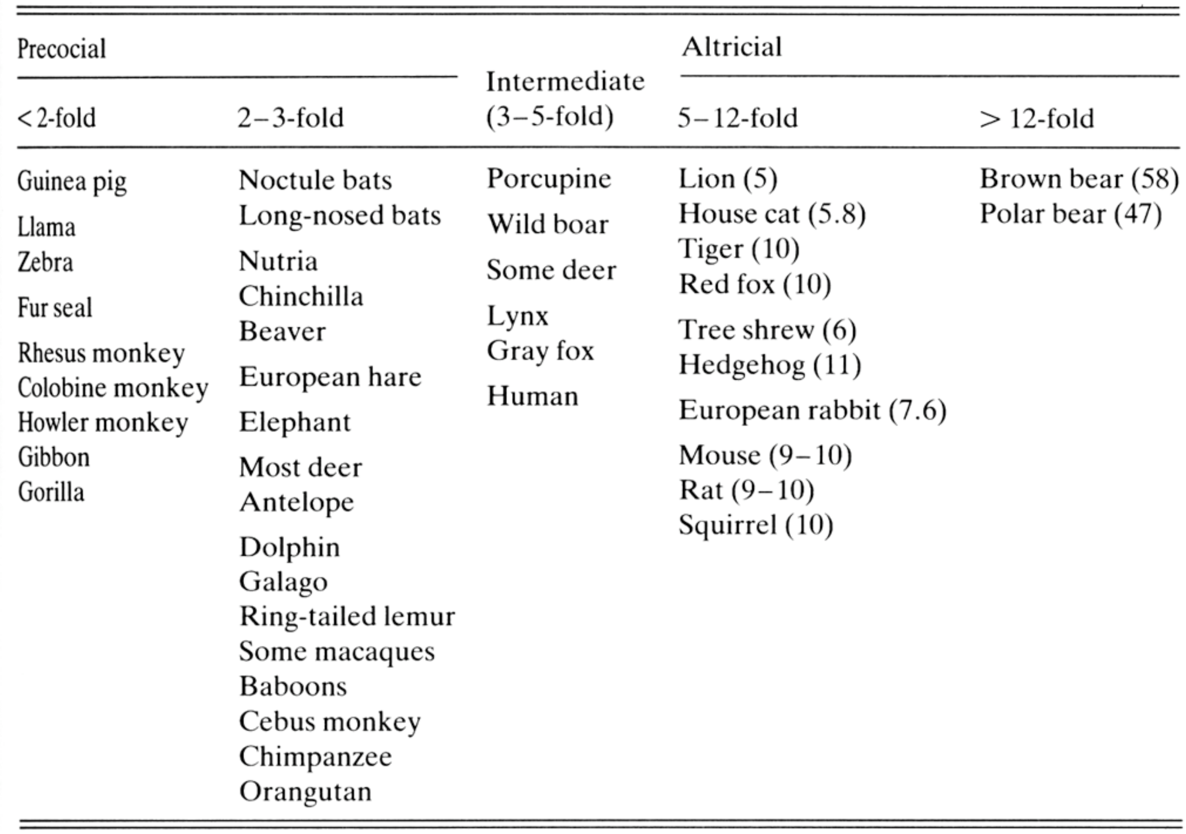
3. In terms of **development**: starlings sing because they have learned the songs of their neighbours.

4. Finally in terms of **evolutionary history**. This answer would involve an analysis of how we suppose that bird song has become more complex through evolutionary time due to sexual selection whereby certain songs are more successful at attracting females and how singing prowess might be an honest advertisement of male fitness.

Of course all these different why’s are not independent. There is an evolutionary component to all of them, and evolution can only function in the context of anatomy and physiology. However they are sufficiently distinct that they are all correct and none are better answers than the others.

Primate brain size is often discussed in terms ‘promotors’ and ‘releasers’. Promotors are physiological and anatomical constraints that either directly directly encourage large brains. Releasers are physiological and anatomical constraints that directly limit brain size and therefore when they are ‘released’ they indirectly encourage large brains. Theories involving these are therefore more in terms of causation than evolutionary history.

Table showing post-natal brain growth in mammals [Parker 1990]

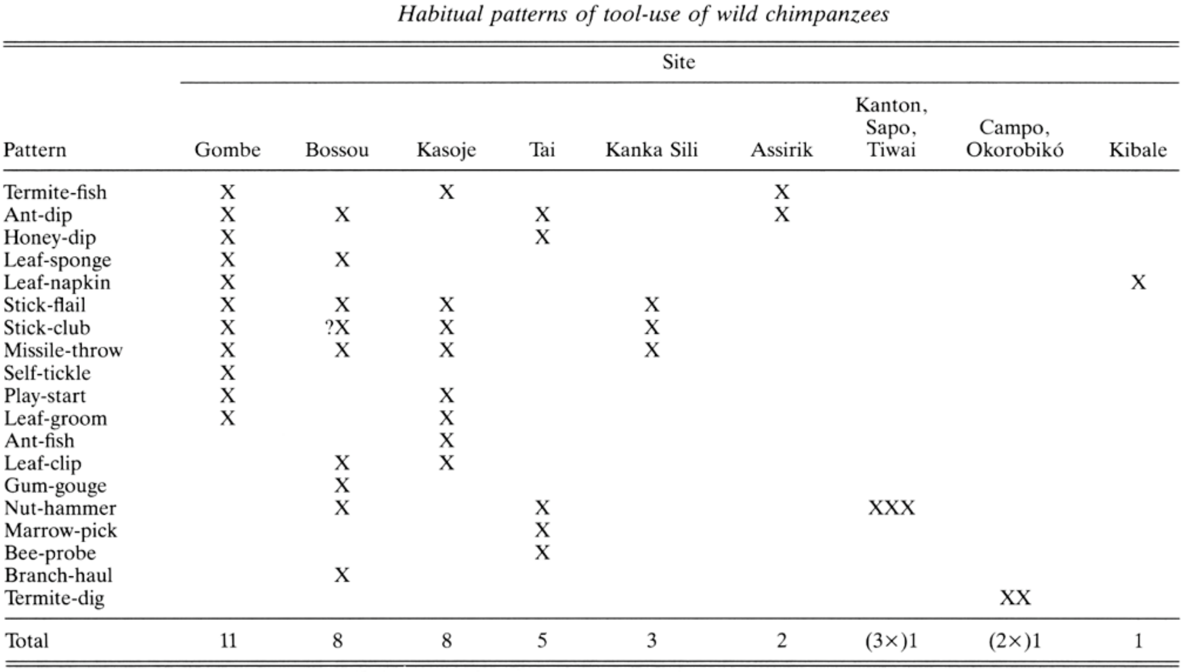


Precocial		Intermediate (3–5-fold)	Altricial	
< 2-fold	2–3-fold		5–12-fold	> 12-fold
Guinea pig Llama Zebra Fur seal Rhesus monkey Colobine monkey Howler monkey Gibbon Gorilla	Noctule bats Long-nosed bats Nutria Chinchilla Beaver European hare Elephant Most deer Antelope Dolphin Galago Ring-tailed lemur Some macaques Baboons Cebus monkey Chimpanzee Orangutan	Porcupine Wild boar Some deer Lynx Gray fox Human	Lion (5) House cat (5.8) Tiger (10) Red fox (10) Tree shrew (6) Hedgehog (11) European rabbit (7.6) Mouse (9–10) Rat (9–10) Squirrel (10)	Brown bear (58) Polar bear (47)

Developmentally, humans have large brains because their postnatal growth is larger than expected.

When we look at evolutionary history directly, there are still a large number of theories but they basically fall into two groups. Firstly there are the theories that assume a direct skill-based advantage to a large brain. Thus this group includes theories that assume large brains have evolved through, for example, tool-use, bipedalism, hand-eye coordination or foraging ability. Secondly there are theories that large brains evolved because of primate social behaviour, whether in the context of tactical deception or coping with large group sizes.

Chimp tool use [McGrew, 1992]

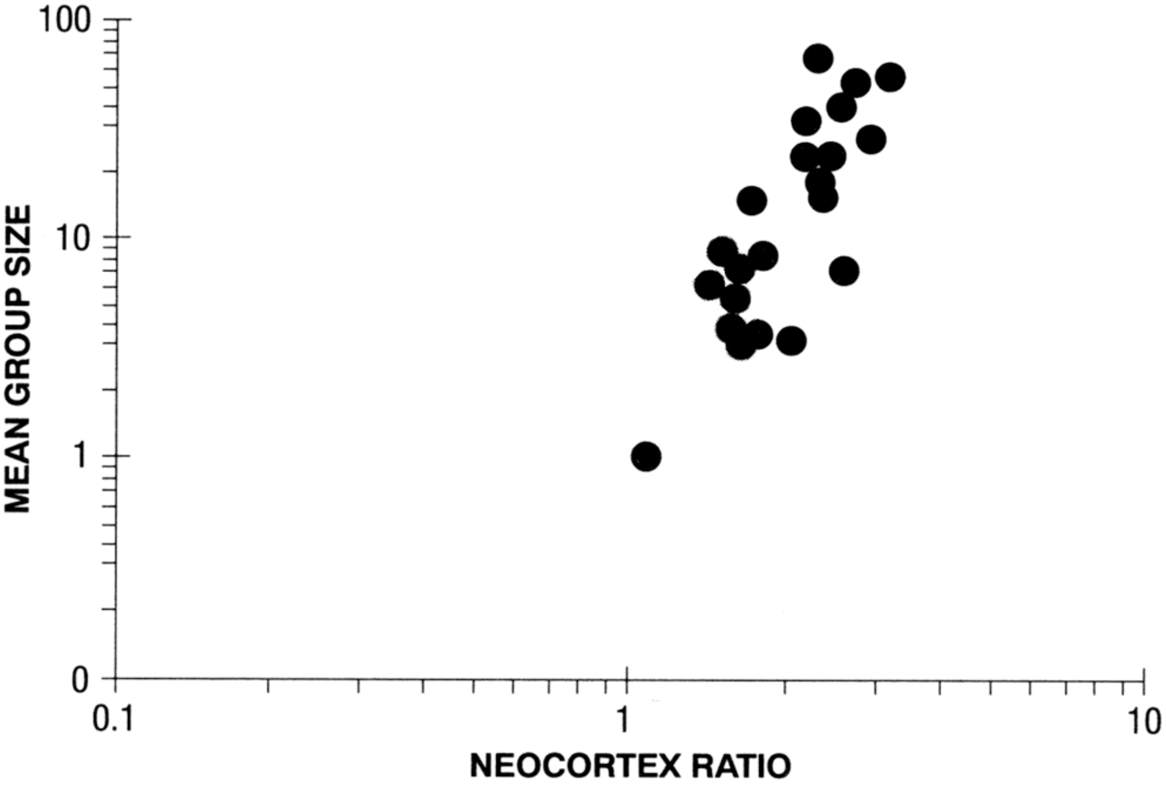


Habitual patterns of tool-use of wild chimpanzees

	Site								
Pattern	Gombe	Bossou	Kasoje	Tai	Kanka Sili	Assirik	Kanton, Sapo, Tiwai	Campo, Okorobikó	Kibale
Termite-fish	X		X			X			
Ant-dip	X	X		X		X			
Honey-dip	X			X					
Leaf-sponge	X	X							
Leaf-napkin	X								X
Stick-flail	X	X	X		X				
Stick-club	X	?X	X		X				
Missile-throw	X	X	X		X				
Self-tickle	X								
Play-start	X		X						
Leaf-groom	X		X						
Ant-fish			X						
Leaf-clip		X	X						
Gum-gouge		X							
Nut-hammer		X		X			XXX		
Marrow-pick				X					
Bee-probe				X					
Branch-haul		X							
Termite-dig								XX	
Total	11	8	8	5	3	2	(3×)1	(2×)1	1

This is probably a question we will never be able to answer with any certainty. In the skill based camp we have the evidence that the sensory-motor areas of primates are large and that this does correspond to fine sensation and fine finger movements – especially in humans. This may well be linked to tool use, hand-preference and complex locomotor and manipulatory tasks and is certainly of advantage to the animal [McGrew, 1992]. Larger brains allow an animal to maintain a larger foraging map and have improved exploitation strategies [Martin, 1984]. However there are plenty of tools using animals that do not have particularly large brains and many animals are extremely acrobatic and able to produce fine, controlled movements. As far as sociality goes, there are some correlations between, for example, neocortex ratio and group size [Dunbar, 1996]. Primates are particularly good at recognising members of their families and social groups and they form complex patterns of alliance and trust. There have been a large number of extraordinary observations of tactical deception and other examples of extremely complex behaviour [Byrne and Whiten, 1988]. Sadly this sort of information is extremely difficult to classify in any sort of objective fashion and unambiguous interpretation is probably impossible. It also needs to be remembered that there is unlikely to be a single factor that caused brain enlargement.

Neocortex ratio and Group Size (Dunbar 1996]



Bibliography

Aiello,L; Dean,C (1990): An introduction to human evolutionary anatomy. Academic Press, London.

Byrne,R; Whiten,A (1988): Machiavellian Intelligence. Oxford University Press, Oxford.

Conroy,GC (1990): Primate Evolution. Norton, London.

Deacon,TW (1992): Primate brains and senses. In: Cambridge Encyclopedia of Human Evolution (Jones,S; Martin,R; Pilbeam,D, eds.) pp 109-114. Cambridge, Cambridge University Press.

Dunbar,R (1996): Grooming, gossip and the evolution of language. faber and faber, London.

Fleagle,JG (1999): Primate Adaptation and Evolution. Academic Press, London.

Foley,R (1987): Another unique species: patterns in human evolutionary ecology. Longman Scientific and Technical, Harlow, UK.

Huxley,JS (1932): Problems of relative growth. Methuen, London.

Jerison,HJ (1973): Evolution of the brain and intelligence. Academic Press, New York.

Krebs,JR; Davies,NB (1987): An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford.

Last,RJ (1978): Anatomy: regional and applied. Churchill Livingstone, Edinburgh.

Martin,RD (1984): Body size, brain size and feeding strategies. In: Food acquisition and processing in primates. (Chivers,D; Wood,B; Bilsborough,A, eds.) Plenum Press, New York.

Mays,S (1998): The archaeology of human bone. Routledge, London.

McGrew,WC (1992): Chimpanzee material culture: implications for human evolution. Cambrideg University Press, Cambridge.

Norton,FGJ (1987): Advanced mathematics. Pan Books, London.

Nowak,RM (1991): Walker's Mammals of the World. John Hopkins University Press, Baltimore.

Parker,ST (1990): Why big brains are so rare: energy costs of intelligence and brain size in anthropoid primates. In: “Language” and intelligence in monkeys and apes (Parker,ST; Gibson,KR eds.) pp 129-154. Cambridge University Press, Cambridge.

Passingham,RE (1982): The human primate. Freeman, Oxford.

Quiring,DP (1950): Functional anatomy of the vertebrates. McGraw Hill, New York.

Radinsky, 1967

Thompson,DA (1917): On Growth and Form. Cambridge University Press, Cambridge.

Tinbergen,N (1963): On aims and methods of ethology. Zeitschrift für Tierpsychology 20: 410-433.