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The evolution of the primate cerebellum

By Bryony Anneke Whiting

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8 NOV 2002

Thesis submitted for the degree of Master of Science (MSc.) in the
Department of Anthropology, University of Durham

2001

To Dad

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Declaration

The work contained in this thesis was carried out by the author in the academic year 2000-2001 whilst a postgraduate in the Department of Anthropology at the University of Durham. None of the work contained in this thesis has been submitted in candidature for any other degree.

Some of the results from this thesis were presented by the author under the title "Great apes: the mystery of the big size of the little brain" at the Human Behaviour and Evolution Society (HBES) 2001 conference.

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ABSTRACT

Investigations into the evolution of the primate brain have consistently focussed on the neocortex as the principal area of change. New evidence is presented here to show that the cerebellum has also shown significant expansion over primate brain evolution indicating that exclusive focus on the neocortex is unwarranted. More detailed analysis shows that individual components of the cerebellar-neocortical system have undergone correlated evolution independently of change in the rest of the brain, providing support for the theory of mosaic evolution. Among primates, the great ape cerebellum is shown to be particularly large, indicating that this area of the brain is more important in great apes than in other primates. Possible ecological, social, developmental and motor correlates are investigated with the aim of accounting for cerebellar expansion. Implications for previous theories of primate brain evolution are discussed.



CHAPTER 1

Introduction

This thesis focuses on primate brain evolution with particular reference to the evolution of the cerebellum, an area of the brain which has received far less attention than it deserves.

The nature of evolutionary change is such that new structures are simply adaptations of those which existed previously (Preuss, 1995). This means that investigations into evolutionary changes in the brain will benefit from comparisons between multiple species with varying levels of relatedness. In looking at the evolution of the primate brain, an investigation will be conducted into the similarities and differences between primates and their closest relatives, the insectivores, as well as those between different primate species.

Chapter 1 presents an overview of previous work on the evolution of the primate brain in which the neocortex (the outermost layer of the brain) has been considered to be the principal area of change. The main theories put forward to account for the large brain, and corresponding high level of intelligence (or competence), of primates will be considered. The general mechanisms of brain evolution will then be addressed, the reader's attention being directed to the idea that particular areas of the brain can change in size even in the absence of changes in the rest of the brain ('mosaic evolution'). This will lead to the demonstration that evolutionary changes in neocortex volume are highly correlated with changes in the volume of the cerebellum. The extent to which there might be a common, underlying causality, is considered, and the structure and functions of the cerebellum are detailed.

Chapter 2 considers a number of methodological issues which need to be resolved. These include scaling, the different types of comparative method available (phylogenetic and non-phylogenetic) and the data to be used.

The empirical contribution of this thesis is presented in the form of three comparative studies which make up Chapters 3 to 5. In Chapter 3, the veracity of the theory of mosaic evolution will be tested by investigating whether the areas connected to the cerebellum have shown correlated evolution with this structure independently of changes in other structures. Chapter 4 looks at whether there are any differences in the size of the cerebellum in primates and insectivores, and whether the cerebellum has shown a similar level of change in all primates. Possible explanations for the change in the size of the cerebellum in primates are considered in Chapter 5, where ecological, social and motor correlates are investigated as well as developmental factors.

Chapter 6 will present the conclusions that can be drawn, along with limitations of this work and suggestions for further investigations.

1.1 The 'Neocortex Theory' of primate brain evolution

1.1.1 Background on comparative studies of the primate brain.

The principles which underlie the comparative method of investigation can be traced back to the early 1800's, specifically to the work of Georges Cuvier, a French zoologist and paleontologist. Cuvier (1812, 1825) carried out systematic comparisons of large numbers of vertebrates and invertebrates and formulated two important guidelines for comparative studies which are, to varying extents, still important today. The first of these guidelines was called the "correlation of parts". This stated that all structures within an organism are so dependent on one another that not only must they be correlated with their own functions, but also with other bodily structures and with the external environment (indicating awareness that selection pressures act on species and affect the way in which they develop). This guideline goes some way towards explaining why comparative studies are important: there are correlations between the structures which make up organisms. While the explicit meaning of "correlations" in Cuvier's guideline is unclear, in comparative studies of

evolution, correlations now refer to statistical similarities in the rate and timing of change in particular structures.

Cuvier's second guideline was called the "subordination of characters". Some structures within animals, it is maintained, are so vital for their survival that there are severe limitations on their possible design. Cuvier argued that uniformity in these structures indicates membership of one of a number of large natural categories (taxa). What is particularly interesting about this guideline is Cuvier's point that the structure which shows the most uniformity within taxa is the nervous system. By arguing that the members of natural taxonomical categories share unusually similar nervous systems, it seems that Cuvier, albeit unintentionally, was one of the first people to suggest that changes in the brain have been important throughout evolution. It is interesting to note here that Cuvier was not an evolutionist, in fact he was an anti-evolutionist, and his guidelines were not formulated to account for evolution *per se* (Webster, 1976). Nevertheless, the "correlation of parts" in particular can be applied to studies of evolutionary change and is in fact a useful guideline in such investigations.

Since the work of Cuvier, while there has been much investigation of the structure and functions of the nervous system (and the brain in particular), there has been a paucity of comparative studies of the brain. Interest in such investigations did not emerge again until well into the 20th century with the work of Jerison in the 1970's.

Jerison was interested in the evolution of intelligence and focused his attention on differences in brain size to explain the variation in intelligence or information-processing capacity among species. His work was based on measurements from fossil endocasts, and referring to his landmark book published in 1973, Jerison claimed that, "This book may be unique in that general principles of behaviour and brain function are derived from the actual record of the evolution of the vertebrate brain." Jerison understood that raw volumetric measurements of the brain are not directly comparable, and therefore put forward a measure that he called the encephalisation quotient (EQ) which takes account of differences in body mass. Jerison used the EQ to compare the relative size of the brains of different species and was the first person to make these direct comparisons. Since this work of Jerison,

other measures of relative brain size have appeared on the scene. One of the most widely used is the Size Index (SI), proposed by Stephan et al. (1981), which, rather than comparing whole-brain size, compares the sizes of specific components of the brain using a base line of the most primitive living mammals, the basal insectivores (Terrecinae).

The comparative method has continued to increase in popularity, with the consequent emergence of more and more methods designed to investigate the evolution of the primate brain. Many of these methods will be encountered in this thesis and their various advantages and disadvantages will be considered as they are met.

The section which follows focuses on more recent work on the evolution of the primate brain, providing an overview of the work that has been carried out and culminating in the identification of various limitations of that work which will be addressed in later chapters. At this point, it must be noted that whereas earlier work, such as that of Jerison, focused on the brain as a whole, more recent studies have focused on one particular area of the brain: the neocortex. The reason for this focus will become apparent in the following section.

1.1.2 The evolution of the neocortex in primates

A fundamentally important finding from comparative investigations of brain evolution is that compared to other mammals of similar body size, primates have evolved an unusually large brain (Passingham, 1982; Deacon, 1990). It is generally accepted that a large brain is a sign of advanced intelligence, and it has therefore been argued that the large size of the primate brain is associated with high levels of intelligence, or at least competence (Byrne, 1995).

More recent work on the evolution of the primate brain, to be considered in this section, has been directed at the relative size of particular brain structures. Such investigations have found that one particular area of the brain, the neocortex, has, "expanded out of all proportion to the rest during the course of primate evolution" (Dunbar, 1995). The neocortex is the outermost layer of the brain and is involved in

the high-level processing of sensory and cognitive information. In contrast to earlier work such as that by Jerison outlined in Section 1.1.1 above, recent work has focused specifically on this structure in attempting to explain the large size of the primate brain. It is accepted by many researchers that the expansion of the whole brain in primates is in fact a reflection of the increase in the size of the neocortex. This in turn has prompted interest in determining why this should be so. The neocortex is thought to be the area where higher processing or conscious thinking takes place, and has therefore been hallmarked as the 'intelligent' part of the brain by many researchers (Barton and Dunbar, 1997). This is clearly an oversimplification, as although the neocortex is most probably involved in intelligence, it is likely that other brain areas are too. Nevertheless, investigators have endeavoured to explain the increase in the size of the primate brain, and the neocortex in particular, by way of the increases in intelligence levels or competence in primates. Hence the conspicuously large and interesting neocortex has monopolised research attention.

In the Chapters which follow, it will be argued that such a near-exclusive focus of attention on the neocortex has resulted in the neglect of other areas that may also have been integral to the expansion of the primate brain.

1.1.3 Why has the brain in general and the neocortex in particular shown such large expansion in primates?

The intelligent behaviours for which the most convincing associations have been found are those associated with the environment in which a species lives, and the social interactions that take place within those environments. These categories have given rise to two theoretical lines of explanation of the increased brain size and associated increased intelligence in primates: the Ecological Hypothesis and the Social/Machiavellian Intelligence Hypothesis. Definitions of intelligence vary, but in general involve "the modification of behaviour on the basis of valid inference from evidence" (Humphrey, 1976). Keeping this definition in mind, the two main theories purporting to explain the increase in intelligence in primates will now be considered.

1.1.3.1 The Ecological Hypothesis

The main idea behind the ecological hypothesis is that the physical environment has played a crucial role in brain evolution. It is hypothesised that increased cognitive skills are needed in order to survive in more complex environments. As a consequence, species which live in diverse, complicated and ever-changing habitats will have evolved larger brains than species living in more simple habitats, the main factor used to distinguish between simple and complex environments being the distribution of food resources.

(i) Distribution and availability of food resources

Some of the first work in this area was carried out by Clutton-Brock and Harvey (1980), who showed that frugivorous primates have significantly larger brains relative to body weight than folivorous species. They proposed that the reason why frugivores have larger brains is that their food-supply is constantly changing. Different fruits become ripe on different trees at different times, and in order to be able to keep track of which food is edible at what time, they required increased intelligence and thus a larger brain. This is in line with previous work on bats by Eisenberg and Wilson (1978) who argued that the foraging strategies of bats with relatively large brains are, "based on locating relatively large packets of energy-rich food that are unpredictable in temporal and spatial distribution".

This idea of monitoring food availability supports work by Mackinnon (1978) and Milton (1981, 1988), who independently referred to this ability as cognitive mapping skill. Mackinnon studied orangutans and noticed that, in the absence of fruit on one particular animal's favourite fruit tree, it moved through the forest following the most energetically economical route to a large number of similar trees which did have fruit. Mackinnon argued that without some kind of internal map to guide it, the orangutan would not have been able to follow such a "perfect" route from tree to tree. In a similar vein, Milton (1981) pointed out that although food might be limited and sparse in dense forests, its whereabouts is essentially predictable making it possible, with the aid of advanced cognitive mental maps, to keep track of edible food resources. She argued that these mental maps would make large demands on memory

and would require an increase in the ability of the brain to constantly store and update information. A mental map does not only have to be formed and maintained, but cognitive manipulation must also be possible in order that it can be used as a reference guide to feeding areas. These are potentially complicated cognitive activities and their effective development would undoubtedly require increased processing power, and thus a larger brain. Support for this possibility of selection for cognitive maps comes from the finding that mean home range size correlates with relative brain size (Clutton-Brock and Harvey, 1980). This is precisely what would be predicted if the cognitive maps idea is correct, as larger and more complex cognitive maps would be needed for larger home ranges.

A matter of controversy over these various findings, however, was the use of relative brain size as the index in the calculations (Shea, 1983; Deacon, 1997). The advantages and disadvantages of the various different scaling methods which could be used will be considered in the next chapter (Section 2.1), however it is important to note here that the practice of using the index of brain size/body size can lead to values that are confounded by differences in body size. Taking folivores as an example, the fact that they need larger stomachs to digest their food means that they have larger bodies and thus the relative size of their brain is smaller. In this way, folivores might be unfairly classed as less intelligent than they actually are because they appear to have a small brain for their body size. Rather than being associated with intelligence, there may in fact be another reason altogether for large-stomached folivores having a relatively small brain. Aiello and Wheeler (1995, 1996), for example, argued that, in metabolic terms, the brain and the gut are two of the most expensive organs of the body, and that in order for one of these to increase in size, there must be a corresponding decrease in the other. This is the 'expensive tissue hypothesis' and it argues that if folivores have a large gut to digest their food, they cannot also have a large brain unless there is a rise in the metabolic rate. Further work is clearly needed here in order to remove the possibility of the results being confounded by differences in body size.

(ii) **Exposing food items**

Having considered how the distribution and availability of food resources in the environment may have influenced the evolution of the primate brain, another important aspect to be considered (which is also associated with the Ecological Hypothesis) is how animals actually get at their food once they have found it. It has been observed that tool use is a fairly common phenomenon in a number of different animal species. Various mammals, and even some species of birds, use objects as tools in order to gain access to difficult food items. However, some primates actually modify items into tools rather than merely using them in the form that they are found. This indicates some kind of advanced cognitive ability which may not be present in non-primates. Chimpanzees (*Pan troglodytes*) appear to be the most advanced non-human primate tool-users as they are able to use tools for numerous different functions, fashioning particular tools appropriately (McGrew, 1992b).

In addition to tool use, there are other mechanisms by which edible food is obtained. Whereas some types of food are readily edible, other foods are more difficult to eat due to protective shells or spiky exteriors. The ability to exploit such foods by removing the outer covering is referred to as "extractive foraging" (Gibson, 1986), and it has been argued that the cognitive demands of extractive foraging have selected for increases in the size of primate brains (Parker and Gibson, 1977; Gibson, 1986). The cognitive demands posed by these inaccessible nutrients are argued to be in the form of particular sets of rules or sequences which animals need to learn so that they can apply them to different foods in various different circumstances. Note that the Gibson/Parker theory is specific to seasonal extractive foraging with tools, which makes it hard to test.

Extractive foraging and tool use are complicated behaviours to quantify as it is difficult to identify a scale of complexity which might be reflected in the differences in primate brain size for these particular behaviours. For mental mapping ability, it was clear that there would be a hierarchy of brain sizes directly related to home range size. With respect to extractive foraging or tool use however, not all primates engage in these activities and there is no clear scale of complexity. This means that it is not

possible to claim that as animals tackle increasingly difficult food items or use increasingly complex tools, they are selecting for increases in their cognitive abilities.

A direct test of whether extractive foraging or tool use do play a role in primate brain evolution would be to look at whether extractive foragers or tool users have larger brains than other primates which do not engage in these activities. Although whole brain size has not yet been compared with extractive foraging ability, a preliminary investigation has shown that one part of the brain, the neocortex, is not significantly larger in animals which carry out this activity, at least when neocortex size is expressed as a ratio relative to the rest of the brain (Dunbar, 1995). This does not rule out the possibility that extractive foraging played a role in brain evolution, but rather provides some indication of the further work required. It seems that if whole brain size is found to correlate with extractive foraging ability, then attention must be focussed on non-cortical areas to find out which area of the brain in particular might have increased in size because of extractive foraging (either in order to be able to carry it out in the first place, or to be able to improve on an already acquired ability).

In summary, the main arguments behind the Ecological Hypothesis are that brain size is associated with the level of intricacy of the environment with which they subject interacts, so that an increase in the size of the brain (and thus an increase in intelligence) is required in more complex environments. The complexity of the environment is measured by two main factors: the distribution of food resources and the nature of food items in terms of the actions required to expose them once they have been located. Thus the Ecological Hypothesis argues that the environments in which primates live are more complex than those of other mammals and that primates have evolved a large brain in order to be able to survive in these environments. The main rival of the Ecological Hypothesis is the Social Intelligence Hypothesis.

1.1.3.2 The Social Intelligence Hypotheses

It was noted at the beginning of this Chapter that primates differ from most other mammals in that they have unusually large brains for their body sizes. In addition, and integral to the Social Intelligence Hypothesis, is the fact that many primates are far more social than the majority of other mammals, suggesting to some researchers

that there may be an association between sociality and intellect (Humphrey, 1976; Byrne and Whiten, 1988).

The fundamental notion underlying the Social Intelligence Hypotheses is that the increased cognitive abilities of primates are adaptations that have evolved to deal with increasingly complex social networks. It is argued that a species' environment does not only include the various different plants and animals, but also other individuals of the same species with which they will interact (this is clearly different to the environment described in the Ecological Hypothesis). It is this type of interaction which is thought to have been especially important in the evolution of primate intelligence.

There is good evidence to show that, in contrast to other mammals, some primates have extremely complicated social relationships and interactions which are subject to constant change and which can be manipulative and even deceptive at times (Whiten and Byrne, 1997). Although a number of primates are solitary (which is probably the primitive condition for primates), many primates live in groups. These groups are very tightly bonded and are characterised by numerous different inter-relationships between the members which often reflect kinship bonds going back a number of generations. In order to be able to exist and continue to interact successfully in such a heterogeneous environment, it is hypothesised that an increase in processing power has been necessary to deal with the massive increase in the volume and complexity of social information. Thus primates are thought to have evolved a specific type of information processing ability, social information processing, and this is argued to be what sets them apart from other mammals.

It is important to note that the term 'Social Intelligence Hypothesis' is often used interchangeably with the term 'Machiavellian Intelligence Hypothesis'. These two are however not totally synonymous. The Social Intelligence Hypothesis is the broad name given to the general claims that the evolution of the brain is related to changes in the social environment, particularly in the level of complexity of social relationships. The Machiavellian Intelligence Hypothesis, in contrast, refers to particular types of intelligent behaviour within social situations. The term Machiavellian derives from the 16th Century political advisor, Niccolo Machiavelli,

and is used here because primates are thought to act as if they were following his advice on social manipulation, a distinctly complex cognitive skill. The Machiavellian Intelligence Hypothesis favours the idea that primate brain evolution is related to advances in particular cognitive abilities such as the manipulation and tactical deception of others. These are clearly socially-related activities and this is why the Machiavellian Intelligence Hypothesis and the Social Intellect hypothesis are sometimes considered to be one and the same. The distinction between these two hypotheses will be considered in more depth at the end of this section, which will focus, primarily, on the more general Social Intelligence Hypothesis as this also encompasses the main ideas behind the Machiavellian Intelligence Hypothesis.

In order to gain a concrete understanding of the concepts behind the Social Intelligence Hypothesis it is necessary to return to its origins in the 1950's. Some of the first investigators to emphasise the importance of the social environment in which an organism lives were Chance and Mead (1953 – see Chance and Mead, 1988) who specifically looked at sexual competition in primates. They noted that, as many primates live in social groups in which females are sexually receptive for an unusually long period of time, males have to be able to simultaneously attend to the females and be aware of what other competing males are doing. Although Chance and Mead did not directly use the term "intelligence", they did show that males are, therefore, continuously faced with novel situations involving different individuals who are constantly on the move. It would be essential for them to deal with these interactions effectively to ensure their reproductive success. Thus, as a result of the constantly changing complex social situations with which male primates have to cope, it would be likely that they evolved to be able to deal with more information more effectively, that is to say they evolved to be more intelligent. However, there are obvious problems with this account, not least the fact that female primates also have large brains and also appear to have advanced cognitive capabilities. As Byrne and Whiten (1988) rightly pointed out, it is not only mates over which there may be conflict but also innumerable other factors including grooming partners, food resources, playmates and sleeping sites. These are clearly not limited to males and thus if competition for mates is involved in the increased size of the primate brain, then it is only part of a very complex network of agonistic and antagonistic social interactions involving both males and females.

The first definite claim that primate intelligence is related to social interactions came from Jolly in 1966, who stated that, "social integration and intelligence probably evolved together, reinforcing each other in an ever-increasing spiral." This conclusion was reached after the observation that much of the social behaviour of monkeys is acquired by watching other individuals and replicating what they do, that is by social example.¹ Jolly noted that a particular group of primates, the ring-tailed lemurs (*Lemur catta*), have evolved a similar complex social environment to other primates in the absence of their ability to manipulate objects. This led her to conclude that a complex social network preceded the advancement of cognitive abilities, and she went so far as to claim that sociality actually enabled the increase in primate intelligence and determined its nature.

Independently of Jolly's work, an important paper on primate social intelligence was published by Humphrey in 1976. Humphrey observed that while laboratory-based tests consistently demonstrated that anthropoid apes possess high levels of cognitive reasoning, he found no evidence of these animals actively using their intelligence in their natural environments. He argued that as "surplus" intelligence is not selected for in evolution, there must have been something else driving the expansion of the cognitive abilities of these primates. Humphrey concluded that this mysterious driving force could only be social complexity. He claimed that great apes, including humans, depend on a wide base of general knowledge about the nature of the environment in which they live as well as more practically applicable knowledge. He argued that this knowledge can only be acquired through social interactions with other individuals, be it through observation or direct communication of an idea or concept. Furthermore, a social group would provide a protective and supportive environment in which animals could be encouraged to learn what the older members of the group could show them, thereby maintaining a strong and stable society.

It was noted by Humphrey (1976) that only individual and kin benefits are accepted as evolutionary driving forces and that group-living is not, although it must be beneficial for it to exist at all. This led him to look into possible explanations for how group-living could stand up to evolutionary pressure, that is how each individual

¹ There has been much controversy over imitation in primates - see Whiten (2000).

animal could benefit from this way of living. Humphrey noted that there are both costs and benefits to individuals from preserving the group structure, as well as from competing with others by exploitation or manipulation. A group includes a highly complex array of ephemeral individual relationships which must be monitored constantly in order that individuals can work out what the consequences of their own and others' behaviour might be, as well as being able to calculate the balance of gain and loss in relation to what others have or do not have. Humphrey claimed that, "[i]n such a situation, "social skill" goes hand in hand with intellect". That is to say that the propensity to carry out these various different calculations, often simultaneously, can be equated with the level of intelligence of an individual.

Humphrey (1976) went further in investigating how increased intelligence could evolve in a group as a whole. In looking more closely at the interactions of individuals within a group, he claimed that an increase in manipulative (or Machiavellian) skill by one "player in the game" would result in an increase in the skill in the other. This assumes either that the second individual learns the skill from the first during its lifetime, or that, over time, members of the group evolve the ability to carry out that skill or another similar one as a result of increased selection pressures. A type of bootstrapping (or evolutionary arms race) must be occurring, whereby the whole group eventually becomes more intelligent.

In summary, the Social Intelligence Hypothesis maintains that brain size is associated with social group size which is considered to be a measure of social complexity. It is argued that the reason why primates have unusually large brains is that they are unusually sociable mammals. They need a large brain in order to be able to keep track of the complex social interactions within their social group.

1.1.4 Testing the theories

It was noted earlier that the neocortex has often been considered to be the 'intelligent' part of the brain (Barton and Dunbar, 1997). For this reason it is important for testing the different hypotheses put forward to account for an increase in intelligence in primates. An association between neocortex size and some measure of either

environmental or social complexity could provide good evidence to indicate which hypothesis is more viable, the Ecological Hypothesis or the Social Intelligence Hypothesis. Work directed towards testing such associations will be considered in this section.

Initial investigations into associations between neocortex size and external influences focussed on sociality. It was found that primates living in larger social groups generally possessed a larger neocortex and that polygynous species had larger neocortices than monogynous species (presumably due to increased numbers of social interactions and relationships) (Sawaguchi and Kudo, 1990). This provided support for the Social Intelligence Hypothesis.

The first investigations which attempted to directly distinguish between ecological and social influences on intelligence were carried out by Dunbar (1992, 1995). He used range area, day journey length, the amount of fruit in the diet and extractive foraging as measures of environmental complexity, and social group size as a measure of social complexity. The results showed that, taking into account differences in body size, there was no significant association between neocortex ratio (the proportion of the brain made up of neocortex) and any of the measures of environmental complexity, thereby raising questions as to the correctness of the Ecological Hypothesis. In contrast, social group size was found to be significantly correlated with all the different measures of neocortical enlargement tested (for example neocortex volume and neocortex ratio), providing support for the Social Intelligence hypothesis. Dunbar explained the association between the neocortex and social group size by suggesting that individuals with small neocortices have limited processing power and thus are limited in the number of social relationships over which they can simultaneously maintain control. This suggests that group size is controlled by neocortex size, so that if the number of members of a group challenges the processing power of the neocortex, the group becomes unstable and may break down. This breakdown will occur because individuals will no longer be able to efficiently monitor the numerous changing relationships and interactions within the group and will, therefore, be unable to decide what actions to take as they will not be able to assess the consequences. In a similar way, as the neocortex increases in size, individuals may be able to monitor more relationships than exist in their current

group. In this case, it is argued that smaller grooming cliques are combined so that the number of interactions and relationships increases over evolutionary time. One inherent problem with this theory is how a stable group size is maintained. This is especially true for smaller cliques joining together, since there would be a dramatic increase in group size immediately after the join which would not correlate with neocortex size. It is highly unlikely that, after such a join, individuals would show a rapid increase in neocortex size to be able to monitor as many of the new relationships as possible. This is because changes in the size of brain structures occur over extended periods of time, periods which are far longer than the lifetime of one individual. What is far more probable is that some individuals would split from the group when it grows beyond a size at which they can manage their relationships. Thus, it seems that neocortical information-processing capacity poses a restriction on maximum group size.

It is important to note that there has been some controversy over Dunbar's findings. A recent study found that social group size does not necessarily show significant correlation with neocortex size (Deaner et al. 2000). Deaner et al. showed that the association between neocortex size (extra-striatal areas in particular) and social group size depends on whether outliers are included and on whether independent contrasts methods are employed. Furthermore, it was demonstrated that associations are found between neocortex size and ecological variables depending on the particular scaling methods used (see Section 2.1) and the data points included. These results indicate that Dunbar's findings may not be robust. However, work by Barton (1996) and Barton and Dunbar (1997) where residuals were used in independent contrasts analyses found that groups size does correlate with neocortex size, supporting Dunbar's findings. Clearly further investigation is required here.

1.1.4.1 Sociality explains intelligence

To summarise, Dunbar's investigations into the association between the neocortex and external factors did not provide support for the Ecological Hypothesis, but strongly supported the Social Intelligence Hypothesis. There has been some controversy over these finding and further attention is clearly needed. The main argument behind the Social Intelligence Hypothesis is that primate group size and

intelligence are closely related to one another. It is claimed that the increased intellectual abilities observed in primates are the result of increasingly complex social group structures which have selected for an increase in the size of the neocortex. The Machiavellian intelligence hypothesis, which supports this idea as a whole, goes further in claiming that it is complex behaviours associated with co-operation and mutual support in particular which have selected for an increase in the volume of the neocortex.

1.1.4.2 Machiavellian Intelligence: variants of the concept

In addition to these behaviours that might benefit society as a whole, a number of more selfish deceptive and manipulative actions have also been associated with increases in neocortex size. The most common type of deceit is the manipulation of attention, where an individual will try to shift attention towards or away from a particular stimulus depending on what will best benefit this individual. Examples of the way in which this is carried out include feigning injury, pretending to have seen a predator, hiding the excited responses which would normally follow the discovery of food and leading animals towards or away from particular places (Byrne, 1995). Manipulative activities, however, do not necessarily involve deception. Manipulation without deception has been observed in hamadryas baboons, where females are sometimes able to threaten others without putting themselves in any danger. They do this by seeking refuge in front of the single leading male over which all the females in the group are fighting, so that if any female tries to return the aggression, it will appear as if they are threatening the male himself (Kummer, 1967). Similar situations have been observed between infants, their mothers and an antagonist, so that after being threatened by the antagonist, an infant will return to its mother to prevent further threatening, since if they continued, the antagonist would be seen to be threatening the mother (Kummer, 1967). This clearly demonstrates that the manipulative and deceptive abilities argued by the Machiavellian Intelligence Hypothesis to be involved in the evolution of intelligence are often complex, and demand a high level of cognitive processing in order to be able to carry out the necessary planning and execution of the deceptions.

1.1.5 Limitations of the Social Intelligence Hypothesis

1.1.5.1 Great apes "don't fit"?

Despite much support for the Social and the Machiavellian Intelligence Hypotheses, there are a number of limitations. The most fundamental criticism is that they may not adequately account for all primates because they cannot explain great ape brain evolution. In great apes, variation in group size does not match neocortex size as would be predicted by the Social Intelligence hypothesis. In this section, this problem will be considered in some detail, together with a number of other limitations of these hypotheses.

(i) Group size in great apes.

As explained above, the main argument behind the Social Intelligence Hypothesis is that increases in social group size involve increasingly complex social relationships and that these select for an increase in intelligence manifested by an increase in brain size (most specifically neocortex size). The problem in accounting for great apes is that their group size does not match their brain size (Byrne, 1997). There is much variation in the social group size of great apes which ranges from solitary orangutans to multi-male, multi-female groups of chimpanzees (Byrne, 1997). This means that there is overlap with the social group size of other primates; great apes do not live in significantly larger social groups than other primates. The problem for the Social Intelligence Hypothesis is that this variation in group size does not necessarily match the variation in brain or neocortex size. Chimpanzees, for example, have large brains and a large social group size, whereas orangutans have a large brain but are solitary (although it has recently been suggested that orangutans are more social than previously thought (van Schaik et al. 1999). Nevertheless, there is more variation in brain size than is explained by group size). A recent explanation put forward to account for this finding is that compared to other primates, great apes have more, "dispersed social groupings combined with increased terrestrialsation" (Dunbar, 2001). Dunbar argues that the social groups in which great apes generally find themselves are relatively small, due to lower predation risk.

In addition to discrepancies in social group size in great apes, a further problem with the Social Intelligence Hypothesis (and indeed the Ecological Hypothesis) is that great apes have been argued to possess certain cognitive specialisations and the theories must be able to account for these (Russon, 1998). The precise nature of these cognitive abilities is considered in parts (ii) – (iv). What will be considered here is whether relative brain size in great apes is significantly large, and thus whether there is support for the possibility of certain cognitive specialisations in these species. In absolute terms, great apes have large brains and large neocortices. However, when body size is taken into account, there is overlap in relative brain size and relative neocortex size in great apes and other haplorhine primates (Deacon, 1990; Dunbar, 1992; Barton 1996). This suggests that there is no uniform increase in the size of the great ape brain or neocortex as might be expected if great apes possess cognitive specialisations. In fact, a number of monkey species have larger neocortex ratios and larger relative brain sizes than some of the great apes, indicating that these species ‘should’ be more intelligent than those great apes. Baboons, for example, have a larger relative neocortex size than gorillas and therefore ‘should’ be more intelligent (Byrne, 1997). The possibility remains, however, that great ape cognitive specialisations, if these exist, are not related to the neocortex, but to another brain structure or structures. If this is the case, then it would not be surprising that great apes do not all have a significantly larger relative neocortex size than other primates.

It is important to note that there has been much controversy over the level of competence of great apes. While some investigators credit these species with very high levels of cognitive abilities (Byrne, 1995; 1997), others argue that such levels are no different to monkeys (Tomasello, 2000). Evidence for and against the ability of great apes to carry out advanced cognitive skills will now be considered, beginning with evidence in support of these skills being present.

(ii) Evidence in support of advanced cognitive abilities in great apes:

Great apes have been singled out as being more cognitively competent than other primates by researchers who believe that they have a special type of insight into behaviour, both their own and that of other individuals. It is argued that they seem to be aware of the intentions of others (Byrne, 1995). This awareness (or possibly even

'theory of mind') is a cognitive advancement which is believed to be manifested in almost all their interactions with other individuals. It is claimed that although the day-to-day activities and behaviours of great apes are not that far removed from those of monkeys, there is a significant difference in the way in which these are carried out due to this supposed awareness of others (Byrne, 1997). One example comes from the use of tools. It is argued that whereas chimpanzees deliberately modify and prepare objects for use as tools (Goodall, 1986), or even collect items for future use as tools (illustrating the ability to plan ahead) (Boesch and Boesch, 1984), the monkeys which use objects as tools do not understand which are functionally appropriate for which task. Researchers therefore argue that the increased cognitive ability of chimpanzees enables them to understand the various aspects of tool use, from what properties a good tool needs to have, to the awareness of which future tasks might be facilitated by the use of tools. This understanding is thought to be lacking in monkeys, thereby demonstrating the existence of a 'jump' in intelligence between great apes and other primates.

Further cognitive abilities which great apes are argued to be able to carry out include: intentional deception (a classic example of Machiavellian Intelligence), the ordering of familiar actions into sequences to attain new goals, the awareness of limitations of the knowledge of infants and the anticipation of the results of actions which they carry out (Byrne, 1995)

One of the most controversial activities which has been attributed to great apes is the imitation of the actions of other individuals (Byrne and Byrne, 1993; Tomasello et al., 1993; Byrne and Russon, 1998). That they engage in certain imitative actions is not controversial; the controversy is over the cognitive abilities behind the imitation. Many researchers believe that imitation illustrates some kind of understanding of the intentions or thoughts of others and that great apes imitate the actions because of this understanding (Tomasello, 1990). However, others argue that imitation simply illustrates that an animal is able to copy the actions of another without having any understanding of the intentions or thoughts of the other (Heyes, 1993). The field of imitation studies is vast and cannot be given sufficient attention here. The main point to be noted is that while there is much support for imitative abilities in great apes, there is little evidence for imitative abilities in monkeys (Whiten and Ham, 1992) and

competence in imitation might therefore be one characteristic which sets great apes apart from the other primates.

(iii) Evidence against advanced cognitive abilities in great apes:

Researchers who do not believe that great apes have superior cognitive abilities than other primates reject the basic assumption underlying the "for" position outlined above. These researchers do not believe that great apes have any special insight into behaviour. They argue that great apes "do not seem to understand their conspecifics as intentional agents like themselves who experience the world in ways similar to themselves" (Tomasello, 2000). This claim is based on the lack of the following types of communication between non-human primates: pointing at objects, showing objects to others, actively giving items to others, and purposefully teaching others. Although it is accepted that non-human primates may show some cooperation, it is argued that this does not involve the understanding of the role of the other individual (Kruger and Tomasello, 1996).

Further evidence against advanced cognitive abilities in great apes comes from Povinelli et al. (2000) who argued that chimpanzees do not have representations of mental states. While they agree that great apes most probably possess mental states, what they are lacking are the representations of these, that is the cognitive abilities necessary to understand or interpret such mental states.

(iv) Conclusions on great ape abilities

Thus there is clearly much controversy over the question of what sort of cognitive abilities are possessed by the great apes. While it may be unclear what the precise nature or level of differences are, the fact that great apes show a number of behaviours not observed in other primates indicates that they do differ and that they do possess certain advanced cognitive abilities.

Having now established that there is a difference in the behaviour of great apes and other primates, it is important to briefly return to the question of whether the Social Intelligence Hypothesis can explain this difference. It was suggested earlier that

although relative neocortex size does not match group size in great apes, it is possible that the cognitive abilities of these species are related to another brain structure and that the variation in the size of this brain structure does match the variation in social group size. If this does prove to be the case, then there may be a chance to rehabilitate the Social Intelligence Hypothesis as an explanation of great ape abilities.

(v) Further abilities of great apes

Recently, Byrne (1997) proposed a new model of great ape cognitive specialisation. He claimed that what sets great apes apart from other primates is that they have a "representational understanding of the world". Great apes are argued to be able to solve both social and technical problems because they can mentally represent these problems, they can mentally rehearse the various possible outcomes of different actions and weigh these up before deciding on which method to choose. Examples of ecological problems which great apes have solved and which Byrne argues involve mental representations, include the construction of 'nests' in which to sleep (Byrne, 1997); the sophisticated use of tools including knowing which tool to use for what purpose and being able to carry out multiple activity stages (Brewer and McGrew, 1990; McGrew, 1992b); and the extraction of hostile food items from hard or spiky casings (Parker and Gibson, 1977). Byrne put forward these ideas in the form of the 'Technical Intelligence Hypothesis' which provides a possible explanation for the behavioural differences observed between great apes and other primates.

Byrne's work is in line with Whiten (1996b) and Suddendorf (1998) who claimed that great apes are capable of what Perner (1991) termed 'second-order mental representations'. This is the ability to simultaneously support multiple mental models. Whiten and Suddendorf independently argued that this ability underlies the various cognitive skills of which great apes are capable. By inference, this work claims that monkeys and gibbons are not able to carry out the same level of cognitive activities as great apes due to their inability to construct mental representations.

Thus, several researchers support the representation argument. The question which must now be answered is how great apes might have come to possess this ability. Byrne associates the emergence of mental representation ability with planning in

great apes. He argues that because of their simple stomachs and their slow locomotion, in order to be able to compete for the ripe foods they needed, great apes evolved the ability to plan; to organise their actions into meaningful sequences which were goal-directed. Planning involves mental representations, the ability to imagine what the outcome of a set of behaviours will be. This would clearly be necessary in hierarchical motor sequences such as those involved in the extraction of hostile food items, as great apes would need to be able to mentally represent the outcome of the various action sequences, to be aware that the execution of these sequences would result in them being able to eat the desired food item. Byrne argued that over time, these representative abilities were applied to other physical objects and even other individuals to predict what their actions might be.

This account appears credible, however it would be much more valuable if it could be associated with changes in the brain. It has been suggested that representation abilities are simply a "by-product" of very large brains, so that when a brain reaches a certain size, a species becomes able to carry out such mental representations (Gibson, 1990). It is submitted that this is extremely unlikely. Complex cognitive abilities such as mental representations do not just appear, they must be selected for over evolution, and in order to determine whether these abilities are what set great apes apart from other primates, it is necessary to look within the brain in order to identify those structures which have changed in size in great apes.

1.1.5.2 Additional factors

Further limitations of the Social Intelligence Hypothesis include the fact that it does not account for a number of the abilities of which primates are capable, but other mammals are not. One of the clearest examples of such an ability is tool use. The use of tools implies some type of understanding that their use will facilitate an activity and there is therefore an intellectual or cognitive component to this ability. As the Social Intelligence Hypothesis attempts to account for the advanced intelligence of primates, it should be able to explain activities such as tool use which are clear examples of the high level of intelligence of these species. By focussing solely on social group size, this hypothesis seems to be missing a number of important factors which set primates apart from other mammals.

Thus, there are clearly limitations to the Social Intelligence Hypothesis. If this hypothesis is to be accepted, and it seems that currently it has more support than the alternative Ecological Hypothesis, then it must be adapted or expanded in order to account for the differences observed in great apes and the particular abilities possessed by primates but not other mammals.

In order to be able to adapt the Social Intelligence Hypothesis, a number of questions must first be answered: Which primates evolved large brains? Did large brains evolve for the same or different reasons in different primate taxa - is it possible that there were several different driving forces behind brain evolution?

It is important to remember that different species show expansions in different brain structures (Barton, Purvis and Harvey, 1995), which suggests that it is necessary to look in more detail at individual brain structures. Species vary greatly and evolutionary changes in their brains should be found to reflect particular adaptations which are favourable to their particular situation or environment. Although the possibility remains that social complexity has played a role in the evolution of intelligence, the presence of additional influences cannot yet be ruled out (particularly in great apes). Perhaps it is these additional influences which can illuminate the differences between competence levels in the various sub-groups of primates.

1.1.6 Conclusions to be drawn from previous work

In summary, the most credible of the previous work has focussed on the neocortex, claiming that an increase in the size of this structure was the main change over primate brain evolution. A strong association was found between the neocortex and social group size, supporting the claim that the neocortex increased in size over evolutionary time in order to deal with increasingly complex social relationships (the Social Intelligence Hypothesis). There are, however, a number of limitations to this hypothesis, and if it is ever to be accepted then modifications are required to account for the particular behaviours of great apes, and to explain why certain complex cognitive abilities such as tool use are possessed by some primates but not by others.

1.2 The bigger picture – how do brains evolve?

Having considered possible explanations for why primate brains might have evolved to be significantly larger compared to other mammals of similar body size, the question of how these evolutionary changes could actually have occurred will now be considered. The processes occurring over evolution will be investigated with the aim of uncovering the principles governing such changes.

1.2.1 Brains are re-arranged, not re-invented

The most important concept to understand in the context of brain evolution is that new structures are formed by the modification of existing ones, they are not produced from scratch (Simpson, 1967; Jacob, 1982; Preuss, 1995). This means that the brains of primates and other mammals are very similar in terms of the types of structures which they contain. Where they differ is in the precise form and arrangement of these structures. Differences can vary from simple changes in size to far more complex re-shuffling of neurons and their connections. Thus, the large size of the primate brain is likely not to be due to the production of new brain structures which are absent in other animals, but to be the result of the modification and expansion of existing structures. It is argued that even the human brain, which is extraordinarily large for a primate, does not contain any new neural structures which other primates or even other mammals do not possess (Holloway, 1968; Tattersall, 1998). To summarize, brains are not re-invented over evolution, they are merely re-arranged.

1.2.2 Mosaic evolution of systems

1.2.2.1 What is mosaic evolution?

In order to look more closely at how these various size changes and re-arrangements occur, it is necessary to be aware of the concept of 'Mosaic Evolution'. This is the idea that the brain does not evolve purely as a coordinated whole, but that individual structures or systems can evolve independently of any changes in other parts of the

brain (Barton and Harvey, 2000). This is in line with the point made in the previous section that brains differ in the size or arrangement of brain structures. If so, it would be necessary for particular parts of the brain to be able to change independently of the rest of the brain in order to produce the wide variation in brains seen today. If the brain had to evolve as a whole, then a change in one area would necessitate a change in all other areas as well.

Mosaic evolution assumes that particular areas of the brain change in response to changes in selection pressures. An example of this is that nocturnal primates have enlarged olfactory structures, most likely a response to the increased need for good olfaction due to the limited visual cues available when it is dark (Barton, Purvis and Harvey, 1995).

However plausible the concept of mosaic evolution may be, it is important to note that there has been some controversy over the idea that different parts of the brain can evolve independently. Finlay and Darlington (1995), for example, argued that the size of each of the major brain subdivisions (excluding the olfactory bulb) can be accurately predicted from whole brain size. Furthermore, their "developmental constraints hypothesis" maintains that in all mammals, the whole brain shows a highly predictable pattern of growth, with strict developmental constraints forcing individual brain structures to enlarge in line with the rest of the brain. Initially, support for this hypothesis seemed to come from studies of the neocortex, as it was found that neocortex size is strongly associated with the size of the whole brain (Hofman, 1989). However, on closer inspection it becomes clear that it is only the white matter of the neocortex which scales with the rest of the brain, the proportion of grey matter appears to be independent of the volume of the rest of the brain (Barton and Harvey, 2000). Thus, it seems that changes in the volume of the grey matter of the neocortex do not necessarily correlate with changes in the rest of the brain, calling into question the Developmental Constraints Hypothesis.

The controversy over the concept of mosaic evolution does therefore not seem to be substantiated, and it is therefore likely that evolutionary changes do occur in a mosaic fashion. It is important to note, however, that the probability that individual brain structures would have evolved entirely independently of any changes in the rest of the

brain is in fact very small. This is because all brain structures have neuronal connections to other parts of the brain and together they form brain systems. Significant changes in the size of one area (increase or decrease) within such a system would almost undoubtedly be paired with changes in the number of connections to and from that area resulting from a change in the number or size of neurons. Consequently, there would be a change in the size of the areas to which it is connected because of a change in the volume of information which would need to be processed. The concept of brain systems will be considered in the next section.

1.2.2.2 What are brain systems?

Brain systems are groups of brain structures which are intimately connected and which cooperate to effectively process a particular type of information. The format of systems is such that the expertise of each of the different brain structures involved is exploited for a particular function of that system of which it forms a part, i.e. these are functional systems with a division of labour. By way of illustration, in the visual system the neurons of the lateral geniculate nucleus (LGN) relay visual information from the eyes to cortical area V1 which crudely analyses the input. V1 then passes information on to extra-striate areas for specialized processing. In this way irrelevant or unimportant information can be sifted out by areas V1 and V2 so that it does not get processed at a higher level, i.e. the different components of the visual system work together efficiently as part of one particular system of the brain.

The brain contains vast numbers of such brain systems and these often work in parallel, thereby increasing the efficiency of the brain. Within a system, efficiency is increased by stronger connections between constituent areas. This can either mean more neural connections or an increase in the strength of existing connections. Such strength increases are manifested either by lowering the threshold of firing in the postsynaptic cell, or by increasing the rate of firing of the presynaptic neuron.

In considering brain structures, it is important to note one situation not explicitly accounted for by the mosaic theory of brain evolution. As outlined in Section 1.2.2.1, the mosaic theory claims that brain structures which make up systems show correlated evolution in the absence of changes in the rest of the brain. The problem is

that brain structures may, and often do, participate in more than one functional system (most notably the neocortex which is involved in a large number of different systems). Changes in the size of one structure may therefore be related to any of a number functional systems, not just one. For this reason, it is necessary to look at sub-parts of brain structures i.e., to look at small-scale changes in the particular areas included in the system of interest. In this way, it should be possible to determine what a change in the size of a brain structure actually means, that is to say, to discover precisely which system this change reflects. If the different sub-areas of the neocortex are investigated and the visual areas, for example, are found to have grown to be significantly larger, whereas the motor areas are found to be slightly smaller, then the overall increase in neocortex size is likely to reflect an increase in the size of the visual system, not the motor system.

To summarise, changes in the overall size of the brain reflect more intricate modifications occurring in the connections between neurons, and the number and the size of neurons within particular brain structures. Brain structures are organised in such a way that they make up functional systems specialised for processing particular types of information. Within these systems, alterations in the number or size or level of connectivity of the component neurons result in changes in the size of those particular brain areas. Thus, specific brain systems could in theory change in size independently of the rest of the brain and it is most likely that the overall increase in primate brain size over evolution is due to changes concentrated in particular areas of the brain rather than a general expansion or contraction. What is particularly important to note is that it is always 'systems' which are being referred to here, not isolated brain areas. The neocortex can be divided into numerous different specialised areas which are involved in various different brain systems. Consequently, it is highly unlikely that in primates the neocortex has shown a significant increase in size in the absence of changes in other areas of the brain, even though neocortex size may have changed most. What is far more likely is that a particular brain system has been selected for over primate evolution and certain areas of the neocortex being involved in that system have, in consequence, become unusually large. Unfortunately, due to a lack of data on the volume of particular neocortical regions in primates, it is currently not possible to assess the validity of this claim. What can be done at this stage is to investigate whether there is any

evidence that other brain structures changed in size as well as the neocortex (see Section 1.2.3). If such evidence is found, then it would support the possibility that it is not the neocortex per se which has expanded in primate brain evolution, but rather a brain system of which particular neocortical areas form a part. Such a hypothesis would be open to confirmation or disproof by evidence of which parts of the neocortex have expanded, when such evidence becomes available.

1.2.3 Co-evolution of the neocortex and cerebellum?

One of the areas of the brain to which the neocortex is most strongly connected is the cerebellum, which plays an important role in motor actions (Holmes, 1917; Thach et al., 1992; Glickstein, 1993; Ito, 1993; Welsh et al. 1995). Recent work suggests that these two areas of the primate brain showed highly correlated evolution independently of change in other structures ($p < 0.0001$) (Barton and Harvey, 2000), indicating that increases in the size of the neocortex were accompanied by changes in the size of the cerebellum. These correlated changes suggest that the neocortex may not be the only area of the brain to have shown significant expansion during primate evolution; the cerebellum may also have been important.

Before taking a closer look at the evolution of the cerebellum (which will be considered in some detail in Chapters 3-5), it is necessary to gain an understanding of what the cerebellum actually is, where it is situated within the brain, what structures it is connected to and what its precise functions are. This will be considered in the following sections.

1.3 The cerebellum

1.3.1 Exploring the cerebellum

The cerebellum (meaning “small brain”) is an important component of the motor system which may also be involved in other cognitive functions. It has strong

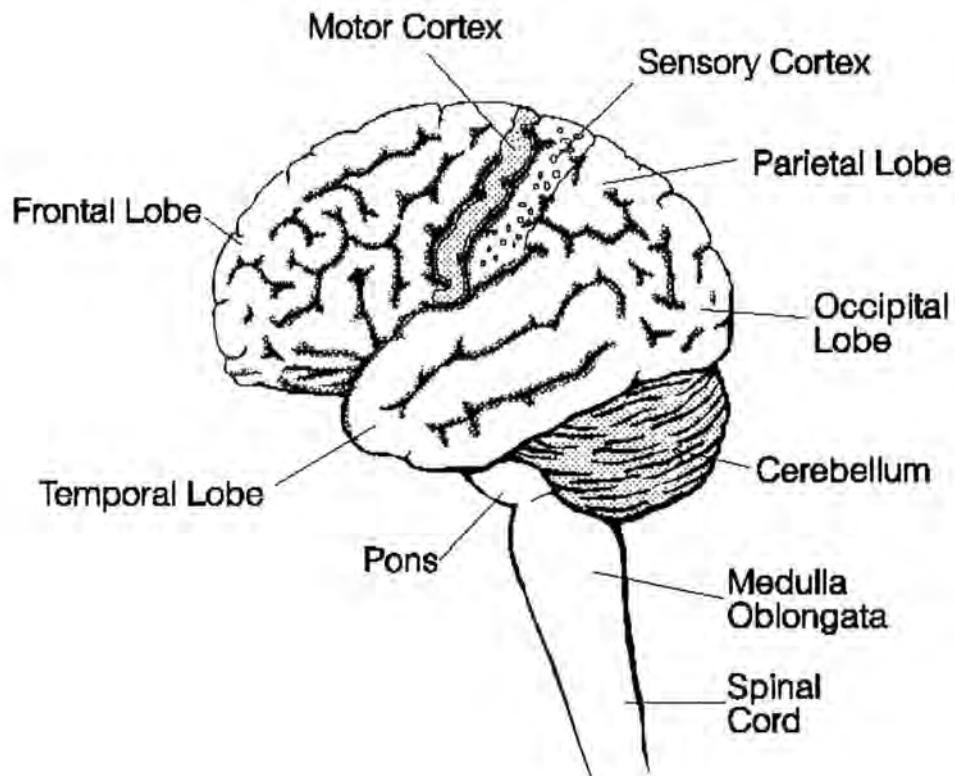
connections to the neocortex as well as to various other motor areas, and this section will look at the structure and functions of this particular area of the brain.

1.3.1.1 Structure of the cerebellum

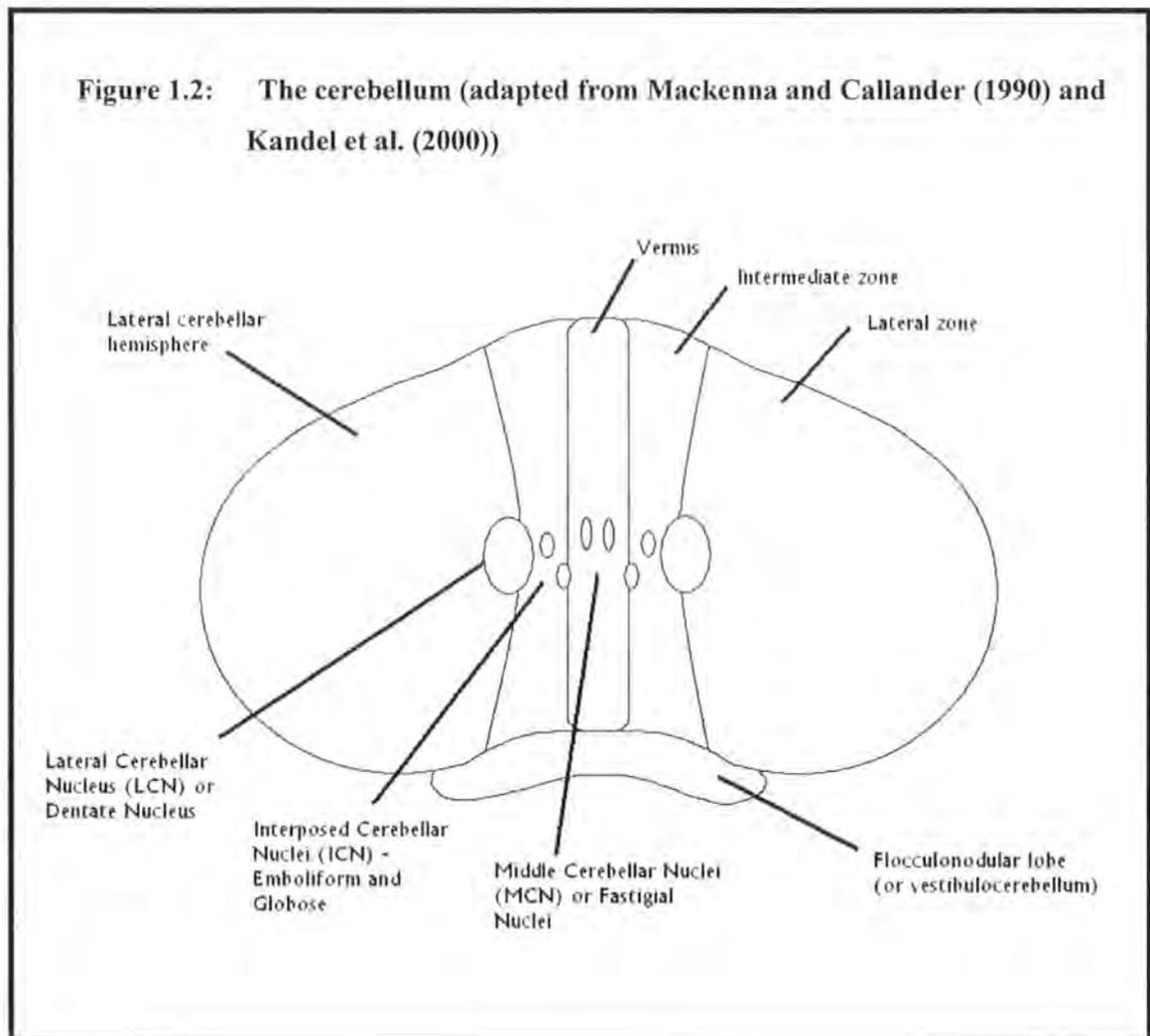
The cerebellum is situated behind the pons in the hindbrain (see Figure 1.1) and is connected to the brain stem and the rest of the nervous system by three clusters of nerve fibres: the inferior (restiform body), the middle (brachium pontis) and the superior (brachium conjunctivum) cerebellar peduncles. The cerebellum has strong connections to the neocortex, particularly to the motor, premotor and prefrontal areas.

Figure 1.1: The Human brain (adapted from the website:

<http://www.neurosurgery.org/pubpages/images/lobesbig.gif>)



The crude structure of the cerebellum is very similar to that of the brain as a whole: it has an outer layer (cortex) composed of grey matter, an internal core of white matter and it is made up of two distinct hemispheres. Since Jansen and Brodal's study (1940) of the cerebellar cortico-nuclear projection, it has generally been accepted that, on the basis of functional variation which is discussed below, the cerebellum can be divided into three longitudinal zones: the lateral zone, the intermediate zone and the vermis (Kuhlenbeck, 1975; Carpenter, 1976) (see Figure 1.2).



Within the white matter of the cerebellar hemispheres lie the major output structures of the cerebellum: four pairs of deep cerebellar nuclei – the fastigial nuclei, the interposed nuclei (emboliform and globose) and the dentate (or lateral) nuclei.

- (i) **The fastigial nuclei:** The fastigial nuclei are situated in the vermis which runs along the midline of the cerebellum. This area receives input from the spinal cord via the spinocerebellar tract; it receives input from the vestibular system via the vestibulocerebellar tract; and it receives visual and auditory information via the tectocerebellar tract. Outgoing signals originate in the Purkinje neurons in the vermis, which send projections to the fastigial nuclei. The nuclei project to the brain stem reticular formation, which then project to the spinal cord via the reticulospinal tract, and to the lateral vestibular nuclei, which project to the spinal cord via the vestibulospinal tract. The fastigial nuclei also send axons which cross to the contralateral side and project to the primary motor cortex via the ventrolateral nucleus of the thalamus.

- (ii) **The interposed nuclei:** The interposed nuclei include both the emboliform and the globose nuclei. They are situated in the intermediate zone of the cerebellar hemispheres which is adjacent to the vermis. The intermediate zone receives projections from the spinal cord via the spinocerebellar tracts. Outgoing projections pass through the superior cerebellar peduncle to the red nucleus, which then projects to the spinal cord (rubrospinal tract) and via the ventrolateral nucleus of the thalamus to the primary motor cortex, which also projects to the spinal cord (lateral corticospinal tract). Collectively, the corticospinal and rubrospinal tracts are called the lateral descending systems.

- (iii) **The dentate nuclei:** The dentate nuclei are situated in the lateral zone (cerebrocerebellum) of the cerebellar hemispheres and receive projections from the cerebral cortex via the corticopontocerebellar tract which passes through the middle cerebellar peduncle. Outputs from the dentate nucleus go to premotor, motor and prefrontal cortical areas via the ventrolateral nucleus of the thalamus.

In addition to these cerebellar nuclei, there is one further area of the cerebellum which sends outgoing projections. This is a small portion of the cerebellar cortex called the flocculonodular lobe (or vestibulocerebellum) situated at the base of the cerebellum. The flocculonodular lobe is closely connected to the vestibular system from where it receives projections and to which it sends outputs.

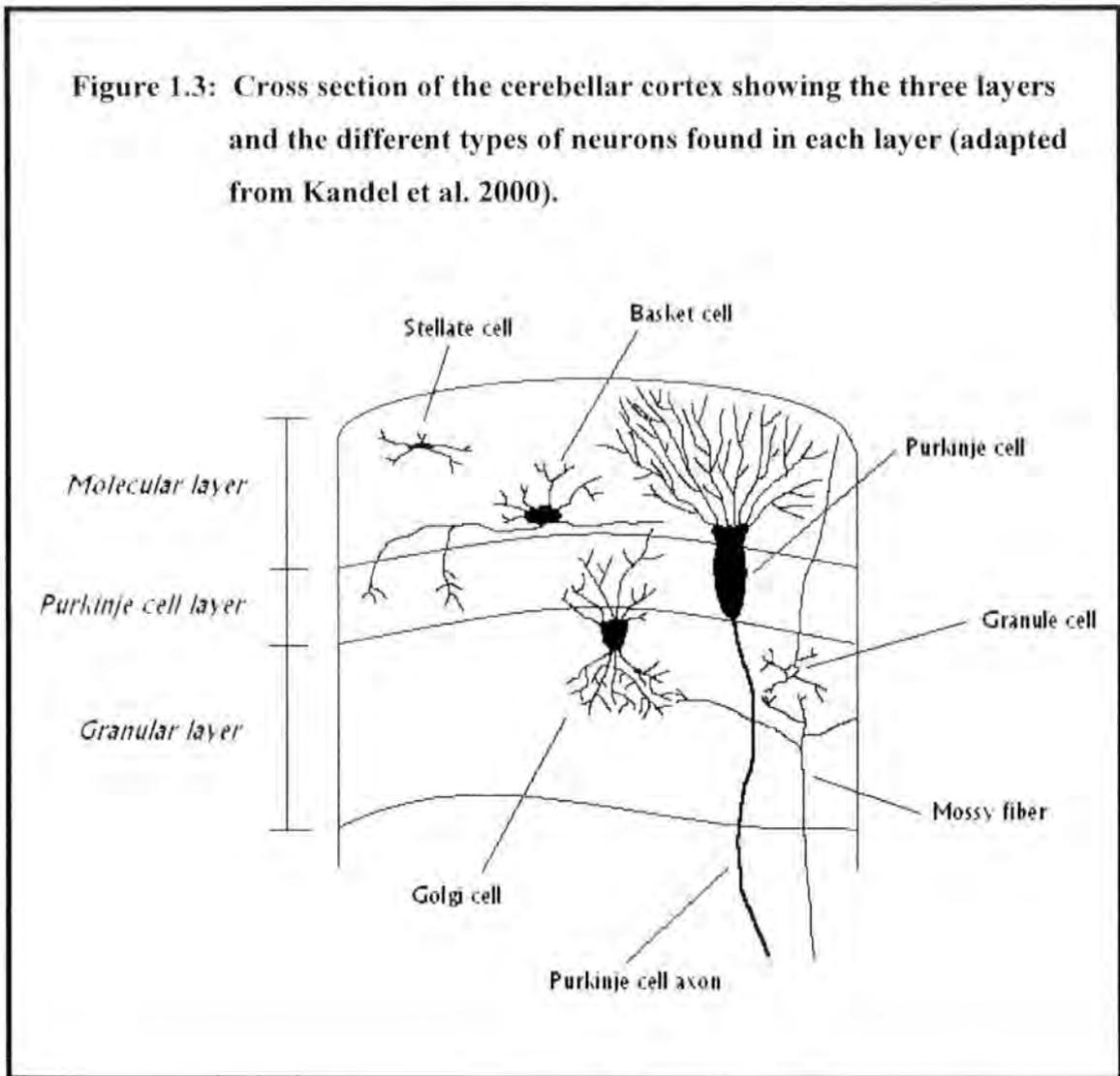
It is important to note that this is only a general outline of the structure of the cerebellum and that there may be variations amongst species. For example, preliminary studies have revealed differences in the relative size of the cerebellar nuclei between gibbons and pongid apes (Matano and Hirasaki, 1997), indicating that although the overall relative size of the cerebellum may be similar between species, the internal arrangement may be different.

(iv) Cerebellar Cortex:

The outer layer of the cerebellum, the cerebellar cortex can be divided into three individual layers: the molecular layer, the Purkinje cell layer and the Golgi granular cell layer, each of which contain varying numbers of five different types of neurons: the inhibitory stellate, basket, Purkinje and Golgi neurons, and the excitatory granule cells (see Figure 1.3).

- a) **The molecular layer:** This is the outermost layer of the cerebellar cortex and is made up of the cell bodies of basket and stellate cells, as well as granule cell axons and dendrites of Purkinje neurons.
- b) **The Purkinje cell layer:** This layer lies directly below the molecular layer and, as its name suggests, is made up of Purkinje cell bodies. Purkinje cells convey all the output of the cerebellar cortex, sending their axons deep into the white matter where they project to the cerebellar nuclei. This inhibitory cerebellar cortical output is mediated by γ -aminobutyric acid (GABA).
- c) **The granular layer:** This layer lies beneath the Purkinje cell layer and forms the innermost layer of the cerebellar cortex. It is made up of an extensive number of granule cells, a much smaller number of Golgi cells, as well as the terminals of mossy fibres. Mossy fibres originate in a variety of brain stem and spinal cord nuclei, and provide the major input to the cerebellum, carrying information from the cerebral cortex as well as sensory information from the periphery. Incoming information is passed from the terminals of these mossy fibres to granule cells and Golgi neurons by means of complex synaptic connections called cerebellar glomeruli.

Figure 1.3: Cross section of the cerebellar cortex showing the three layers and the different types of neurons found in each layer (adapted from Kandel et al. 2000).



1.3.1.2 Functions of the cerebellum

Although, on average, the cerebellum makes up only 10% of the volume of the whole brain, it contains more than half of all the brain's neurons (Kandel et al. 2000). The large numbers of neurons attest to the information processing power of the cerebellum. As discussed in Sections 1.2.1 - 1.2.2, brains evolve by modifying the number and arrangement of neurons in different areas. The fact that the cerebellum has such a high concentration of neurons suggests that this is an important area of the brain. It is impossible to know whether the number of neurons in the cerebellum dramatically increased over evolution or whether even very primitive brains had such a large proportion of neurons in this (or the corresponding) area. Nevertheless, the

fact that the cerebellum still contains this proportion of neurons indicates that it carries out very important functions and some of these will now be considered.

In investigating the functions of the cerebellum, it seems sensible to start by looking at the nature of the information that it receives and that which it sends out.

- (i) **Inputs:** Extensive numbers of axons project to the cerebellum (40 times more than project from it), indicating that the cerebellum receives an extraordinary amount of information. Inputs come from the cerebral cortex (primarily motor areas), the vestibular system and the spinal cord, suggesting that incoming information is principally concerned with the planning and execution of movement (Kandel et al. 2000).
- (ii) **Outputs:** The major outputs of the cerebellum project to the motor areas of the cortex and brain stem, including the motor, premotor and prefrontal cortices, the vestibular nuclei, the thalamus and the red nucleus. These are areas which directly innervate motor neurons, indicating that the cerebellum can have a strong influence on motor activity.

Thus, there can be little doubt that the cerebellum is involved in motor actions. However, a role for the cerebellum in a number of sensory and cognitive functions has recently been proposed (Fiez et al., 1992; Leiner et al., 1993) (although this is controversial, especially the proposal of a cognitive role e.g. language (Fabbro et al. 2000)), and it is therefore possible that the cerebellum is not a purely motor-gearred structure. The various functions of the cerebellum will now be considered, and the controversy over whether or not some of these functions may be of a sensory or cognitive nature will be addressed. The first functions to be considered are motor functions, which range from planning movements to executing them and to controlling them once underway.

The cerebellum (lateral zone in particular) has consistently been implicated in the planning of motor actions (Allen and Tsukahara, 1974; Eccles, 1977; see Brooks and Thach, 1981, for a review). It is argued that motor actions are formed on the basis of previous experience of similar sensory inputs (Smith et al. 1993) which implies that

memory is involved in that it must be necessary to store information about a previous encounter with similar stimuli in order to be able to produce the same actions again. There are, however, a number of unresolved points in this account, including the question of how similar stimuli need to be to evoke a particular stored motor action. Furthermore, this account offers no explanation as to how the first motor actions are ever produced when there are no similar experiences to relate to (for example in young children learning to move). Thus, there are a number of questions which must be resolved before this account can be accepted as an explanation for precisely how the cerebellum is involved in planning motor actions.

There has, however, also been some controversy over the very idea that the cerebellum is involved in the planning of motor actions at all. Dagher et al. (1999) carried out a PET study in humans to investigate which brain areas are involved in motor planning. In this study, subjects were required to carry out the Tower of London (TOL) task which is a test of planning where the problem posed can be solved by mentally going through possible sequences of actions before actually producing the final, hopefully correct, solution. By looking at which areas of the brain are active during such mental rehearsal, it is possible to see which areas are necessary for this planning to occur. The results of Dagher et al.'s study showed that the dorsolateral prefrontal, lateral premotor, anterior cingulate and caudate areas are the areas of the brain involved in planning motor actions. There is no mention here of the cerebellum, indicating that it was not found to be active during the planning stage of the TOL. However, a limitation of this study is that the TOL is not the best task to use, since it does not accurately reflect the normal processes that would be employed to plan movements. In this task, subjects mentally rehearse possible courses of action, so they most probably use active mental imagery to imagine what results different actions would have. This is clearly not what happens in the planning of everyday motor actions, since if it did, any movement would take an inordinate amount of time. Furthermore, the lack of cerebellar activity could be due to a lack of a motor component in the planning of the task. There is no reason why subjects should imagine themselves moving the objects within the task, it is very possible that they simply imagined the objects moving by themselves or already having moved, thus taking away the motor component. In addition, the task used in Dagher et al.'s experiment in particular was carried out using images on a computer screen. Thus,

even when actively carrying out the task (i.e. putting coloured balls in a specified order), the level of motor activity required is limited. Therefore, when planning this final active part of the task, there would be a limited amount of activity in motor areas of the brain corresponding to the small amount of motor actions that would actually be required to carry out the task. In short then, at this point in time, although PET studies are a very useful way in which to determine the functions of particular brain areas, the lack of activation in the cerebellum in Dagher et al's study should not be taken to mean that the cerebellum is not involved in motor planning.

Moving on to movement execution, evidence suggests that it is the intermediate and medial regions of the cerebellum in particular that are involved in the execution of motor actions (Allen and Tsukahara, 1974; see Brooks and Thach, 1981 for a review). This execution requires accurate timing and it has been argued that particular areas of the cerebellum act as some kind of "internal timing system" (Ivry et al., 1988). Ivry et al. looked at patients with particular damage to different areas of the cerebellum. They found that although patients with damage to medial cerebellar regions were able to determine when to make a response (i.e. they had intact timing abilities), they were unable to actually carry out a particular task at the correct time. Patients with lateral cerebellar lesions, on the other hand, had problems with timing their actions. This led Ivry et al. to conclude that it is the lateral regions of the cerebellum which are important for the timing of motor actions. This finding was supported by Akshoomoff and Courchesne (1992), who went further to argue that it is not just the lateral regions, but the whole of the neocerebellum (cerebellar nuclei, vermis and posterior lobe hemispheres), that is involved in the coordination and precise timing of a planned sequence of motor actions.

Once a movement is underway, the cerebellum appears to be involved in controlling that movement. It has been suggested that the cerebellum should be seen to be "a large collection of individual lines", analogous to Eccles's "beams" (Eccles et al. 1967), each of which responds selectively to particular sequences of events by producing appropriate sequences of output signals (Braitenberg et al., 1997). In this way, the cerebellum can monitor motor activity and, by having such specialisation within the structure (with particular areas responding to particular types of information), more accurate or detailed monitoring of motor actions is possible. The

particular area of the cerebellum that has been implicated in these functions is the cerebellar cortex, and it is suggested that the output produced by this area in response to particular input sequences is in the form of inhibitory neural firings which "sculpt" the motor sequences in order to "adapt them to the complicated requirements of the physics of a multijointed system" (Braitenberg et al. 1997). It is important to note that there has been some criticism of this model. It has been argued, for example, that it cannot adequately account for recent findings that the cerebellum is involved in attentional and sensory systems as well as the motor systems which have been well documented (Courchesne, 1997), nor can it explain the whole of the temporal range of processing in which the cerebellum is involved as it cannot account for discrete movements of between 200 to 1000 milliseconds (Grethe and Thompson, 1997). A further limitation of this model is that it is unclear how the output signals are formed, to what extent they are innate and how they are influenced by learning; if they are learned then classification is required to explain how this learning might take place. This model clearly requires some modification.

In addition to the control of movements, another important action to be carried out once a movement is under way (and perhaps even beforehand) is the fine-tuning of motor actions. This is thought to be one of the principal functions of the cerebellum. Fine-tuning motor actions involves the assessment of disparities between the intended action and that which was actually produced, followed by the sending of projections to adjust the action of motor cortical and brain stem regions accordingly (Thach et al. 1992; Kandel et al. 2000). The neocerebellum in particular has been argued to carry out these functions (Jueptner and Weiller, 1998).

The ability of the cerebellum to monitor and then adjust or fine-tune movements means that it is possible to learn from experience and constantly improve on the accuracy of the movements executed. Some of the earliest work on the role of the cerebellum in motor learning was carried out by Marr (1969), who argued that it is the cerebellar cortex in particular that is involved in learning motor actions. More recently, evidence to support the idea that the cerebellum can learn from experience has come from experiments using positron emission tomography. It has been shown, for example, that there is a decrease in regional cerebral blood flow in the cerebellum during repeated execution (i.e. practice) of a motor task, despite any improvement in

performance (Jenkins and Frackowiak, 1993). This indicates that the cerebellum learns the precise actions required as they are repeated during a motor task so that with further repetitions, there is less activity in the cerebellum as an activity becomes automatic and no (or at least less) new learning is required. Support for cerebellar involvement in motor learning comes from Schweighofer et al. (1998) who used a complex cerebellar neural network to model cerebellar activity in a particular type of motor learning (learning to control arm movement). At a neural level, the ability of the cerebellum to learn from experience is dependent on long-term depression (LTD). This occurs on the mossy fibre input to the cerebellum when both of the excitatory inputs (parallel fibers and climbing fibres) to the Purkinje cells are activated simultaneously (Kano, 1996). This activation results in an increased response from the cerebellar nuclei that is then transmitted to the thalamus and on to the motor cortex.

Particularly fine motor actions (which presumably result from the types of learning considered above), have been associated with one particular cerebellar nucleus: the dentate nucleus. This nucleus is thought to be involved in skilled movement sequences (Rao et al., 1997) and it has been argued that the development of the lateral zone in humans in particular is related to the manual dexterity which evolved after bipedalism when hands became free (Matano and Hirasaki, 1997).

Thus, there is good evidence to suggest that the cerebellum is involved in the planning, execution, control, fine-tuning and learning of motor actions. These are all very motor-oriented, however it is important to note that the cerebellum has also been found to interact with the somatosensory system, and may therefore also play a role in sensory processing (Paulin, 1993). Possible sensory functions of the cerebellum will now be considered.

Studies of brain-damaged patients have implicated the cerebellum in non-motor perceptual and spatial reasoning problems. Fiez et al. (1992), for example, tested a patient with right cerebellar damage on a number of non-motor tasks. They found that although he performed well on tests of intelligence, memory and language, he had great difficulty in practice-related learning and in the detection of errors. This indicates that the cerebellum is normally involved in these non-motor tasks and

therefore that the cerebellum may be involved in tasks which are not purely motor-oriented. Further evidence for the role of the cerebellum in perceptual or spatial reasoning comes from Paulin (1993), who argued that together with the somatosensory system, the cerebellum plays a role in the tracking of stimuli in the environment (or smooth pursuit eye movements) as well as tracking movements made by the animal itself. The cerebellar cortex in particular was implicated in this function and Parkins (1997) went so far as to claim that rather than being a structure for motor control, the cerebellum is primarily a tracking system which plays an important role in motor control and coordination. There has, however, been limited support for this proposal, especially since it cannot account for the possible cognitive functions of the cerebellum which are considered below.

Further work on sensory functions of the cerebellum was carried out by Gao et al. (1996). Their experiments used magnetic resonance imaging to show that the dentate nucleus is active during the processing of sensory information in the absence of any motor activity. This led them to the rather radical claim that the lateral cerebellum is active during motor activities only because it is involved in the processing of the associated sensory information not because it plays a role in motor actions. Support for this argument comes from Jueptner et al. (1997), who argue that the neocerebellum is much more concerned with sensory information processing than has been considered previously. However, it is important to note that while Jueptner et al. are arguing that the neocerebellum is more deeply involved in sensory information processing, it appears that Gao et al. are arguing that the dentate nucleus is *only* involved in sensory information processing. This is a very bold claim to make, as will be seen later, not least because the dentate nucleus is the area of the cerebellum argued to be particularly involved in cognitive functions.

Further work on the role of both the dentate nucleus and the lateral zone as a whole in sensory processing was carried out by Parsons et al. (1997). They argued that the lateral cerebellum is involved in the acquisition and discrimination of tactile sensory stimuli rather than being involved in actual motor control. In their experiment, MRI scans were carried out on subjects performing both passive and active sensory tasks. The results showed that the dentate nucleus was activated in response to tactile stimulation in the absence of any finger movements, that this nucleus was not

activated by finger movements which were not associated with the discrimination of tactile stimuli, and that the strongest activation occurred when sensory discrimination and finger movements were carried out simultaneously. This led them to conclude that the dentate nucleus is involved in the acquisition and discrimination of sensory information and that related to this function, it plays a role in modulating and repositioning the surfaces of the fingers in response to incoming sensory information. In contrast to Gao et al.'s claims, these results suggest that the dentate nucleus is not solely involved in sensory processing but that it also has a motor component. However, the activity of this nucleus does seem to be more related to sensory processing than to motor coordination, as fMRI studies show (Liu et al. 2000).

Leaving aside the question of the degree to which the cerebellum is involved in sensory processing, what is most important here is simply the fact that it is involved in this type of processing and that it is therefore not a purely motor structure. Having considered the motor and sensory functions that have been attributed to the cerebellum, it is now important to look at the most controversial area: the cognitive functions. The cognitive activities in which the cerebellum has been proposed to play a role include lexical processing (Petersen and Fiez, 1993; Leiner et al., 1993; Fabbro et al. 2000), mental imagery (Ryding et al., 1993) and attention (Akshoomoff and Courchesne, 1992; Allen et al. 1997)

One area of the cerebellum in particular has been implicated in cognitive activities. This is the cerebrocerebellum (or lateral zone), the only cerebellar area to receive projections from the cerebral cortex. Investigations into the projections from the cerebellum to the prefrontal cortex have identified distinct output channels from the dentate nucleus, supporting the hypothesis that this nucleus is involved in motor and cognitive operations (Middleton and Strick, 2001). Middleton and Strick specifically looked at thalamic regions that send projections to the prefrontal cortex and compared these with the thalamic areas that receive projections from the cerebellum. The results showed that the cerebellum projects to a number of prefrontal cortical areas (46 and 9). As the prefrontal cortex is not a strictly motor area, but is involved in various types of high-level cognitive processing Middleton and Strick concluded that the cerebellum must be involved in cognitive functions in addition to the well-documented motor functions.

Within the cerebrotocerebellum, it has been suggested that it is the neodentate in particular that is involved in non-motor functions (Leiner et al. 1986). This is because stereotaxic lesions in this area do not result in any of the motor problems which typically arise after cerebellar damage (Siegfried et al. 1970). Direct tests of the role of the dentate nucleus in cognitive operations was carried out by Kim et al. (1994). Using MRI, these workers found significant bilateral activation of the dentate in subjects who were trying to solve a pegboard task. This task has both cognitive and motor components, and what is particularly interesting about the results is that the area activated during this task was up to four times greater than the area activated in a task that only involved simple movements of the pegs, a purely motor task. This means that a large area of the dentate seems to be specifically involved in the cognitive aspects of behaviour.

The possibility that it is the dentate in particular that is involved in cognitive abilities suggests that there might be a significant difference between the size of this nucleus in humans (who are generally believed to have highly developed cognitive abilities) and other primates. This does in fact appear to be the case (Matano, 2001). The neodentate in particular has been found to be far more developed in humans than monkeys and more enlarged in humans than in apes. It is therefore very possible that this area is involved in the attributes which set humans apart from other primates: higher level cognitive functions (Leiner et al., 1993)

To summarize, the cerebellum has been implicated in numerous different activities including the planning, execution and control of motor actions, spatial reasoning, the tracking of stimuli in the environment, sensory processing, lexical processing, mental imagery and attention. As these activities require sensory and cognitive abilities, it seems that the cerebellum is not a purely motor structure. It is far more likely that particular areas of the cerebellum have primarily motor or cognitive functions, but that as a whole the cerebellum is involved in a variety of different activities. One point which it is important to note is that many of the functions in which the cerebellum is argued to play a role should not be classified as purely motor, or sensory or cognitive. Many functions involve aspects of more than one of these areas, (probably because they involve more than one area of the cerebellum). Motor planning, for example, is not a purely motor activity because planning implies some

cognitive awareness that the action will be needed in the future. Correspondingly, the lateral zone which has been implicated in motor planning actually contains the dentate nucleus which has been implicated in cognitive functions. Thus, in explaining the evolution of the cerebellum, it is not sufficient to look for correlations with the whole cerebellum, it is necessary to look *within* the cerebellum to determine which particular areas have changed in size as each area has its own specific functions.

1.3.2 Development of the cerebellum

There has been relatively little work carried out on the development of the cerebellum and consequently there is a paucity of knowledge in this area. One very important point which is known, however, is that the cerebellum, which is one of the first brain structures to begin to differentiate in the development of the brain, is one of the last areas to reach maturity (Wang and Zoghbi 2001). This is particularly interesting in the light of the possibility that the cerebellum and neocortex showed correlated evolution (Barton and Harvey, 2000), as the other parts of the brain that also develop late are areas within the neocortex. The prefrontal cortex in particular is known to develop late when there is a large amount of external stimulation. This is interesting given the strong connections between the prefrontal cortex and the cerebellum (Middleton and Strick, 2001) and the finding that many cognitive functions in which the prefrontal cortex is involved also involve the cerebellum (Diamond, 2000). Furthermore, it is common for both the cerebellum and the prefrontal cortex to be damaged in a number of developmental disorders (Diamond, 2000). The development of the cerebellum will be considered in more detail in Chapter 5, where the importance of the timing of development of brain parts will be investigated from an evolutionary stand-point.

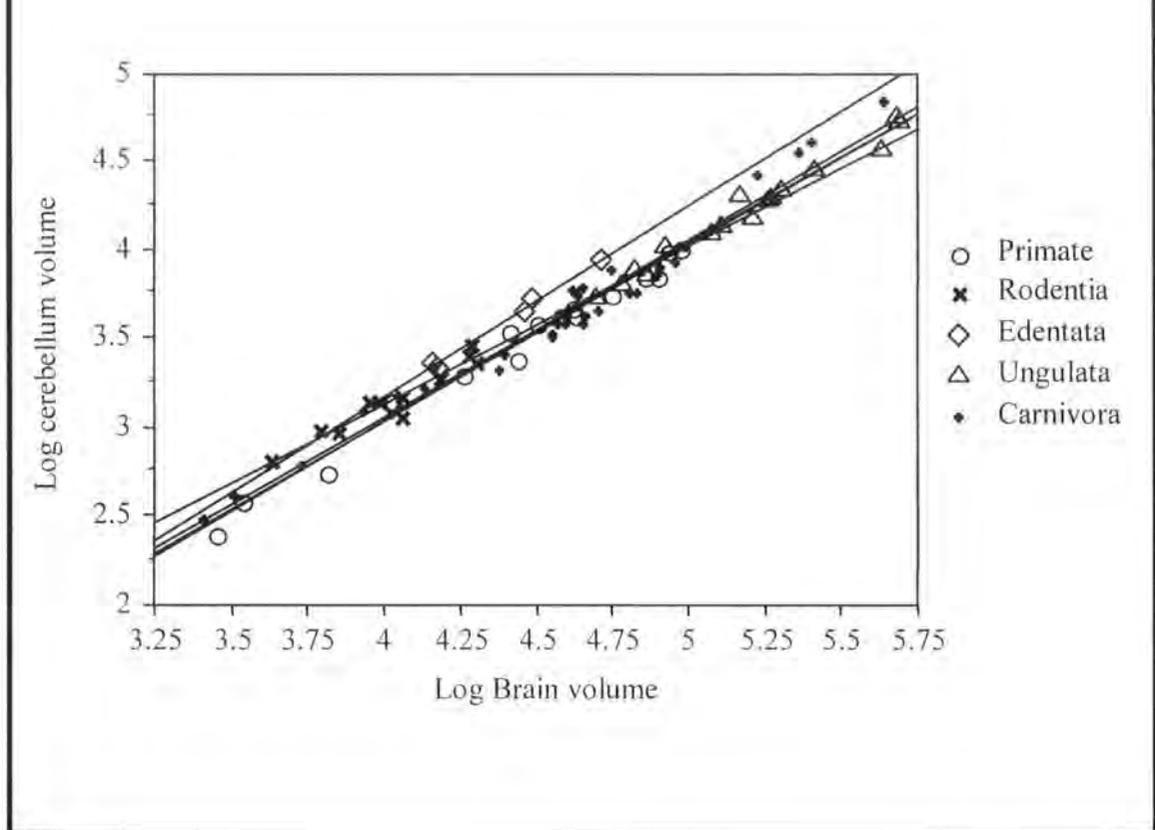
1.3.3 Evolution of the cerebellum

Investigations into the evolution of the cerebellum have been limited to comparative studies because not only are there no fossil cerebella, but cerebellar imprints into fossil skulls which might give some indication of crude size are extremely rare and, when they are found, faint.

Before looking at work on the evolution of the cerebellum, it is important to first refute a very recent claim that cerebellar size is constant across species (Clark, Mitra and Wang, 2001). If this were the case then the cerebellum might not be such an interesting area of the brain to study, however there are a number of flaws in Clark et al.'s paper. Clark et al. used the cerebellum as a proportion of brain volume as the comparable variable in their investigation. They compared these variables for 20 mammalian taxa, with the rest of the mammalian taxa combined to determine whether any of these sub-groups differed significantly from all the other mammalian taxa combined, finding that relative cerebellar size remains constant across different mammalian taxa.

The main problem with this method is that by pooling all the other mammalian taxa, any variations which may exist between taxa will be evened out. Therefore it is not surprising that they found that no taxa differed significantly from this combined group. An analysis of variance on the cerebellum as a proportion of the brain in mammals has since been found to be significant (Barton in preparation), indicating that the cerebellum does vary in relative size in different mammals. Furthermore, Figure 1.4 below shows the results of a least square regression analysis of the relative size of the cerebellum in a number of different primate species. An analysis of covariance showed significant differences between mammals in the proportion of the brain made up of cerebellum ($p < 0.0001$, $F = 8.129$, $d.f. = 4$).

Figure 1.4: Cerebellum volume plotted against whole brain volume for five different groups of mammals.



These results clearly show that there is significant variation in the relative size of the cerebellum between different mammalian taxa. This indicates that the cerebellum has shown different evolutionary changes in different taxa and that it is, therefore, most likely an important brain area to study although it may well be that among taxa, neocortex size varies more than cerebellum size does.

Having demonstrated that investigations into the cerebellum are worthwhile, it is necessary to look at the previous work that has been carried out in this area. Recent investigations into the evolution of the cerebellum have found that among mammals, primates, particularly apes, have a relatively large cerebellum (Rilling and Insel, 1998). The investigation which led to this finding involved carrying out *in vivo* MRI scans on eleven different haplorhine species. The results showed that the cerebellum of apes (not including humans) is approximately 45% bigger than that of

monkeys, prompting Rilling and Insel to argue that monkeys and apes have evolved different grades of relative cerebellum size. This difference between the size of the cerebellum in monkeys and apes is highly significant, and suggests that some function of the cerebellum was more beneficial or more necessary in apes than in monkeys, and that the increase in cerebellar volume must have been specifically selected for over the course of evolution.

The obvious question that follows from these findings is why apes need a larger cerebellum than monkeys; what is the behavioural advantage for apes of investing in such a large cerebellum? Very little work has focussed on the precise role of the cerebellum in non-human primates, which means that there is currently no obvious explanation for why apes might have evolved an unusually large cerebellum. The best option currently available might be to look at the human cerebellum since much work has been carried out on this area. However before jumping into such investigations it is important to note that this finding of an increase in cerebellum size in apes may not necessarily hold true for humans. It has in fact been claimed that humans have a smaller cerebellum than would be predicted for a primate brain of human size (Semendeferi and Damasio, 2000). Semendeferi and Damasio used MRI scans to reconstruct 3D images of the human brain from which they could estimate the volumes of a number of brain structures, including the cerebellum. In absolute size, the cerebellum was found to be at least twice as large as the cerebellum of any of the other apes. However when the cerebellum as a proportion of the whole brain was compared between species, the relative size of the human cerebellum was significantly smaller than would have been predicted for an ape brain of human size.

This finding of a small cerebellum in humans may nevertheless be caused by confounding effects of the large neocortex. It was noted earlier in this paper that primates have a large neocortex. Even within primates, the human neocortex is exceptionally large, being almost three times larger than would be predicted for a primate brain of human size (Passingham, 1982, Deacon, 1997). Including the neocortex in the “rest of the brain” is likely to obscure trends in cerebellum size. This is because any brain structure that is compared to the volume of the rest of the brain including the neocortex will inevitably appear smaller than it actually is due to the large size of the neocortex to which it is being compared. It is predicted that on

removing the effect of the large neocortex, the human cerebellum will be found to have shown similar increases in size relative to other brain structures, as was observed in other apes. Furthermore, in line with the cognitive functions of the cerebellum outlined in Section 1.3.1.2, it is predicted that great apes who appear to have superior cognitive abilities, will be found to have significantly larger cerebella compared to the other apes (gibbons). These predictions will be directly tested in the following chapter.

In summary, although previous investigations into the evolution of the primate brain have focussed on changes in the size of the neocortex, recent evidence suggests that the cerebellum may also have played an important role, as this structure has shown correlated evolutionary changes with the neocortex (Barton and Harvey, 2000). The aim of this thesis is to investigate the changes that have taken place in the cerebellum over primate evolution and to determine the importance of these changes and the implications for previous theories of primate brain evolution. This requires the testing of a number of hypotheses which include the following:

- 1) In line with the theory of mosaic evolution, it is predicted that the areas of the brain that are connected to the cerebellum will be found to have shown correlated evolution with the cerebellum, independently of change in other structures.
- 2) As the primate neocortex is unusually large and as the cerebellum has shown correlated evolution with this structure, it is predicted that the primate cerebellum will also be found to be unusually large compared to that of other mammals.
- 3) Within primates, it is predicted that the great ape cerebellum will be found to be particularly large because great apes seem to have advanced cognitive and motor abilities in which it is likely that the cerebellum is involved.

Further investigations will also be carried out, prompted by the results obtained by testing these hypotheses. These investigations will focus on identifying environmental variables that correlate with relative cerebellum size in an attempt to explain the evolutionary size changes that have occurred in the primate cerebellum.

CHAPTER 2

Methods

The focus of this thesis is the evolution of the cerebellum and the areas to which it is connected, most notably the neocortex. It appears that these structures have shown correlated evolutionary changes, an issue that will be investigated in some detail in the chapters which follow. Before moving on to these investigations, there are a number of methodological issues that need to be addressed in order to justify their design. Section 2.1 addresses the issue of scaling and Section 2.2 the logic behind the analyses. In Section 2.3 detail is provided about the data to be used in the current analyses. The different types of comparative method (phylogenetic and non-phylogenetic) will be considered in Section 2.4 with particular focus on the method of independent contrasts which will be critical to these investigations.

2.1 Scaling

In the empirical sections that follow, the evolution of the cerebellum will be explored by comparing the volume of different brain structures among species. It is important to note that comparisons of absolute volume are unlikely to be useful, due to confounding factors such as body size and whole brain size. This means that in order for structures to be usefully compared they must be scaled. There has been much controversy over the various different scaling methods available, so much so that it has been argued that results obtained are artifacts of the particular scaling method adopted (Deaner et al, 2000). The three types of scaling most commonly used are:

- (i) Regressing the volume of the brain structure against body mass (e.g. Clutton-Brock and Harvey, 1980; Gibson, 1986).

- (ii) Regressing the volume of the brain structure against the volume of another brain structure (e.g. Sawaguchi and Kudo, 1990; Barton, 1996, 1998; Joffe and Dunbar, 1997).
- (iii) Calculating the ratio of one brain structure to another (e.g. Dunbar, 1992, 1995).

Note also that some have advocated the use of absolute neocortex size (Falk and Gibson, 2001). For (i) and (ii), the residuals of the regressions for different species are then compared to determine what differences are present. For (iii), the ratios for different species are directly compared. Note that for (i) and (ii) the slope is set empirically and the residuals are then taken, whereas for the ratio method (iii), the slope is set as 1 and the residuals are then taken.

The argument that the results obtained depend on the scaling method employed stems from the observation that work supporting the ecological hypothesis outlined in Chapter 1 mainly used method (i), whereas work supporting the social brain hypothesis used methods (ii) and (iii); the implication being that more support for the ecological hypothesis would have been found if methods (ii) or (iii) had been used. Clearly the possibility that methods of investigation bias results is a serious issue, one that must be investigated and resolved if the findings of comparative studies are ever to be accepted.

A recent investigation directly tested the effect on results of using each of the three methods (Deaner et al., 2000). In this study, extra-striate cortex was scaled using methods (i), (ii) and (iii). Two environmental variables: group size (a social variable) and home range size (an ecological variable), were then regressed against the scaled values to determine whether either of these could better explain the variation in extra-striate size and whether the results differed depending on which scaling method was used. The results showed that for method (ii), group size predicted extra-striate cortex size most accurately. For methods (i) and (iii) there was no significant difference between the accuracy of the predictions of group size and home range size. Any variation was associated with whether or not outliers were included, whether home range size was scaled to body mass and whether independent contrasts were used. Deaner et al. concluded that there is "no reasonable basis" for choosing any of

the scaling methods over any of the others. There was no difference in the explanatory power of the social or ecological hypothesis for explaining the variation in the size of the extra-striate cortex. Therefore, it was argued, previous research using comparative methods are inconclusive and that what is needed is a scaling method that produces consistent correlations between the relative size of brain structures and observed behaviours. As the principal aim of the current analyses is to investigate the evolution of brain structures in relation to one another, these analyses will show whether mosaic evolution is likely to have taken place. It will not be possible to determine this by calculating brain size relative to body size. This means that while Deaner's findings are interesting and need to be investigated in general by other comparative studies, they do not, however, undermine the specific purpose of this particular study.

The empirical work which follows is focused on the evolution of the cerebellum and related structures relative to variation in the rest of the brain. Method (ii) will be used because the focus is on the evolution of particular brain structures and on the evolutionary changes in these structures relative to one another (for example, do the neocortex and cerebellum correlate independently of their general correlation with whole brain size?). In Chapter 6, when environmental correlates such as those used in Deaner et al.'s study, are investigated, three different scaling methods will be used to evaluate the effect this has on results. These are: brain - (neocortex+cerebellum) (see section 3.3 for rationale behind removing neocortex and cerebellum); medulla (because this structure shows little variation relative to body size); body weight (because many traits scale with body size).

2.2 Investigating systemic brain evolution

The cerebellum and neocortex are discrete brain structures and these will be compared to one another and with the rest of the brain in the investigations which follow. This means that there will be three major non-overlapping brain parts to compare: the cerebellum, the neocortex and the rest of the brain (brain - (neocortex + cerebellum)).

In addition, a number of structures functionally and anatomically linked to the cerebellum will also be compared. They include the pons, the thalamus and the vestibular system. Each of these structures will be regressed onto the three non-overlapping brain parts detailed above in order to investigate the evolution of the cerebellum and the structures to which it is most intimately connected.

2.3 Data

The majority of the measurements of the volumes of different brain structures comes from Stephan et al. (1981). This includes data on the volume of the cerebellum, the neocortex, the vestibular system (including the lateral vestibular nucleus) and the thalamus for a large number of primates and insectivores. Data on the volume of the pons in primates and insectivores comes from Matano et al. (1985). Data on the volume of the cerebellum and the whole brain in *Pan paniscus* and *Pongo pigmaeus* (which was not included in the Stephan et al. data set) come from Semendeferi and Damasio (2000) and measurements of the volume of the neocortex in these species comes from Rilling and Insel (1999). Volumes of the cerebellar nuclei are obtained from Matano and Hirazaki (1997) and volumes of the non-nuclear cerebellum are calculated by subtracting the volumes of the nuclei from whole cerebellum volume. "Rest of the brain" volumes are calculated by subtracting the relevant brain structures from whole brain volumes for the various different calculations. All data is analysed in logarithmic form making them suitable for standard regression (Purvis and Rambaut, 1995).

It is important to consider a number of limitations in this data, particularly in the data from Stephan et al. (1981). Firstly, in accounting for the shrinkage which occurs during fixation of a brain structure, the method used by Stephan et al. assumed that grey and white matter showed uniform changes in size. Work by Kretschmann, Tafesse and Herrmann (1982) has since shown this assumption to be invalid. Secondly, the effects of old age or illness may be reflected in some of the brains measured, as the post-mortem brains were taken either from animals which had been sacrificed, or from those which die of natural causes. Thirdly, once brains have been sliced in a particular plane in order to measure one brain part, it is not possible to re-slice them in order to measure another brain structure more accurately. Fourthly, and

perhaps most importantly for this study, the Stephan et al. data set only includes measurements for three out of the five great ape species. Although data for the two other great apes has been found from other sources, it is possible that there is some discrepancy in the data due to different measuring techniques. Despite these various problems, the data from Stephan et al. is by far the most comprehensive set of its kind and has been used by many researchers since it was first published. Therefore, in the absence of any other data whether more accurate or more comprehensive, the data from Stephan et al. will be used in the current analyses, together with data from Semendeferi and Damasio (2000) and Rilling and Insel (1999) for the other two great apes. The limitations outlined should not, however, be lost sight of.

Data on the ecological variables encountered in Chapter 5 (home range, day journey length and percentage fruit in the diet) are taken from Smuts et al. (1987) and Barton (1999), measures of social group size come from Dunbar (1992), locomotor data comes from Matano and Hirazaki (1997) and Rowe (1996) and measures of fine motor actions come from van Schaik et al. (1999) (Tool use and bimanual asymmetric coordination - BAC), and Gibson (1986) (Extractive foraging). The data on neocortical and adult brain volumes used in this chapter comes from Smuts et al. (1987).

2.4 Comparative Methods

There are two main types of comparative method: those which incorporate a phylogeny and those which do not. As both types will be used in this thesis, the details of each are laid out below.

It has long been appreciated that species are not independent data points and that they should not be treated as such in comparative investigations (Nunn and Barton, 2001). Nevertheless, in the absence of any comprehensive method by which to take account of the phylogenetic relatedness of species, early researchers assumed that species are independent data points (Eisenberg and Wilson, 1978). Some of the first work which attempted to take account of the relatedness of species was carried out by Clutton-Brock and Harvey (1980) who looked for patterns within different taxonomic levels.

However, the first researcher to provide a principled solution to the phylogenetic problem was Felsenstein (1985) who put forward a method of independent comparisons. Thus, phylogenetic methods are a relatively recent phenomenon.

2.4.1 Non-phylogenetic methods

The statistical method most commonly used in non-phylogenetic analyses of size data is the method of least-square regression. It is important to note that least-square regressions are also used in phylogenetic methods. Least-square regression provides a general means by which to look at patterns in the data, whether or not a phylogeny is incorporated in the analysis.

One of the most important uses of least-square regression analyses is in the production of residuals. The residuals are the amount by which a measure differs from the expected value, calculated on the basis of all the measurements included in the analysis. By using residuals rather than absolute volumes in analyses, it is possible to take account of a confounding factor.

In this thesis, least-square regression analyses of species values will primarily be used for initial comparisons in order to identify possible grade shifts between different species. In order to assess the significance of these grade shifts and to look at actual evolutionary relations between brain parts, these simple regressions may not be sufficient (Nunn and Barton, 2001). For this reason, methods which take account of phylogenetic effects will also be employed. These methods are considered in the next section.

2.4.2 Phylogenetic Methods

The logic behind the incorporation of a phylogeny in the analysis is three-fold. Firstly, it enables phylogenetically independent data points to be identified. This means that it is possible to determine whether a particular trait has evolved repeatedly in association with another variable (either an environmental variable or another trait)

from multiple independent origins. It is important to distinguish between this situation and the one in which traits are shared between species as a result of inheritance from their common ancestor. The second reason why a phylogeny is important is that it minimizes the effects of unmeasured or unknown confounding variables that are correlated with phylogeny (Purvis and Webster, 1999; Nunn and Barton, 2001). Finally, information from a phylogeny enables the reconstruction of the changes that have taken place over evolutionary time. As the purpose of the comparative studies in this thesis is to look for correlated evolutionary change, the ability to reconstruct evolutionary change is particularly useful.

It is interesting to note here that there has been some question of how important a phylogeny really is, so much so that tests have been formulated with the specific aim of assessing the need for a phylogeny in particular comparative analyses (Losos, 1999). These tests look at whether specific traits are correlated with phylogeny and if they are, then a phylogenetic method is advised. If they are not, then it is argued that species values can be assumed to be independent and a phylogenetic method is not necessary (Bjorklund, 1997; Abouheif, 1999). This suggestion has received some criticism. Nunn and Barton (2001) for example argued that biological traits are invariably correlated with phylogeny. Furthermore, they argue that rather than relying on the rejection of an alternative hypothesis, this method depends upon the assumption that there is no correlation with phylogeny, that is, it depends upon the acceptance of the null hypothesis. Nunn and Barton claim that this is problematic because the incorrect acceptance of the null hypothesis could lead to seriously flawed results. While further investigation is clearly required here, it seems that at this point in time, the consensus is that most accurate results are obtained in analyses which do incorporate a phylogeny.

Further support for phylogenetic methods comes from recent simulation studies (Purvis et al. 1994; Nunn, 1995). One particular investigation showed that when phylogenetic relatedness is ignored, Type I error rates can be as high as 44%, an enormous value especially when compared to the expected error rate of 5% (Harvey and Rambaut, 1998).

One problem with phylogenetic methods is the limited availability of accurate comprehensive phylogenies. However, even the use of incomplete phylogenies has been shown to provide results that are more statistically valid than non-phylogenetic methods (Purvis et al. 1994). This result indicates that, in line with Nunn and Barton (2001), phylogenetic methods should be used in investigations of evolutionary change. Phylogenies will, wherever possible, be used in the studies that follow. Non-phylogenetic methods will also be used, but these will primarily be preliminary investigations to look for general differences between taxonomic groups. The phylogeny to be used comes from Purvis (1995).

Having considered the importance of including a phylogeny, it is now important to look at the details of the methods themselves. The phylogenetic method which will be used in this thesis is the method of independent contrasts. This method, which is detailed below, can be used to analyse both continuous data and a mixture of continuous and discrete data.

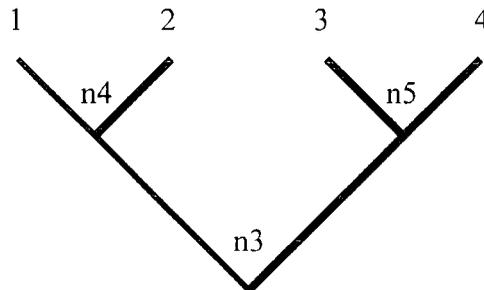
2.4.2.1 Independent contrasts

The method of independent contrasts works by identifying cases of correlated evolution (for example of particular brain structures) amongst multiple independent evolutionary events, based on the phylogenetic relatedness of the taxa.

A contrast is the difference between species or between reconstructed nodes higher in the phylogeny for the particular trait in question. These contrasts should be independent, allowing one to examine evolutionary associations between different traits by correlating these contrasts with one another. The traits of interest in this thesis are the sizes of different brain structures and it is assumed that different lineages can, independently, evolve similar traits as a result of similar selection pressures (Harvey and Pagel, 1991).

The logic of independent contrasts is best illustrated in diagrammatic form and can be seen in Figure 2.1 below.

Figure 2.1: Branching phylogeny which illustrates the logic of independent contrasts analysis



The branching phylogeny contains three sets of independent differences between pairs (species 1 versus 2, species 3 versus 4 and node 4 (n4) versus node 5 (n5)).

In this example, species 1 + 2 are more closely related to each other, hence likely to be more similar than they are to 3 + 4 (and vice versa). In that sense, species within clades are not independent of one another. However, the differences between pairs of species at each node in the phylogeny should be independent. These differences are referred to as “contrasts”. The reason why the contrasts are independent of one another is that they only reflect changes which have come about since the two species split from their common ancestor. This is best demonstrated by focusing on two particular species. In the diagram above, the contrast at n4 only reflects changes which have occurred since species 1 and 2 split from their common ancestor. Any similarities they may share are not considered here. This eliminates the possibility of the phylogenetic relation between the two species biasing the results.

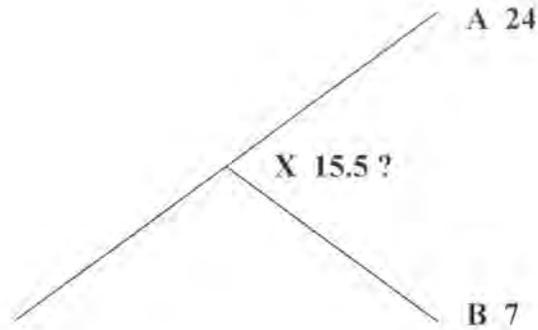
In summary, by splitting the variation among the species (1,2,3,4) into three separate evolutionary events, the comparisons at the three nodes in this phylogeny can account for all of the variation between the species. Thus, independent contrast analyses work by splitting variation between species into smaller "chunks" which can then be used to look at the relation between species.

One of the most widely used applications which employs the method of independent contrasts, and which will be used throughout this thesis, is the C.A.I.C. (Comparative analysis by independent contrasts) computer package (Purvis and Rambaut, 1995). This package is based on Felsenstein's (1985) method of independent comparisons (outlined above). Within C.A.I.C. there are two different methods of analysis, one for continuous data and one for a mixture of continuous and discrete data. The particular algorithms employed for each of these are outlined in the relevant chapters together with details on the statistical methods used to assess significance levels.

One of the advantages of C.A.I.C. is that it can take account of branch lengths, that is the relative amount of evolutionary change thought to have taken place. It is assumed that, the longer the branch, the greater the amount of evolutionary change. The incorporation of branch lengths overcomes problems of heteroscedasticity by standardising the contrasts. The standardisation method is based on a Brownian motion model of evolution where evolutionary change at each node is assumed to be independent of any previous changes which have occurred (Felsenstein, 1985, 1988). This method can control for increased changes on longer branches because the variance of the independent evolutionary changes is proportional to the branch length. Recently, however, there has been some controversy over the assumption of Brownian motion in that it has been argued to be an oversimplification (Harvey and Rambaut, 2000). Nevertheless, a simulation study showed that independent contrasts produce much more valid results than non-phylogenetic analyses when data was used which evolved under other models but was analysed under Brownian motion (Diaz-Uriarte and Garland, 1996).

One problem with the independent contrasts approach is that actual ancestral trait values are not known and are simply estimated on the basis of existing values. This is illustrated in Figure 2.2 below.

Figure 2.2: Branching phylogeny to illustrate limitations of the C.A.I.C. computer package.



In this phylogeny, the value of the ancestral trait X is calculated as a mean of the trait values of A and B. The validity of this method is questionable as there is no reason why A and B should have shown the same level of change in a particular trait after splitting from their common ancestor. After the split, A and B will most likely have faced different external selection pressures and so it is very unlikely that they would have shown the same amount of change in a particular trait. It is very possible for one species to show no change in a particular trait over time. For example, it is possible that the trait value at X is 7. In this case, A has shown a large increase in that trait whereas B has shown no change.

Having understood some of the limitations of this method it has to be said that it is very difficult to see how these problems could be overcome. Without any direct evidence of the values of ancestral traits, calculating averages may be the best compromise at this point in time. Despite these limitations, when compared to other methods, independent contrasts have been found to provide accurate patterns of known evolutionary change and while the actual values calculated for the different nodes may not be highly accurate, the patterns produced by this analysis appear to be

good. Furthermore, simulation studies tend to support the robustness of C.A.I.C. in the face of violations (Grafen, 1989; Purvis et al., 1994). It seems that at this point in time, C.A.I.C. is the most reliable method to use to look at evolutionary change and it will therefore be used in the analyses that follow.

CHAPTER 3

Investigating systemic evolution

3.1 Introduction

Previous studies of primate brain evolution have consistently focused on the neocortex as the principal area of change. Recent work, however, has indicated that the cerebellum may have shown correlated evolution with the neocortex (see Section 1.2.3). This would suggest that the neocortex may not be the only area of the brain that has expanded over primate evolution and that it may not be the only region that sets primates apart from other animals. If the cerebellum is found to have shown significant changes in size together with the neocortex, this would have major implications for theories of primate brain evolution. Previous theories proposed to explain the expansion of the neocortex in particular would either have to be adapted in order to encompass the evolution of the cerebellum, or be discarded.

This chapter further investigates the evolution of the cerebellum in order to determine the extent of its correlated evolution with the neocortex. It is important, in this respect, to remember that both the neocortex and the cerebellum form part of the same functional system (see Figure 3.1). Also note that the definition of functional systems in neuroscience is an unresolved issue, see for example Swanson and Petrovich (1998) who question the term amygdala). The mosaic theory of brain evolution outlined in Chapter 1 maintains that individual systems are able to change in size independently of changes in the rest of the brain, i.e. the brain does not necessarily evolve strictly as a whole. If this theory is correct, then the cerebellum and neocortex, forming part of the same system, would be predicted to have shown correlated evolution.

In order to investigate the evolution of the cerebellum and, in so doing, assess the validity of mosaic evolution, it is necessary to look at the other brain structures that

form part of the cerebellar systems. As outlined in Chapter 2, the cerebellum receives input from the neocortex (via the pons), the vestibular system (lateral vestibular nucleus) and the spinal cord and its major outputs go to the neocortex (via the thalamus) and the vestibular nuclei. These connections are shown in Figure 3.1 below.

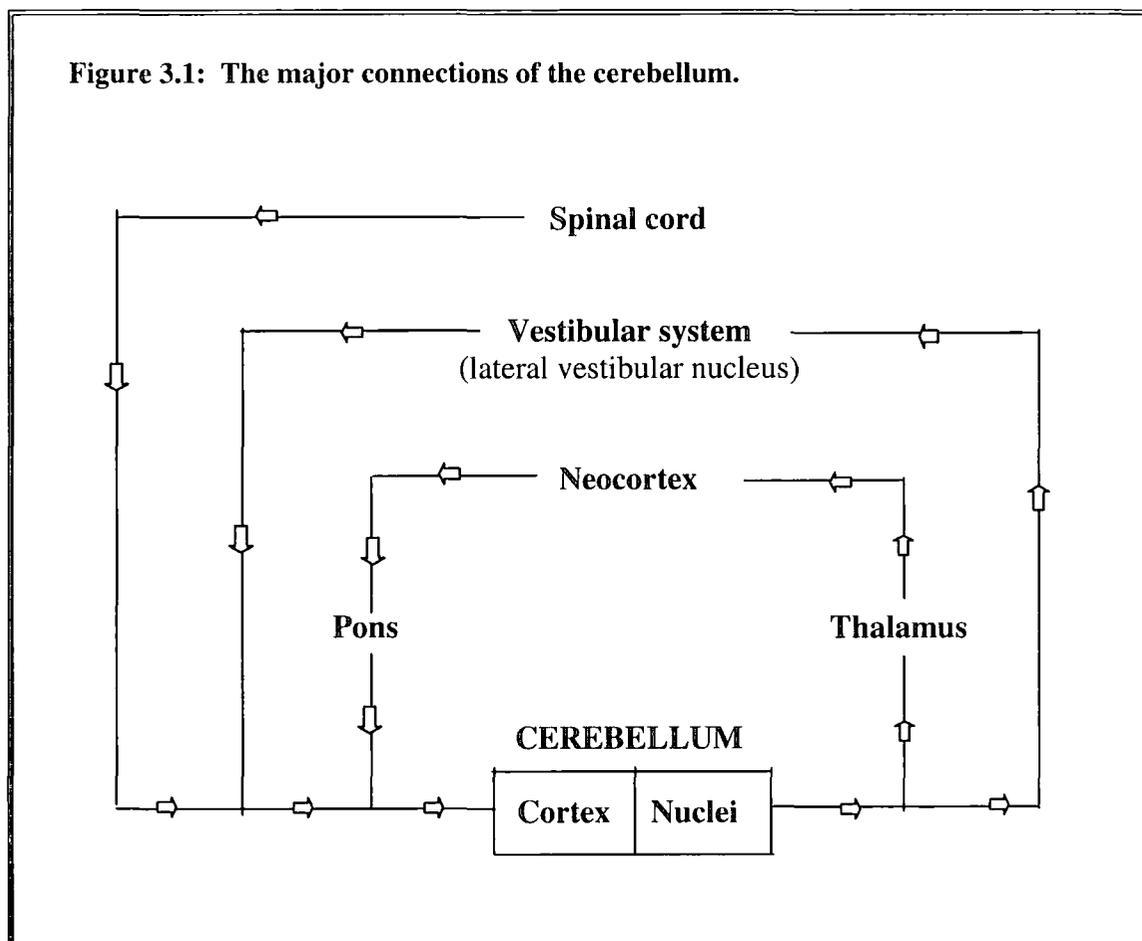


Figure 3.1 depicts two systems: a cerebellar-vestibular system and a cerebellar-neocortical system. The evolution of each of these systems will be investigated in this chapter by looking at correlated changes of the cerebellum and the individual brain structures that make up each system. The investigation can be split into the following three parts:

(i) The neocortex and the cerebellum

The first part will look at the evolution of the cerebellum and the neocortex in more detail to determine which particular areas of the cerebellum have shown correlated evolutionary changes with the neocortex. Data is currently available for the volume of the cerebellum as a whole and for the volume of the cerebellar nuclei, and these are used to calculate the volume of the non-nuclear cerebellum (which includes the cerebellar cortex, the major input area of the cerebellum). In line with the association already found between the whole cerebellum and the neocortex, it is predicted that positive correlations with the neocortex will be found for the non-nuclear cerebellum (which receives information from the neocortex) and for the cerebellar nuclei (which send information out to the neocortex).

(ii) The pons and the thalamus

In the second part, the pons and the thalamus will also be factored into the calculations. This is important because there are no direct neural connections between the neocortex and the cerebellum. Projections from the neocortex to the cerebellum pass through the pons, and projections from the cerebellum back to the neocortex pass through the thalamus (the ventrolateral nucleus in particular). By looking at evolutionary changes in these areas it will be possible to determine whether they have shown correlated evolution with the neocortex and cerebellum. If the results show correlated evolution of the neocortex, the cerebellum, the pons and the thalamus then, in line with the concept of mosaic evolution, it would seem plausible that the neocortex and cerebellum evolved together and in fact that the whole of the cerebellar-neocortical system evolved as one. If, on the other hand, no evolutionary associations are found with the pons and the thalamus, then it would seem that the cerebellum and neocortex did not evolve together, but coincidentally showed similar volumetric changes over evolutionary time. This would not support the idea of mosaic evolution.

(iii) The vestibular system

The final part will look at the other projections to and from the cerebellum. As can be seen in Figure 3.1, in addition to the neocortical circuit, the cerebellum also receives information from, and sends information to, the vestibular system. It is the lateral vestibular nucleus in particular that has connections to the cerebellum. This nucleus projects to the flocculonodular lobe of the cerebellum. Outputs back to the lateral vestibular nucleus come from the middle cerebellar nucleus (MCN). Unfortunately data are currently lacking on the volumes of the ventrolateral nucleus of the thalamus and of the flocculonodular lobe of the cerebellum. The volume of the whole thalamus and the volume of the non-nuclear cerebellum, respectively, will therefore be used instead.

3.2 Materials and methods

3.2.1 Data

The measurements of the volumes of the various brain structures included in the current analyses come from Stephan et al. (1981), Semendeferi and Damasio (2000), Rilling and Insel (1999), and Matano and Hirazaki (1997). Please see Section 2.3 for more detailed information about the data.

3.2.2 Method

The method used in this chapter is the method of independent contrasts, which enables the assessment of evolutionary relations between different brain structures. Details of this method and the particular program to be employed here (the computer package C.A.I.C.) were outlined in Chapter 2. Multiple regression analysis on the results of C.A.I.C. will reveal whether the two structures show correlated evolution. It should be reiterated that the focus of this investigation is on the relation between the cerebellum and neocortex and their relation to the rest of the brain. For this reason, in the analyses that follow, both neocortex and cerebellum volume will be excluded in calculations of the volume of the 'rest of the brain'. This is to avoid any possibility of confounding the results due to possible co-evolution of these two structures.

3.3 Results

The tables and graphs below report the results of independent contrast analyses of the cerebellum and its parts in relation to the neocortex and the other structures to which it has functional connections. In each case the significance level is set at $p < 0.05$. The graphs are provided only for those correlations which are significant.

(i) The neocortex and the cerebellum

Relative contrasts for the neocortex (that is the residuals for the regression of that structure on the brain-(neocortex+cerebellum)) were regressed on relative contrasts of each of the following structures: the whole cerebellum, the non-nuclear cerebellum and the cerebellar nuclei.

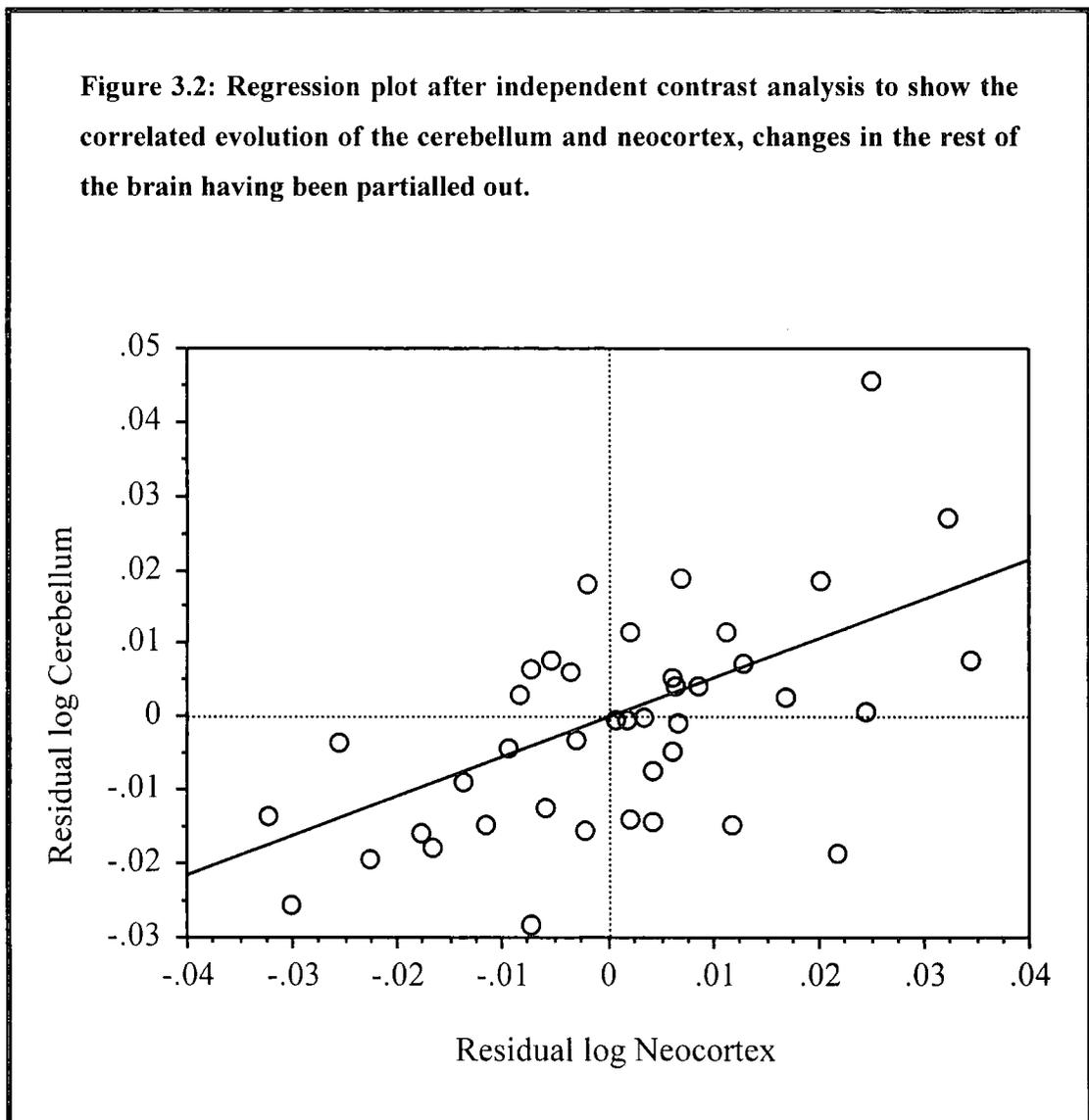
Table A: Correlated volumetric evolution of the neocortex and cerebellar areas as revealed by multiple regressions of independent contrasts.

	Whole Cerebellum		Non-nuclear cerebellum		Cerebellar nuclei	
Neocortex	p	<0.0001	p	0.0003	p	0.0035
	f	18.997	f	16.045	f	9.768
	r²	0.322	r²	0.308	r²	0.213
	d.f.	1, 37	d.f.	1, 37	d.f.	1, 37

P values, f values, regression coefficients (r^2) and degrees of freedom (d.f.) are given for each correlation. Significant f values indicate that the two structures in question have shown highly correlated change over evolution after the effects of evolutionary change in the rest of the brain has been removed.

Figures 3.2-3.4 below shows the significant evolutionary relations for this data set. All three of the comparisons between the neocortex and the cerebellum were found to be significant. The most significant relation was between the neocortex and the whole cerebellum ($p < 0.0001$), the least significant relation was between the neocortex and the cerebellar nuclei ($p = 0.0035$).

a) The whole cerebellum and the neocortex



This figure clearly shows that the cerebellum and neocortex have shown highly correlated volumetric changes over evolutionary time ($r^2 = 0.322$).

b) The non-nuclear cerebellum and the neocortex

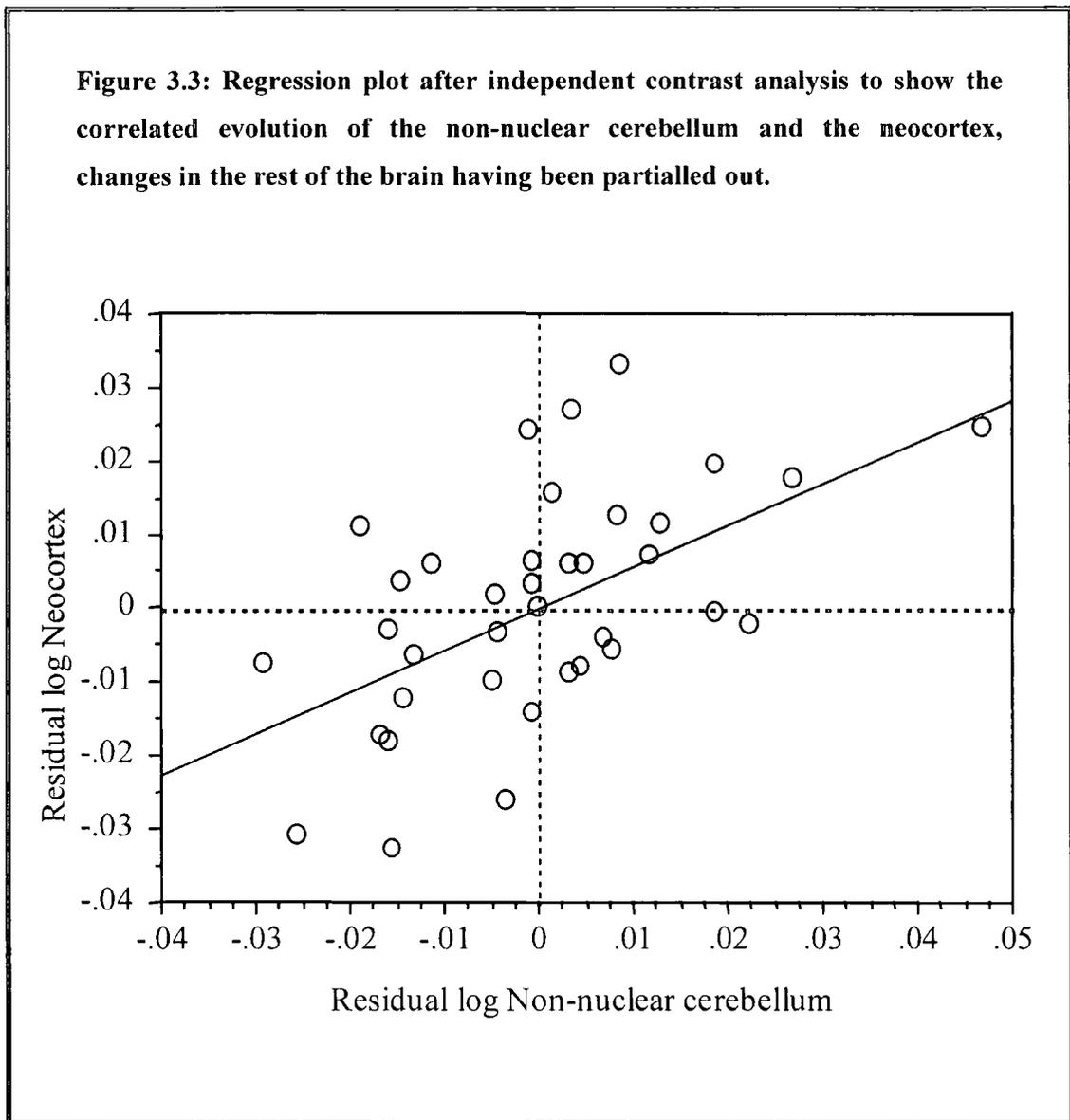


Figure 3.3 shows there to be a strong correlation between the evolutionary changes in the neocortex and in the non-nuclear cerebellum ($r^2 = 0.308$).

c) The cerebellar nuclei and the neocortex

Figure 3.4: Regression plot after independent contrast analysis to show the correlated evolution of the cerebellar nuclei and the neocortex, changes in the rest of the brain having been partialled out.

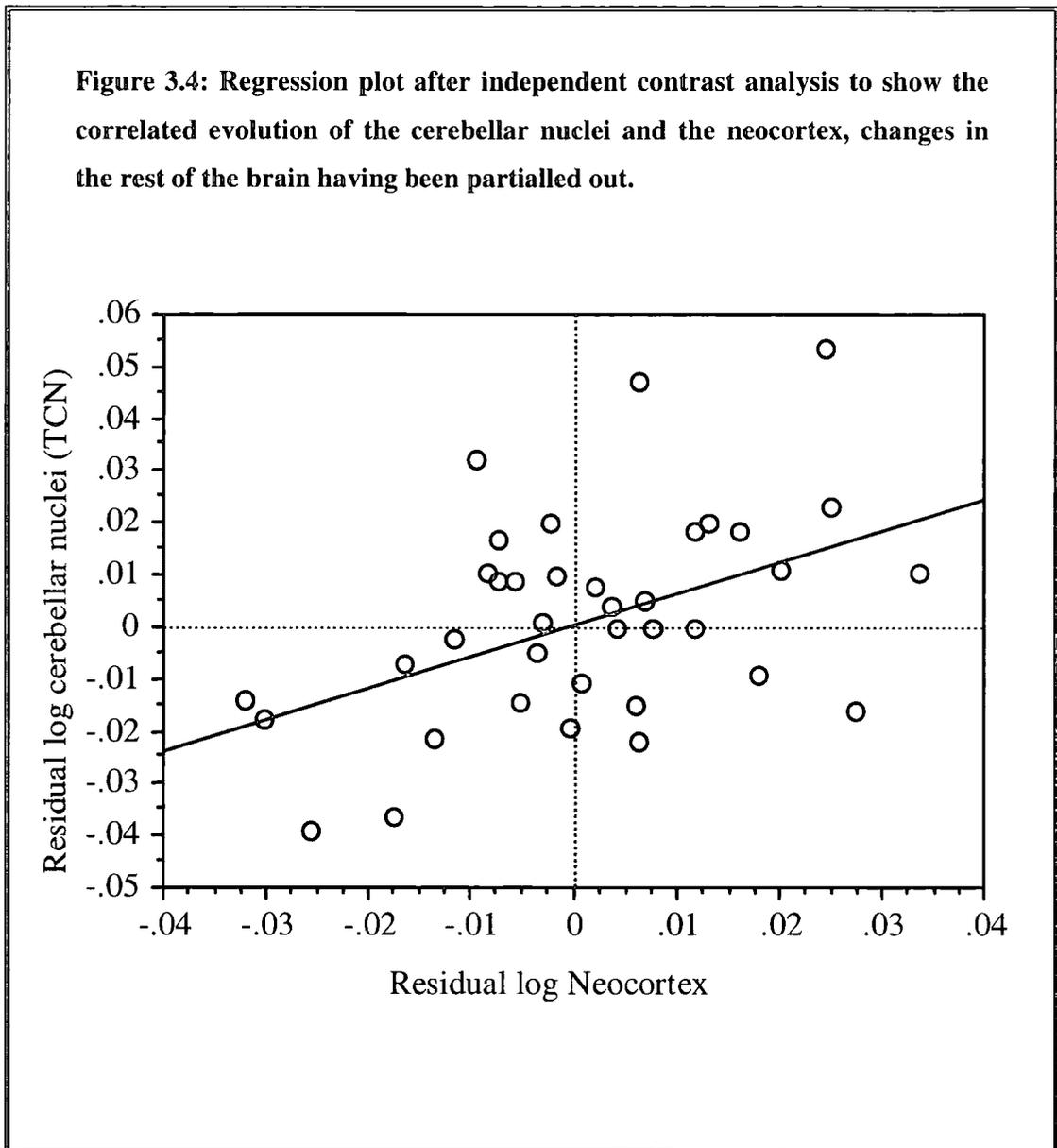


Figure 3.4 shows that the neocortex also shows highly correlated evolution ($r^2 = 0.213$, $p = 0.0035$) with the cerebellar nuclei, although this correlation is not as significant as that between the neocortex and the whole cerebellum ($r^2 = 0.322$, $p < 0.0001$) or between the neocortex and the non-nuclear cerebellum ($r^2 = 0.308$, $p = 0.0003$). The amount of variance explained is marginally lower with the non-nuclear cerebellum.

(ii) The pons and the thalamus

The pons and the thalamus both contain nuclei and fibres that are part of the cerebellar-neocortical system. It is predicted that, in line with mosaic evolution, the pons and thalamus will be found to show correlated evolution with the neocortex and cerebellum, and particularly strong correlations with the cerebellar areas (nuclei or non-nuclear regions) to which they are connected.

Changes in the volume of the pons relative to the brain – (neocortex + cerebellum + pons) were regressed on changes in the volume of each of the following structures relative to the volume of the brain – (neocortex + cerebellum + pons): the neocortex, the whole cerebellum, the non-nuclear cerebellum and the cerebellar nuclei (see table B).

Changes in the volume of the thalamus relative to the brain – (neocortex + cerebellum + thalamus) were regressed on changes in the volume of each of the following structures relative to the volume of the brain – (neocortex + cerebellum + thalamus): the neocortex, the whole cerebellum, the non-nuclear cerebellum and the cerebellar nuclei (see table B).

Table B: Correlated volumetric evolution among brain structures involved in the cerebellar-neocortical system as revealed by multiple regressions on independent contrasts.

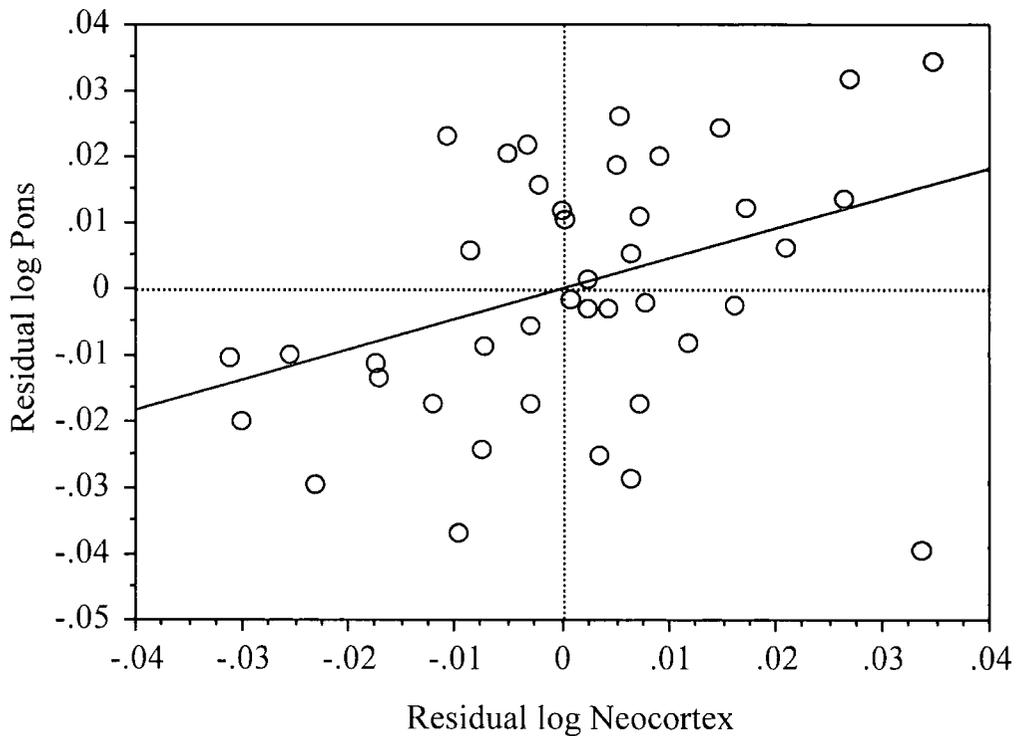
	Neocortex		Whole Cerebellum		Non-nuclear cerebellum		Cerebellar nuclei	
Pons	p	0.0152	p	0.0049	p	0.0035	p	0.1518
	f	6.436	f	8.867	f	9.786	f	2.144
	r²	0.139	r²	0.181	r²	0.214	r²	0.056
	d.f.	1, 41	d.f.	1, 41	d.f.	1, 37	d.f.	1, 37
Thalamus	p	0.3413	p	0.7455	p	0.8498	p	0.0253
	f	0.946	f	0.108	f	0.037	f	5.846
	r²	0.041	r²	0.005	r²	0.002	r²	0.226
	d.f.	1, 23	d.f.	1, 23	d.f.	1, 21	d.f.	1, 21

P values, f values, regression coefficients (r^2) and degrees of freedom (d.f.) are given for each correlation. Significant f values indicate that the two structures in question have shown highly correlated change over evolution after the effects of evolutionary change in the rest of the brain has been removed.

Figures 3.5 – 3.8 below show the significant evolutionary relations between a) the neocortex and the pons, b) the whole of the cerebellum and the pons; c) the non-nuclear cerebellum and the pons; d) the cerebellar nuclei and the thalamus.

a) The neocortex and the pons

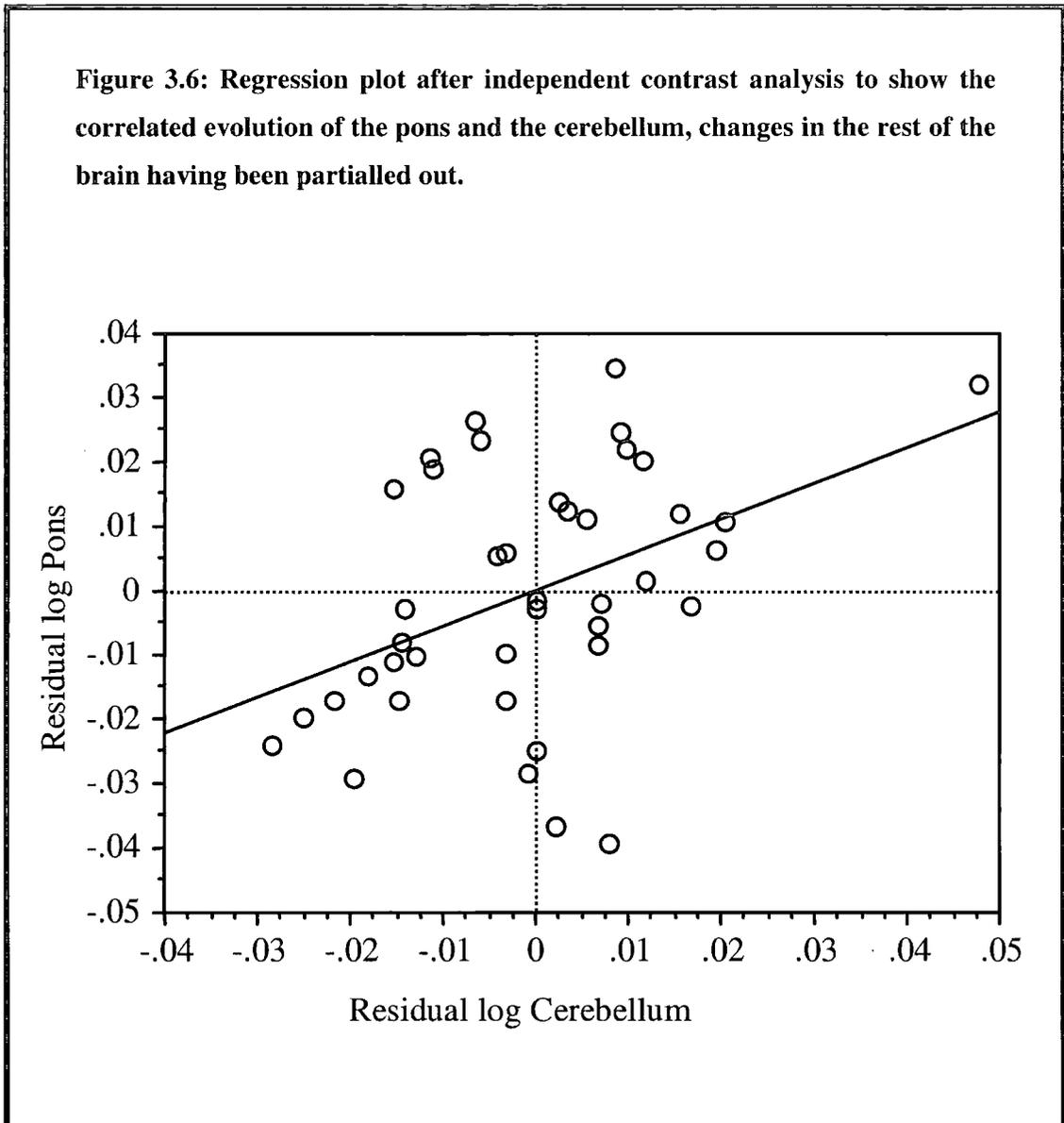
Figure 3.5: Regression plot after independent contrast analysis to show the correlated evolution of the pons and the neocortex, changes in the rest of the brain having been partialled out.



This Figure shows that the pons and the neocortex have shown highly correlated volumetric changes over evolutionary time ($r^2 = 0.139$, $p = 0.0152$).

b) The whole cerebellum and the pons

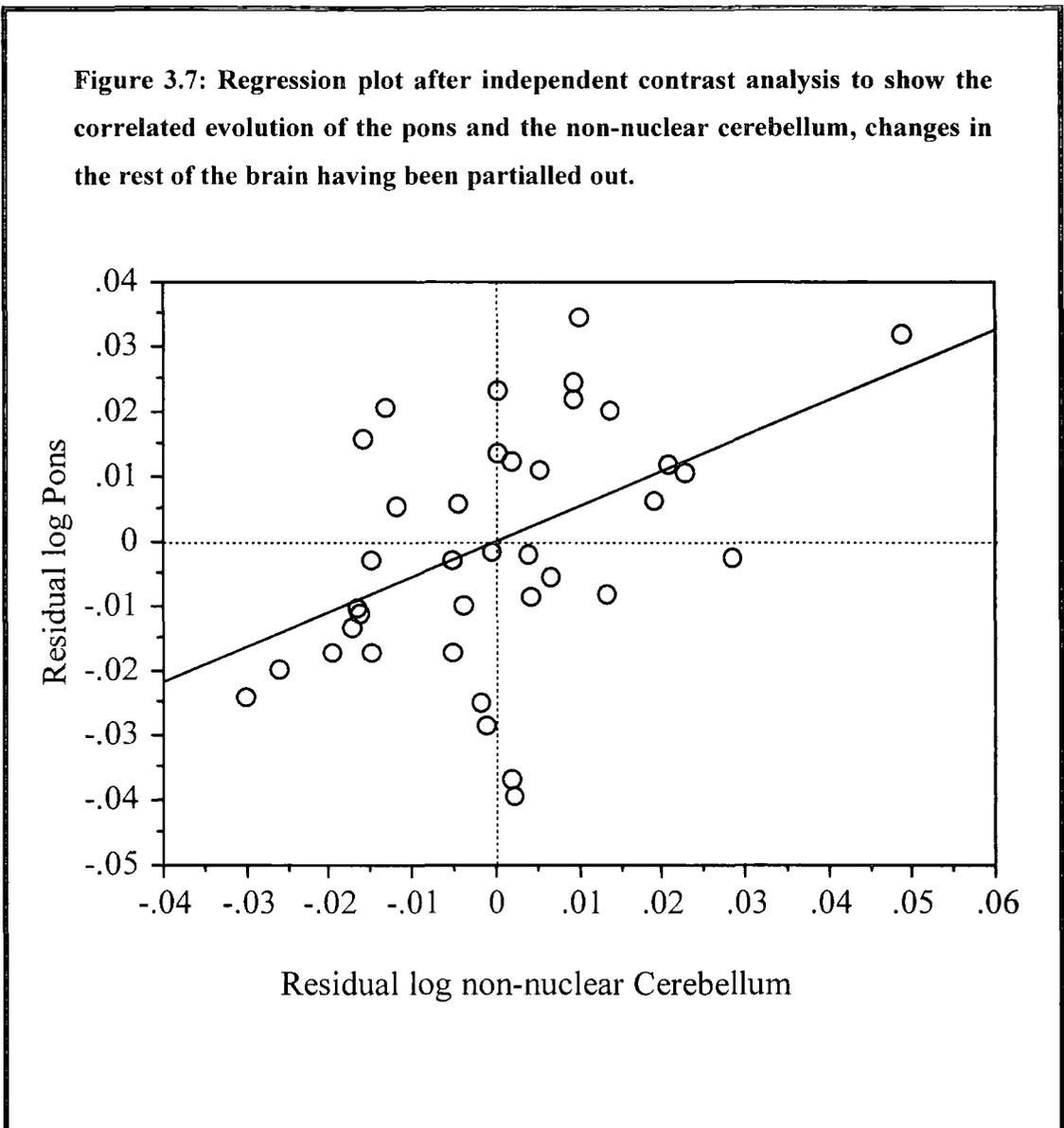
Figure 3.6: Regression plot after independent contrast analysis to show the correlated evolution of the pons and the cerebellum, changes in the rest of the brain having been partialled out.



The correlation between the cerebellum and the pons is significant ($r^2 = 0.181$, $p = 0.0049$). It is more significant than the correlations between the neocortex and the pons ($r^2 = 0.139$, $p = 0.0152$). The amount of variance explained is marginally lower with the pons.

c) The non-nuclear cerebellum and the pons

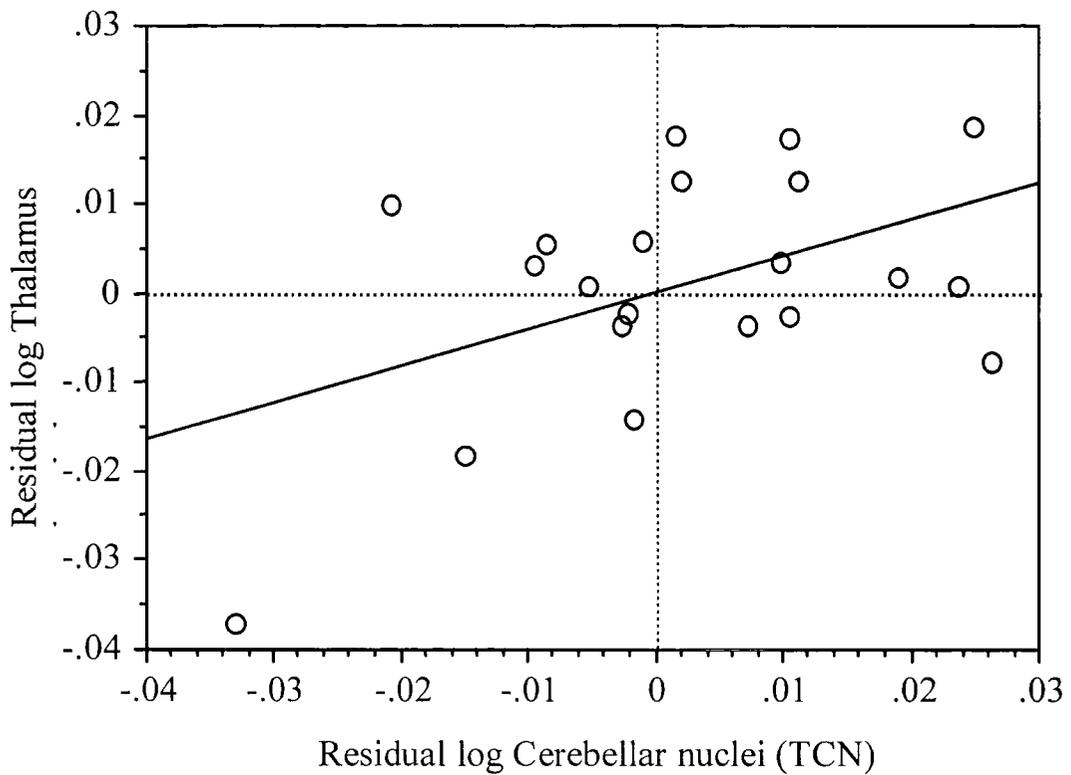
Figure 3.7: Regression plot after independent contrast analysis to show the correlated evolution of the pons and the non-nuclear cerebellum, changes in the rest of the brain having been partialled out.



The strongest relation in the cerebellar-neocortical system (excluding the correlations between the neocortex and cerebellum seen in part i) is between the non-nuclear cerebellum and the pons. This is interesting because the non-nuclear cerebellum is precisely the area to which the pons projects.

d) The cerebellar nuclei and the thalamus

Figure 3.8: Regression plot after independent contrast analysis to show the correlated evolution of the thalamus and the cerebellar nuclei, changes in the rest of the brain having been partialled out.



The thalamus and cerebellar nuclei show correlated evolution ($r^2 = 0.226$, $p = 0.0253$). These nuclei are the only structures within the neocortex-cerebellum system with which the thalamus has shown correlated evolution which accords with the projections of the thalamus which pass to the cerebellar nuclei.

(iii) The vestibular system

In addition to the neocortex, the other major connection of the cerebellum is to the vestibular system, the lateral vestibular nucleus in particular. This nucleus receives projections from the Middle Cerebellar Nucleus and the evolutionary changes in these areas are included in the analyses.

Changes in the volume of the vestibular system relative to the volume of the brain – (neocortex + cerebellum + vestibular system) were regressed on changes in the volume of each of the following structures relative to the volume of the brain – (neocortex + cerebellum + vestibular system): the whole cerebellum, the non-nuclear cerebellum and the cerebellar nuclei (see Table C).

Changes in the volume of the lateral vestibular nucleus relative to the volume of the brain – (neocortex + cerebellum + vestibular system) were regressed on changes in the volume of each of the following structures relative to the volume of the brain – (neocortex + cerebellum + vestibular system): the whole cerebellum, the non-nuclear cerebellum, the cerebellar nuclei and the middle cerebellar nucleus (MCN) (See Table C).

Table C: Correlated volumetric evolution among brain structures involved in the cerebellum-vestibular system as revealed by multiple regressions on independent contrasts.

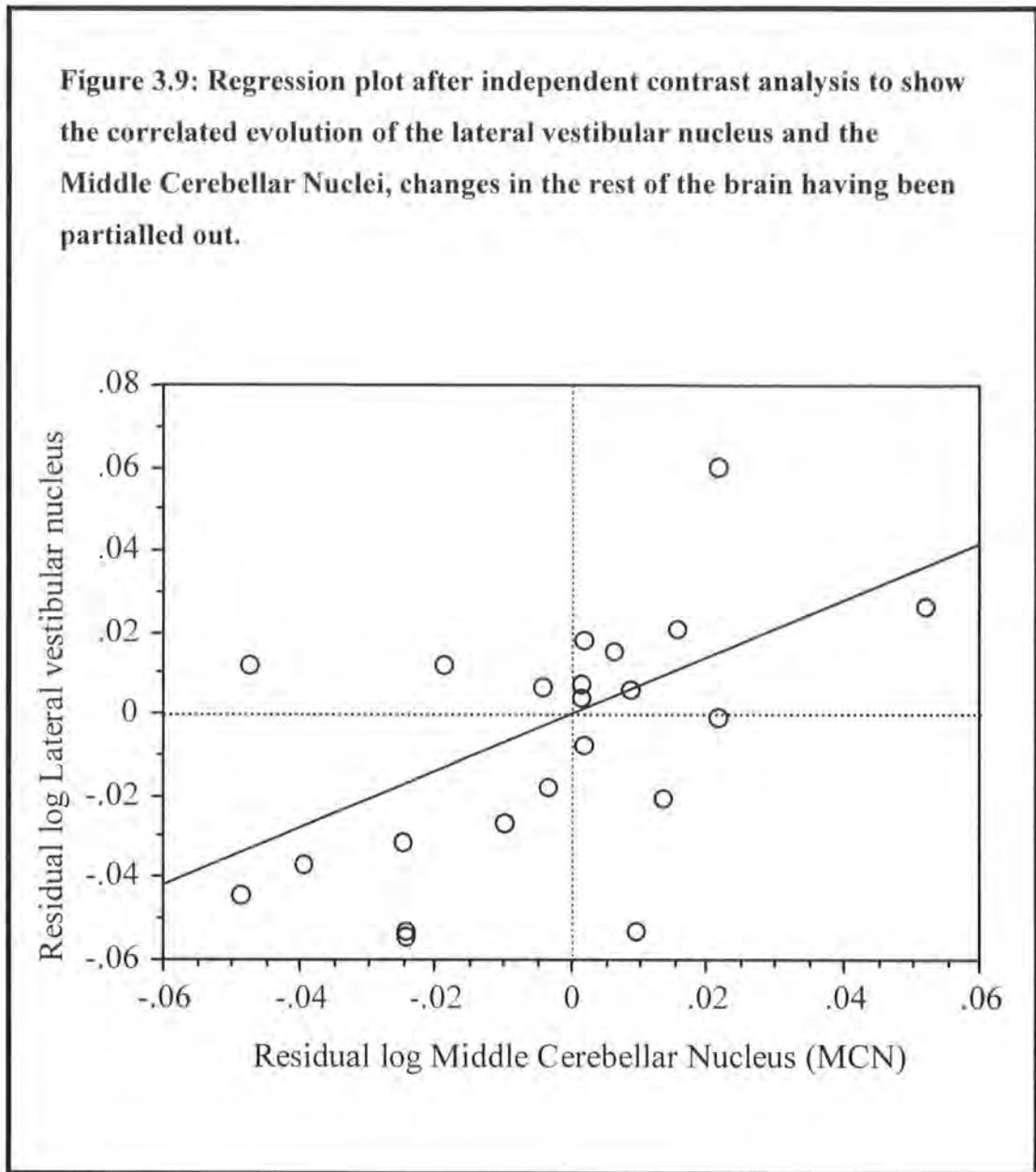
	Whole Cerebellum		Non-nuclear cerebellum		Cerebellar nuclei		MCN	
	p		p		p		p	
Vestibular System	f	0.3507	f	0.1497	f	0.2035	f	-
	r ²	0.908	r ²	2.245	r ²	1.723	r ²	-
	d.f.	0.038	d.f.	0.101	d.f.	0.076	d.f.	-
		24		21		22		-
Lateral vestibular nucleus	p	0.8844	p	0.2906	p	0.9247	p	0.0061
	f	0.022	f	1.175	f	0.009	f	9.310
	r ²	0.001	r ²	0.053	r ²	0.0004	r ²	0.307
	d.f.	24	d.f.	22	d.f.	22	d.f.	22

P values, f values, regression coefficients (r²) and degrees of freedom (d.f.) are given for each correlation. Significant f values indicate that the two structures in question have shown highly correlated change over evolution after the effects of evolutionary change in the rest of the brain has been removed.

The only significant evolutionary relation for the vestibular system and the cerebellum is the relation between the Middle Cerebellar Nucleus (MCN) and the lateral vestibular nucleus. These are precisely the areas which have strong connections with one another. This relation is shown in Figure 3.9 below.

The middle cerebellar nucleus (MCN) and the lateral vestibular nucleus

Figure 3.9: Regression plot after independent contrast analysis to show the correlated evolution of the lateral vestibular nucleus and the Middle Cerebellar Nuclei, changes in the rest of the brain having been partialled out.



Taken together, the results presented here show that the cerebellum has undergone correlated evolution with the brain structures to which it is most intimately connected, providing evidence that the different parts of the cerebellar system have evolved together. Furthermore, this is true at a fine level of detail: specific areas which are connected to one another have the strongest correlations.

3.4 Discussion

The results provide strong support for the theory of mosaic evolution as structures involved in the same functional systems have shown highly correlated evolution independently of change in the rest of the brain. The cerebellum is involved in two major functional systems, and almost all the component parts in both systems have shown highly correlated evolutionary size changes. What is particularly interesting is that this holds true at a very detailed level of analysis. For the cerebellar-neocortical system, it was found that the input (non-nuclear) areas of the cerebellum have shown the most significant correlation with the pons and the neocortex – precisely the areas that project to the non-nuclear cerebellum. The output areas (cerebellar nuclei) were found to have shown the most significant correlation with the thalamus, the area to which they project the output of the cerebellum. For the cerebellar-vestibular system, correlated evolution was found at the level of individual cerebellar nuclei. In these analyses, the component correlating the most strongly with the lateral vestibular nucleus was the MCN, which is the nucleus known to project to the vestibular system, and to the lateral vestibular nucleus in particular. These findings provide very strong support for the mosaic theory: functionally connected brain structures appear to show especially strong correlated evolution.

It is important to note that, although it has strong connections with the neocortex, one structure, the thalamus, did not show significantly correlated evolution with this area. This may simply be due to the fact that there was a reduced sample size for which data on thalamus volume was available, or that data was not available for the particular area of the thalamus which is involved in the cerebellar-neocortical system (the ventrolateral thalamic nucleus) and that whole thalamus volume had to be used instead. A further possible explanation for this anomaly is that the thalamus is involved in a number of other brain systems and, therefore, is also affected by changes in their size. It is plausible that, over evolutionary time, there were changes in the connections in one of the other systems and that these were stronger than the changes in the cerebellar-neocortical system. This would mean that, overall, the correlated evolution between the thalamus and the neocortex would not be significant. Preliminary support for this possibility comes from the finding that the

volume of the diencephalon as a whole does correlate with neocortex volume in a larger data set (Barton and Harvey, 2000).

Relating these results to previous work, strong support is provided for the finding that the cerebellum and neocortex have shown correlated evolution (Barton and Harvey, 2000 (note that this finding is disputed by Wang et al. on the basis that the cerebellum is a relatively constant proportion of total brain volume while the neocortex proportion varies much more extensively). Furthermore, it is demonstrated that it is not just these structures which have shown similar changes over evolutionary time. The fact that the areas to which the cerebellum is connected (the pons and the thalamus) also showed correlated evolution with both the cerebellum and the neocortex (although less so for the thalamus) suggests that it might be the whole of the cerebellar-neocortical system that has shown significant changes over primate evolution. This means that rather than simply finding an explanation for why the neocortex is so large in primates, researchers should perhaps also focus their attention on why this cerebellar-neocortical system as a whole is so large. One area of enquiry would be comparisons between the relative sizes of components of the cerebellar-neocortical system in primates and insectivores. If all the systemic components were found to be significantly different in size in primates, then it would be likely that the whole of the cerebellar-neocortical system has shown significant evolutionary size changes in primates, compared to other mammals. If, however, it is only the neocortex and cerebellum that have changed in size in primates then there may be another story to tell. Unfortunately, it is not possible to investigate the relative size of the whole of the cerebellar-neocortical system in primates here because measures of the pons and the thalamus in insectivores are missing. This important piece of research will have to wait until such measures are available. It is, however, possible to look at the relative size of the cerebellum and the neocortex in primates and insectivores and this will be considered in the next chapter.

Having found evidence that the cerebellar-neocortical and cerebellar-vestibular systems seem to have evolved in their entirety, it will be instructive to consider why it is that structures evolve together as systems, and hence why areas connected to the cerebellum might be affected by changes in the size of this particular brain structure.

The most basic explanation for the correlated evolution of systems is that changes in the size of any brain structure will be associated with changes in the projections of those structures. This point was well documented by Matano and Hirazaki (1997) when they explained what happens to neural connections as the cerebellar nuclei change in size. They claim that a decrease in the size of a nucleus reflects either a decrease in the number of neurons that it contains, or a decrease in the size of the arborization of dendrites and thus a decrease in the number of synaptic terminals. Therefore, a decrease in the size of one area might indicate that there are simply not enough neurons for the number of synaptic connections that existed before, or that the level of dendritic arborization is not high enough to support the same level of connectivity. Either way, a decrease in the size of a cerebellar nucleus will result in a decrease in the connections of that nucleus. Conversely, an increase in size would either reflect an increase in the number of neurons, or an increase in the number of synaptic terminals available for forming new connections, thus increasing the number of projections. This clearly shows that changes in the size of a structure affect the connections of that structure and consequently also the areas to which it is connected.

The events which Matano and Hirazaki associated with changes in the size of particular nuclei can also be applied to the cerebellum as a whole. A change in the size of this structure will result in changes in the volume of information that it is able to receive or send out. If a species is observed to have an increase in cerebellum size, then this would indicate that there is an increase in the number of neurons and opportunities for synaptic connections in the cerebellum of this species. It is likely that this means that the cerebellum can handle more information and so can be more efficient. Conversely, a decrease in cerebellum size would indicate a decrease in the efficiency of the cerebellum due to fewer neurons and a lower level of dendritic arborization. This rationale can also be applied to the neocortex and in fact most other brain structures, as the neuronal make-up shows little variation across brain structures.

Keeping in mind this explanation for why connected structures might show correlated size changes, it will be argued here that the most significant size changes are those of the neocortex and the cerebellum. The main reason why the pons and the thalamus showed correlated evolution is likely to be that there were changes in the connections

to these areas, that is there were changes in the size of the cerebellum and the neocortex and consequently changes in their connections, which pass through the thalamus and pons.

It seems likely that the changes in size of the primate cerebellar-neocortical system over evolution were in fact increases in size as it is already known that one area, the neocortex, certainly did expand in primates. This prediction will be tested in the next chapter where the relative size of the cerebellum and its parts (nuclear and non-nuclear) in primates and insectivores will be investigated. In addition, the aim of Chapter 4 is to determine whether the cerebellum has changed in some primate species more than in others. If this should prove to be the case then it might shed some light on why the cerebellum showed such significant size changes over evolution. By comparing various behavioural attributes of species with and without relatively large cerebella, it should be possible to gain an idea of what sort of pressures selected for an enlarged cerebellum.

Summary

To summarize, the aim of this chapter was to investigate the possibility that the cerebellum and neocortex showed correlated changes in size over evolution. The results provided strong support for this hypothesis and went further to show that the whole of the cerebellar-neocortical system showed correlated evolutionary size changes.

CHAPTER 4

Investigating the expansion of the cerebellum

4.1 Introduction

In the previous chapter, it was demonstrated that the primate cerebellum has shown highly correlated evolutionary changes with the neocortex, and with the other brain structures to which it is most strongly connected. This indicates that in addition to the neocortex, there might have been important changes in the cerebellum over primate brain evolution. The questions that must now be answered, and that will be addressed in this chapter, are how cerebellum size varies within the primate order, and what might explain such variation.

Preliminary investigations into the evolution of the cerebellum have suggested that among primates, a distinction can be drawn between apes and monkeys in relative cerebellum size: apes are argued to have relatively larger cerebella than monkeys (Rilling and Insel, 1998 - see Section 1.3.3). In this chapter different primate taxa will be compared in order to test this finding, to determine whether there are any other significant differences between different primate sub-groups, and if so to determine the nature of such differences.

The chapter is split into two main sections. The first section (4.3) looks at the relative size of the cerebellum both in primates as a group (4.3.1) and among primates in different sub-groups (4.3.2). It is predicted that, as the primate neocortex is unusually large and as the cerebellum showed correlated evolution with the neocortex, that the cerebellum will also be found to be significantly large in primates compared to insectivores. There are no *a priori* reasons for predicting that any primate group

would have a significantly larger cerebellum than any other group and this part will therefore be approached as a novel investigation without predictions being made.

The second section (4.5) will take the findings of Section 4.3 further by investigating precisely which areas of the cerebellum showed significant changes in size. As was explained in Chapter 1, a brain structure as heterogeneous as the cerebellum may be involved in numerous different functional systems. It is, therefore, necessary to look at changes in the particular sub-structures that are involved in the systems being investigated. Was it the whole cerebellum or particular regions within the cerebellum that expanded? The particular regions that will be investigated are the cerebellar nuclei and the non-nuclear cerebellum as these are the only regions for which data are currently available. On the basis of the claim that the size of the longitudinal zones² of the cerebellum is reflected in the size of the cerebellar nuclei (Matano and Hirazaki, 1997), it is predicted that the cerebellar nuclei will be found to have shown a similar change in size to the rest of the cerebellum (i.e. an increase). Very little work has focussed on evolutionary changes in the primate cerebellar cortex and there is little reason for predicting that this area of the cerebellum should be found to have shown significantly more or less changes in size than the cerebellum as a whole. This section will therefore also be treated as a novel investigation.

4.2 Materials and Methods

4.2.1 Data

The primate data used in this chapter comes from the same sources as that used in Chapter 3. The volume of the insectivore cerebellum, neocortex, cerebellar nuclei and whole brain come from Stephan et al. (1981).

4.2.2 Method

The analyses in this chapter primarily involve least-square regressions. Brain structures are regressed against one another in order to look at differences in their relative size amongst different species. The particular scaling method which is used is based on method (ii) outlined in Section 3.1. Brain structures have been regressed against the "rest of the brain" in order to assess cerebellar variation relative to other structures (as in the previous chapter, "rest of the brain" means brain – (neocortex + cerebellum) as these structures seem to have evolved to some extent as a unit). The aim of the current analyses is to examine the differences in particular brain structures relative to the other structures, that is relative to the rest of the brain. This means that any possibility that observed differences reflect global changes in whole brain size are effectively ruled out.

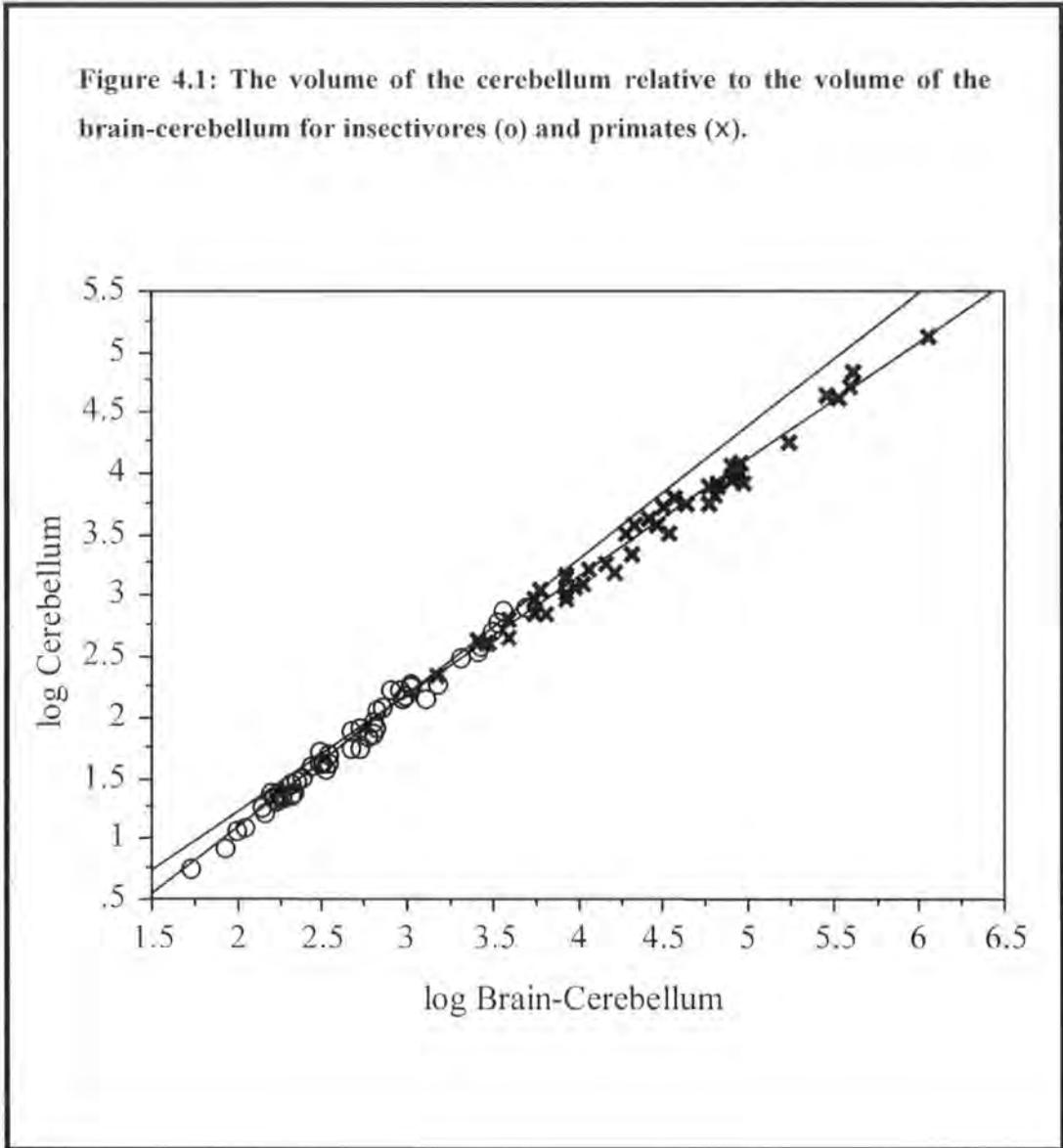
In order to determine whether there are significant differences between groups in the relative size of the cerebellum or its parts, analysis of covariance (ANCOVA) is used. To overcome the possibility of phylogenetic effects, Purvis's grade shift method (Purvis and Rambaut, 1995) was used in addition to the least square regression analyses. This method involves running the data through the computer package C.A.I.C. used in Chapter 3. If the resultant slopes for the different groups are not significantly different (t-test on the residuals), then the contrast at which the two groups split is investigated to determine whether it differs significantly (more than two standard deviations) from the mean of all the contrasts. A significant difference indicates that there is a grade shift between the two groups being considered for the particular trait of interest.

4.3 Results (1)

Figures 4.1 – 4.6 below show the results of least-square regression analyses on the relative size of the cerebellum in primates and insectivores (Section 4.3.1) and in a number of primate groups (Section 4.3.2).

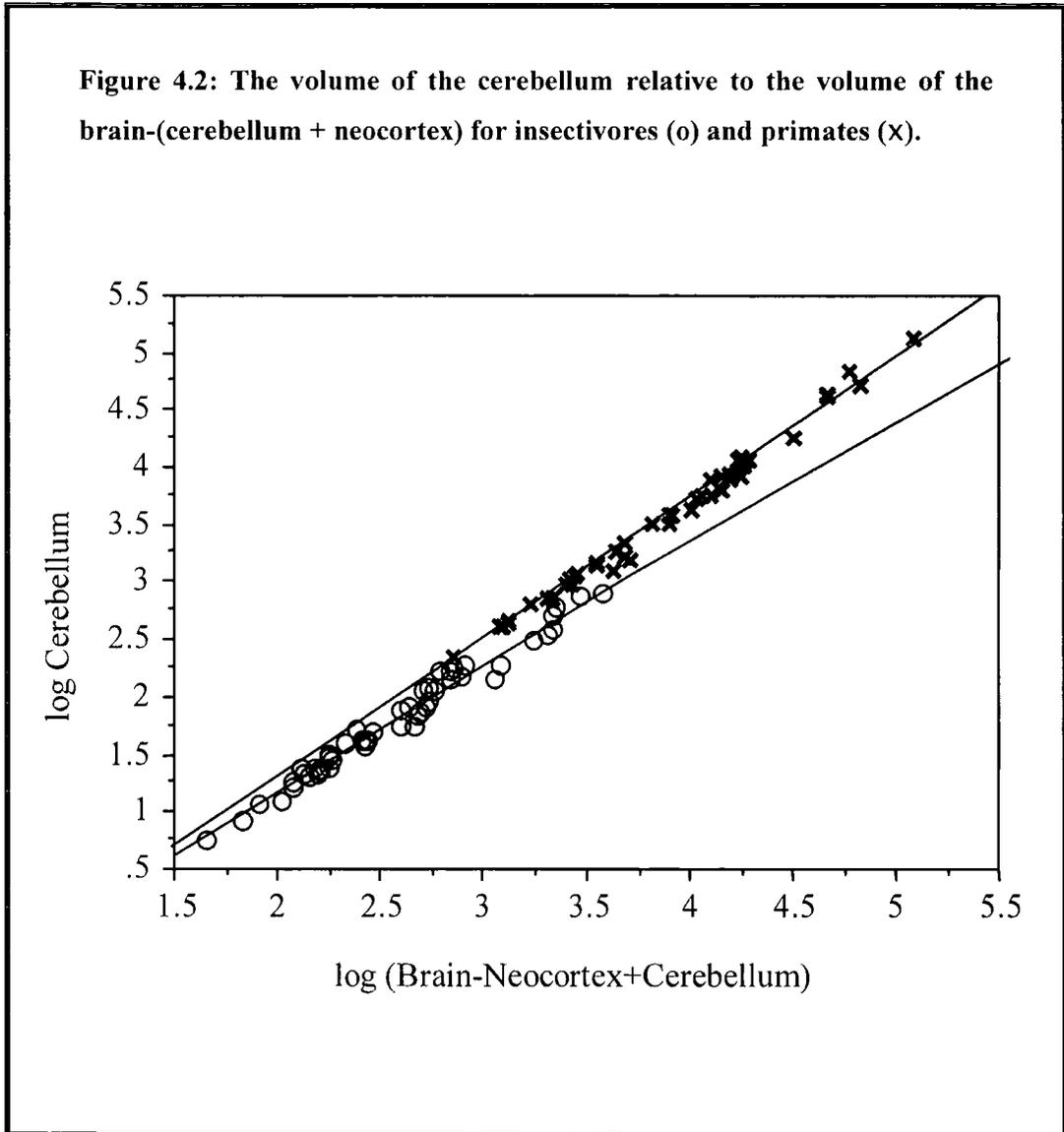
² There are three longitudinal zones in the cerebellum: the lateral zone, the intermediate zone and the vermis. See Carpenter (1976) for the logic behind these distinctions.

4.3.1 The cerebellum in insectivores and primates



ANCOVA indicates that the relative volume of the cerebellum in primates does not differ significantly from that in insectivores ($p < 0.1777$, $f = 1.845$, d.f. 93). These results are, however, likely to be misleading due to confounding effects of the neocortex which is known to be exceptionally large in primates and is included here as part of the independent variable.

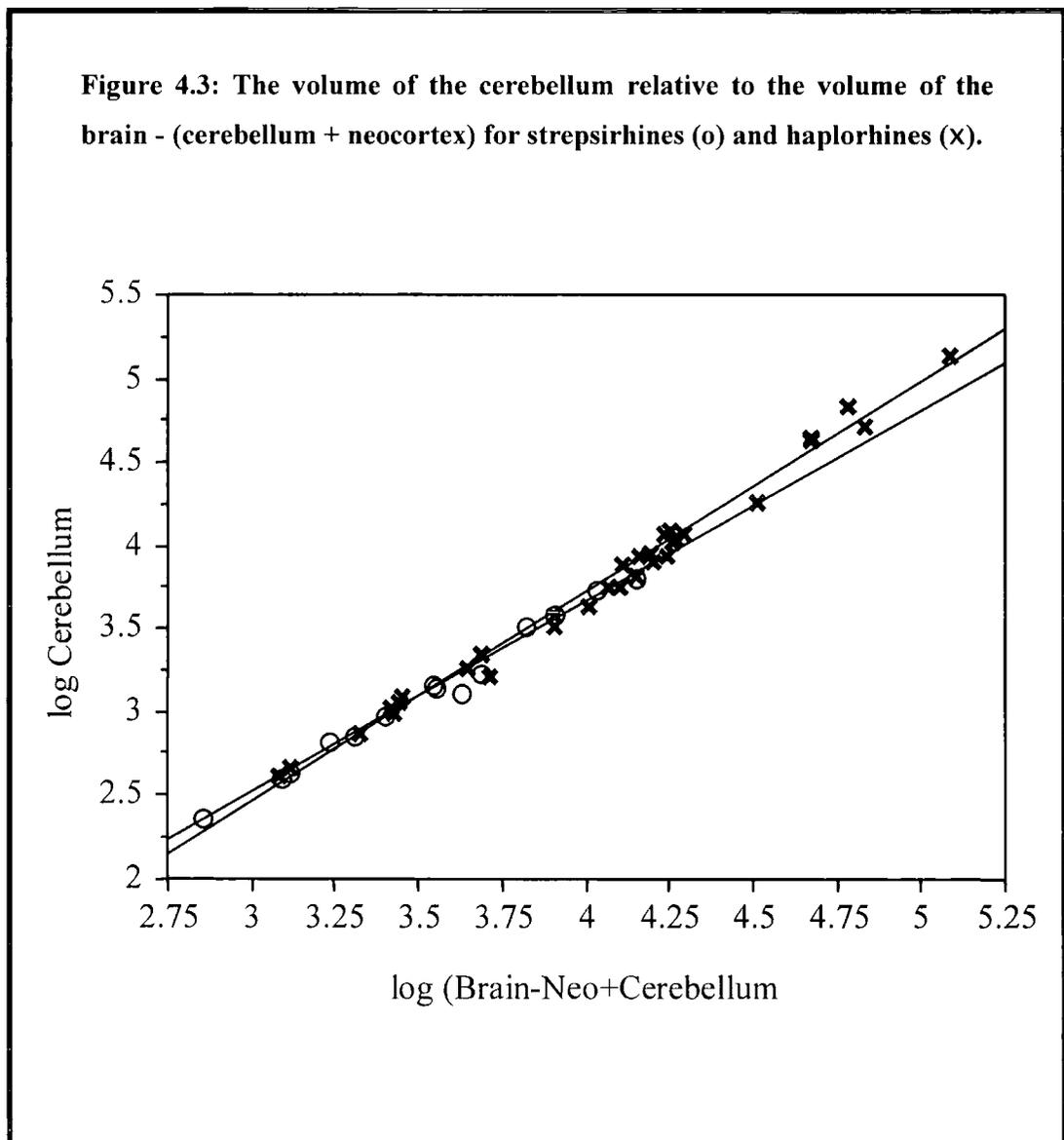
Figure 4.2 shows that when the neocortex is subtracted from the “rest of the brain”, the primate cerebellum is significantly larger in relative size than that of insectivores (ANCOVA: $p < 0.0001$, $f = 50.604$, $d.f. = 93$).



4.3.2 Differences between different primate groups

Figures 4.3 – 4.6 below show the relative size of the cerebellum in different pairs of primate groups.

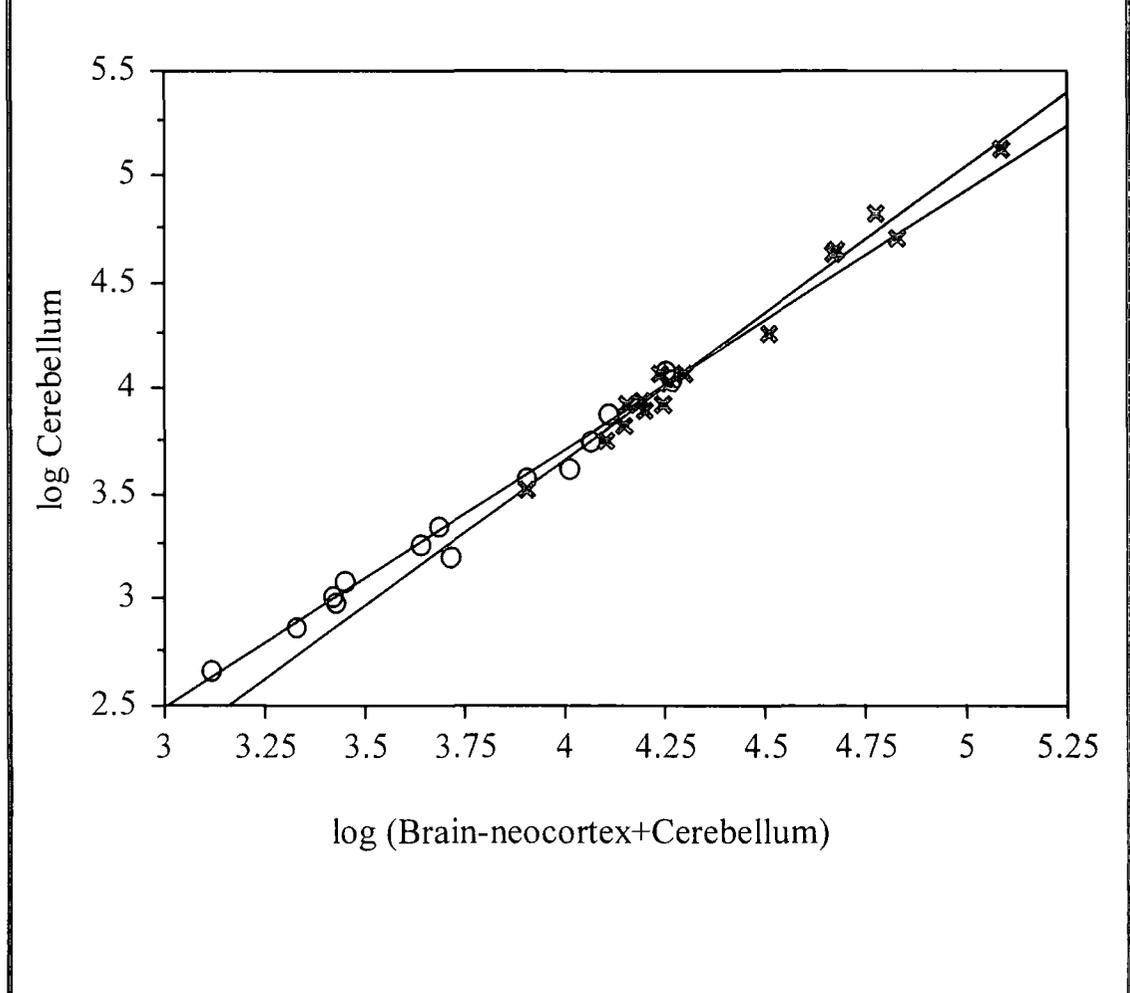
(i) Strepsirhines/Haplorhines



This Figure shows that the relative size of the cerebellum in strepsirhines and haplorhines does not differ significantly (ANCOVA: $p = 0.2779$, $f = 1.208$, d.f. = 43).

(ii) Platyrrhines/Catarrhines

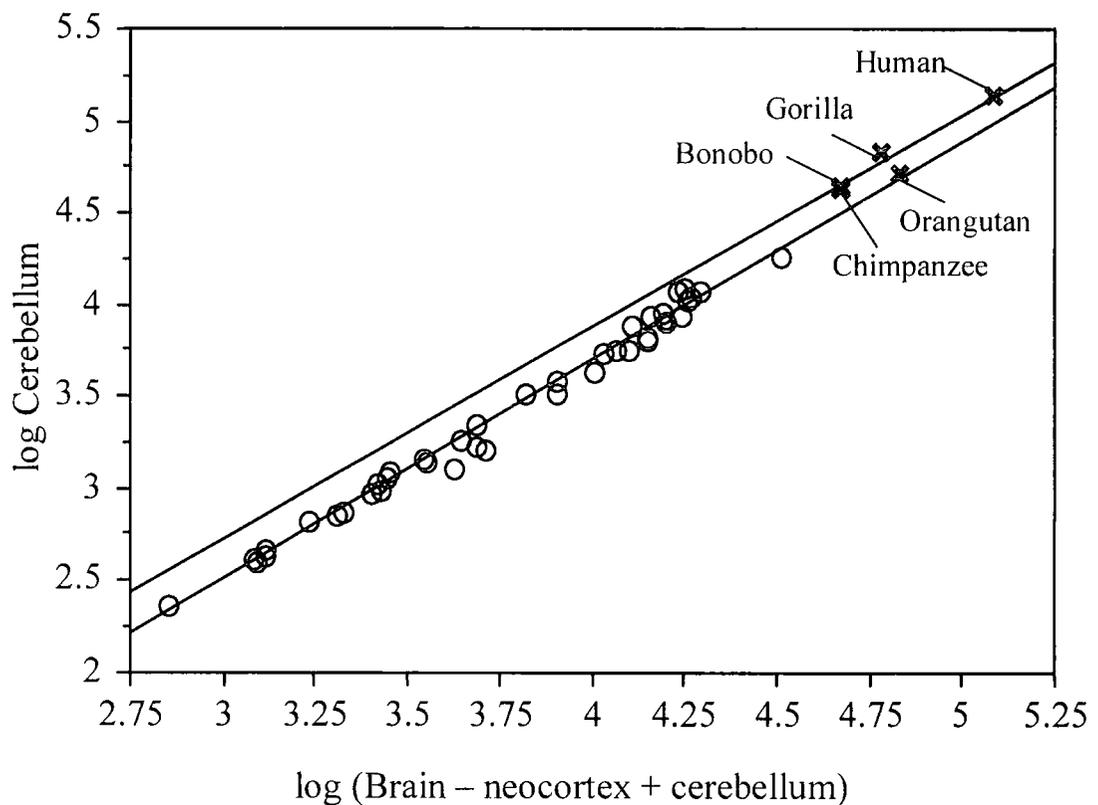
Figure 4.4: The volume of the cerebellum relative to the volume of the brain- (cerebellum + neocortex) for platyrrhines (o) and catarrhines (x).



There is no significant difference between relative cerebellum size in platyrrhines and catarrhines (ANCOVA: $p = 0.3688$, $f = 0.835$, $d.f. = 27$).

In all of these graphs, it is clear that there are a number of points which are consistently above the plotted lines. These are the values for the great apes, which suggests that there might be a significant difference in the size of the cerebellum in these animals compared to other primates. This possibility is investigated in Figure 4.6 below.

Figure 4.6: The volume of the cerebellum relative to the volume of the brain- (cerebellum + neocortex) for great apes (x) and other primates (o). The values for the chimpanzee and bonobo are overlapping, giving the impression that there are only four great ape species.



This Figure clearly shows that there is a significant difference between the relative size of the cerebellum in great apes and other primates (ANCOVA: $p = 0.0001$, $f = 17.920$, $d.f. = 43$). This difference is far more significant than the differences

between any of the other primate groups, suggesting that great apes have an unusually large cerebellum.

In Figure 4.5, a significant difference was found between apes and monkeys, however it seems that this difference was due to the large size of the cerebellum in great apes in particular. It is clear from this Figure that the great ape values fall well above the line for the other primates, whereas the other apes (gibbons) falls much closer to the monkey values. Therefore, amongst primates, it seems that great apes may have unusually large cerebella. The great ape falling on the lower line is the orangutan which suggests that the evolutionary shift might have occurred after the split between African apes and orangutans.

Having carried out initial least-square regression analyses to look for patterns in relative cerebellum size, independent contrasts analyses, which take into account the phylogenetic relatedness of species, are now necessary. The particular method to be used is the Purvis grade shift method outlined in Section 4.2.2 which tests for grade shifts between different taxa.

Table D presents The results of t-tests on Independent Contrasts analyses for the cerebellum and the brain - (neocortex + cerebellum) in the different groups to test for differences in the slopes of the lines:

Table D: The probability that the gradient differs for different primate groups

Species	p value	t value	d.f.
Primates/Insectivores	0.5629	0.581	74
Strepsirrhines/Haplorhines	0.0429	-2.091	40
Platyrrhine/Catarrhine	0.2246	-1.243	27
Apes/monkeys	0.3850	-0.883	27
Great apes/others	0.3918	-0.866	40

These results show that for all but one of the paired comparisons, there is no significant difference between the slopes of the two lines. The only exception is the strepsirhine/haplorhine comparison and no further analysis can be carried out on this pair because the statistical method used (the Purvis grade shift method) depends on the gradients being the same. For all the other groups, it is now necessary to determine whether there has been a grade shift for one group compared to the other. This involves looking at the residual at the split of the two groups in the phylogeny and determining whether this differs significantly from the other residuals. If the residual is found to be more than two standard deviations away from the mean of the residuals, then the result is taken to be significant and will indicate that there is a grade shift between the two species in question. Table E below shows which pairs are significantly different in relative cerebellum size.

Table E: Statistics for the residuals from independent contrasts analyses which show whether there is a significant difference in relative cerebellum size between taxonomical pairs.

Paired comparisons	Mean of residuals	Standard deviation	Standard error	Value of residual of interest	Significantly different?
Primate / Insectivore	0.021	0.020	0.002	0.084	yes
Platyrrhine / Catarrhine	0.013	0.010	0.002	0.016	no
Ape/monkey	0.013	0.010	0.002	0.019	no
Great apes/ other primates	0.011	0.009	0.001	0.030	yes

These results show that, once phylogeny has been taken into account, the only differences in relative cerebellum size are between primates and insectivores and between great apes and other primates. Although the ape/monkey pair was shown to be significantly different by ANCOVA on species values, the phylogenetic method has shown the difference not to be significant, presumably because gibbons fall with 'other primates', leaving great apes as the only primate group to have an unusually large cerebellum³.

4.4 Discussion (1)

As a group, primates seem to have unusually large cerebella (compared with insectivores). In addition, relative cerebellum size is generally very similar among primates except that African great apes appear to possess significantly large cerebella compared to the other primates.

The finding that African great apes have an unusually large cerebellum differs from the results of Rilling and Insel (1998). They found that the difference in cerebellum size lies between apes and monkeys, that is to say that gibbons fall within the range of the great apes. They also found that humans did not have enlarged cerebella, like other apes. However, Rilling and Insel included the neocortex in the rest of the brain. When this area is excluded it is clear that the gibbons fall well within the cluster of the values for the monkeys, and the group which still differs significantly is the African great apes. This suggests that, relatively speaking, the cerebellum is more important in African great apes than in other primates and possible reasons for why this might be the case will be considered in Chapter 5. It is interesting to note that humans fall within the values of their closest relatives and the results presented here seem to suggest that as far as relative cerebellum size is concerned, humans are just another African great ape. What is not yet known, however, is whether it is the same

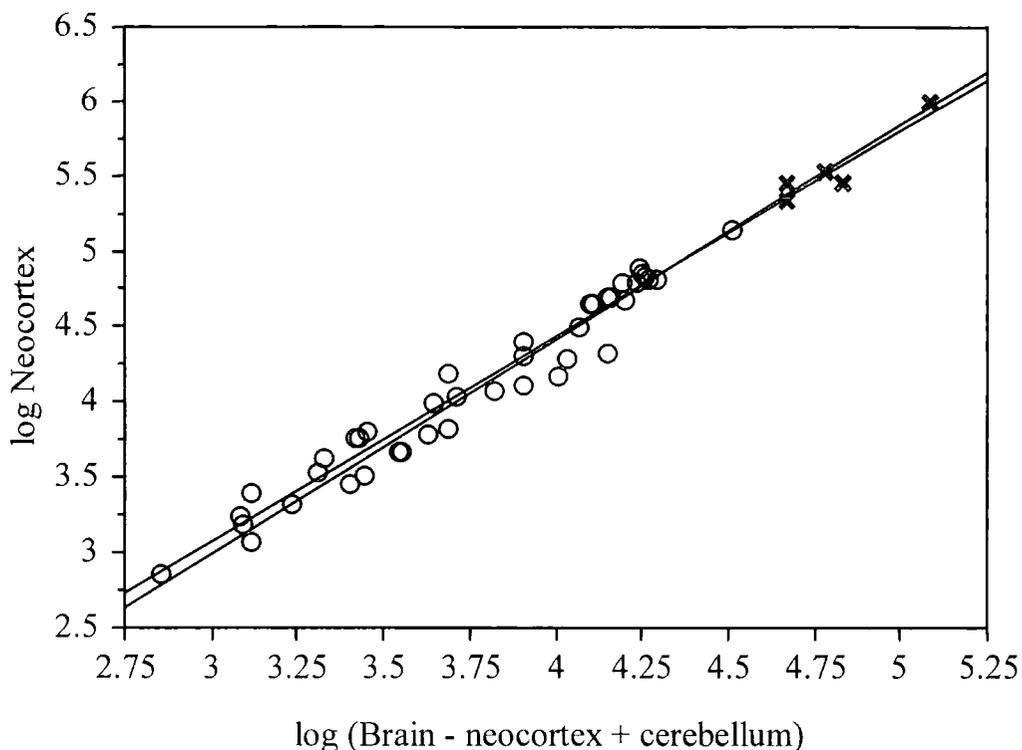
³ For further information about the Purvis grade shift method which was used in these analyses, please see Purvis and Rambaut (1995).

parts of the cerebellum that have increased in size in all of the African great apes or whether different parts have increased in different species.

Having suggested that humans may just be another African great ape with respect to cerebellum size (relative to other structures), it is interesting to note that one of the great ape values falls slightly away from the others, but that this is not the value for the human. This is the value for the orangutan and it almost falls on the line of the other primates indicating that orangutans may not share the large cerebellum possessed by the other great apes. While it is unclear why this might be the case, it suggests that an expanded cerebellum evolved after the split between the African great apes and Pongo. Detailed investigation of the different selection pressures on African and Asian great apes might therefore shed some light on the reason for the increase in cerebellum size in great apes, although that is the subject for another paper.

One very interesting point concerning great apes is that whilst the great ape neocortex is a similar proportion of the total brain to other primates' neocortex, the African great ape cerebellum is a far larger proportion of the brain than other primates' cerebellum. In other words, what holds African great apes out as different from other primates is their large cerebellum. Figure 4.7 shows that the great ape values fall almost exactly on the line of other primates, indicating that the relative size of the great ape neocortex is very similar to that of the other primates. This finding indicates that in African great apes, in addition to the cerebellum being unusually large, this area of the brain has in fact shown more significant size changes relative to other primates than has the neocortex, indicating that the most significant evolutionary changes in great ape brains may have been changes in the size of the cerebellum, not changes in the size of the neocortex, a difference which clearly sets great apes apart from other primates.

Figure 4.7: Neocortex volume plotted against the volume of the rest of the brain for great apes (x) and other primates (o)



Summary

In line with the aim of this thesis to determine what has been most important in the evolution of the primate brain, for great apes it seems that the expansion of the cerebellum is more important than the expansion of the neocortex. This is not to question whether the neocortex expanded in great apes, but simply to argue that the focus of previous work on the neocortex as the principal, or even sole, area of change in primate brain evolution is simply not justified for great apes. The results presented here show that researchers should be focussing their attention on the cerebellum, or at least on the cerebellar-neocortical system as a whole, as it is in the size of the cerebellum that great apes differ from other primates.

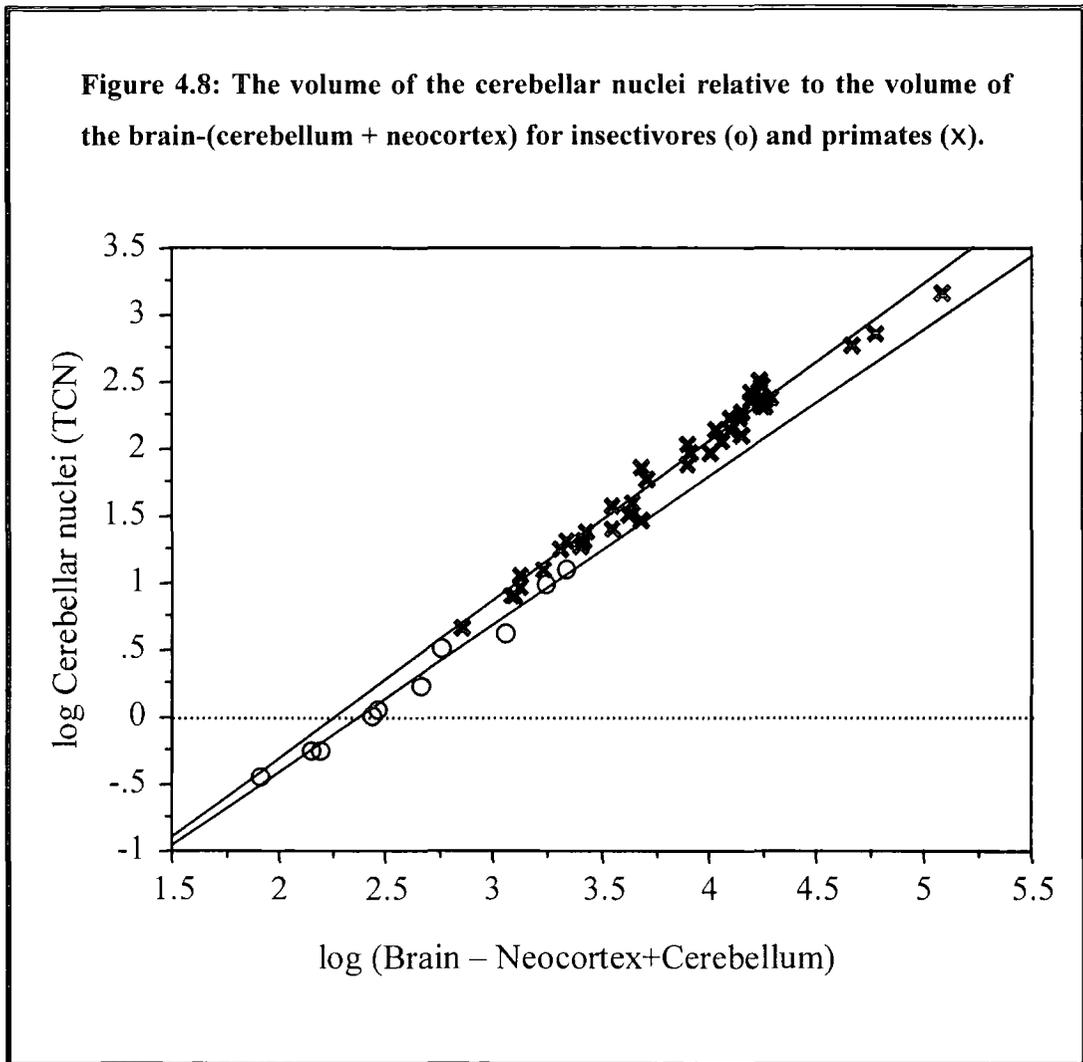
The following section attempts to identify exactly which parts of the cerebellum increased in size in primates and which parts increased in size in great apes. This is important because there is much functional variation within the cerebellum. If the areas that have shown significant increases in size can be identified, then by looking at the functions of these areas it might be possible to shed some light on the reason for the cerebellar expansion, and to draw cognitive and functional conclusions from this.

4.5 Results (2)

The relative sizes of the cerebellar nuclei (TCN), and of the non-nuclear cerebellum in (i) primates compared to insectivores and (ii) great apes compared to other primates are shown in Figures 4.8 – 4.11 below. Unfortunately data for the volumes of the nuclei in bonobos and orangutans is not currently available and these species will therefore have to be excluded from the analyses.

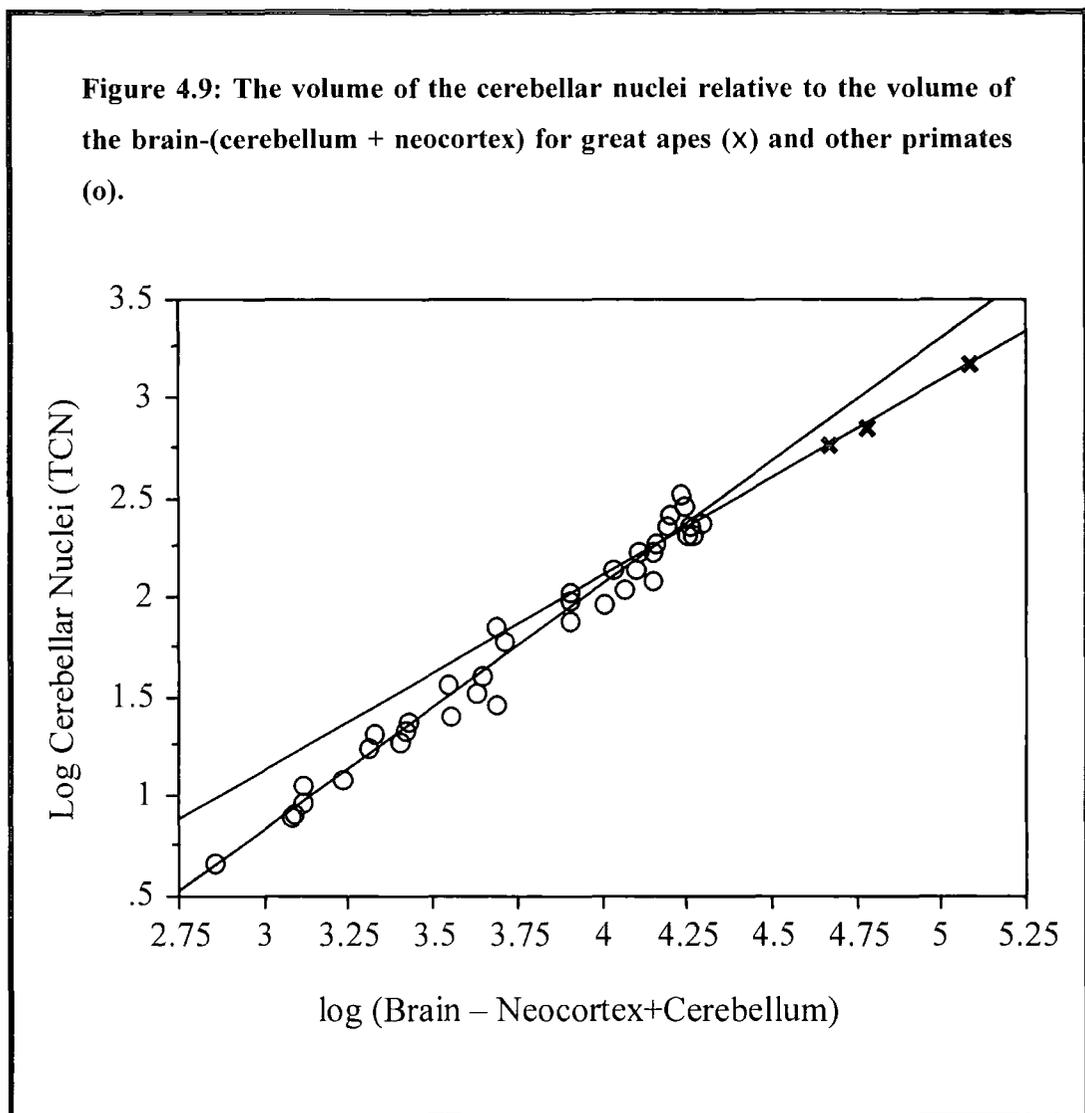
4.5.1 The Cerebellar Nuclei (TCN)

(i) Primates and insectivores



This figure clearly shows that there is a significant difference between the relative size of the cerebellar nuclei in primates and insectivores (ANCOVA: $p = 0.0003$, $f = 15.689$, d.f. = 47). Unfortunately, it is not possible to determine whether this difference is more or less significant than the difference between the relative size of the whole cerebellum in primates and insectivores because it was not possible to carry out ANCOVA on that difference due to differences in the gradients (see Figure 4.2).

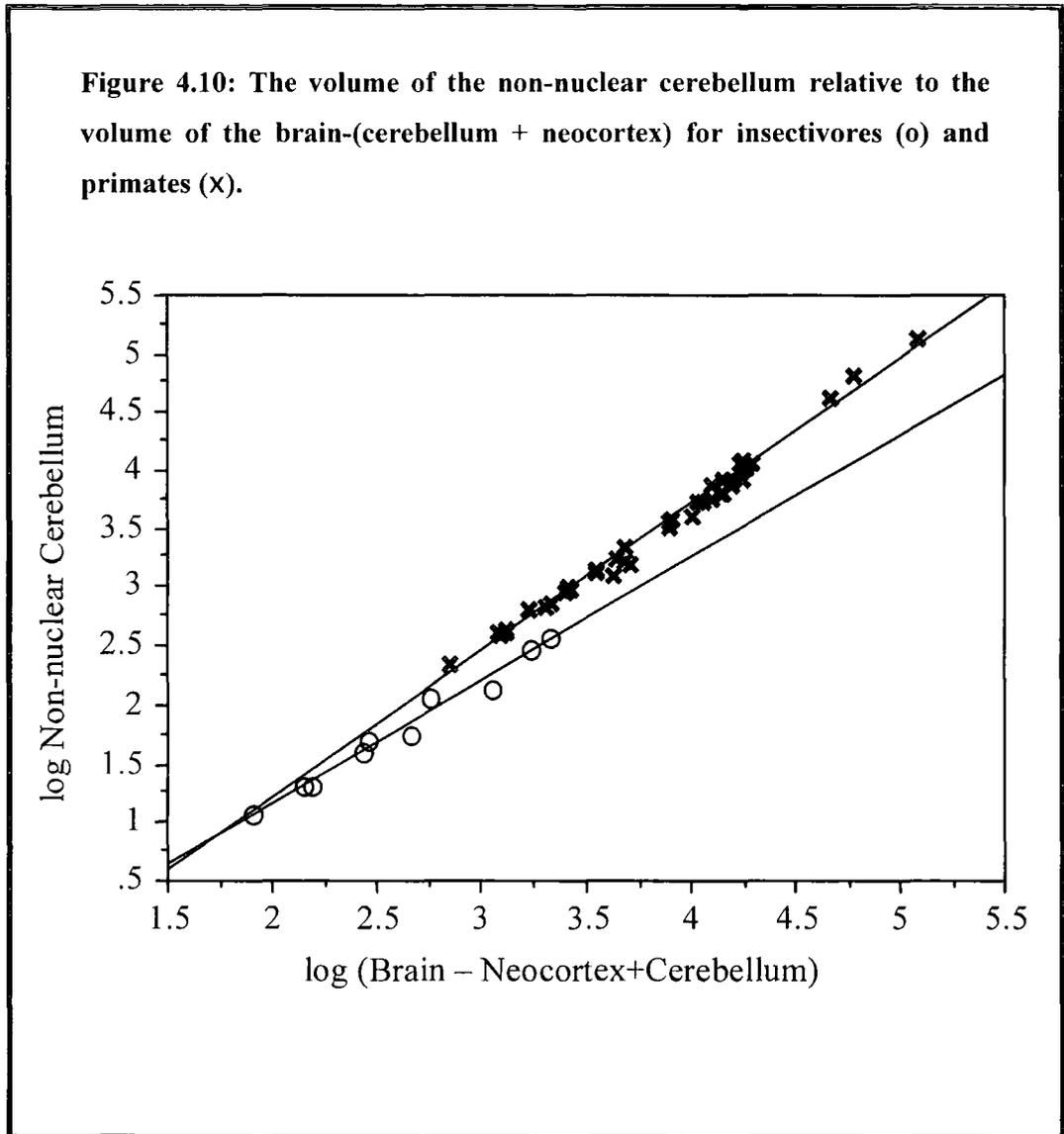
(ii) Great Apes and other primates



This figure shows that there is a significant difference in the relative size of the cerebellar nuclei in great apes and other primates ($p = 0.0130$, $f = 6.814$, $d.f. = 37$). What is particularly interesting about this graph is that the cerebellar nuclei appear to be relatively smaller in great apes than other primates - this is the opposite to the results for the whole cerebellum which was found to be significantly larger in great apes.

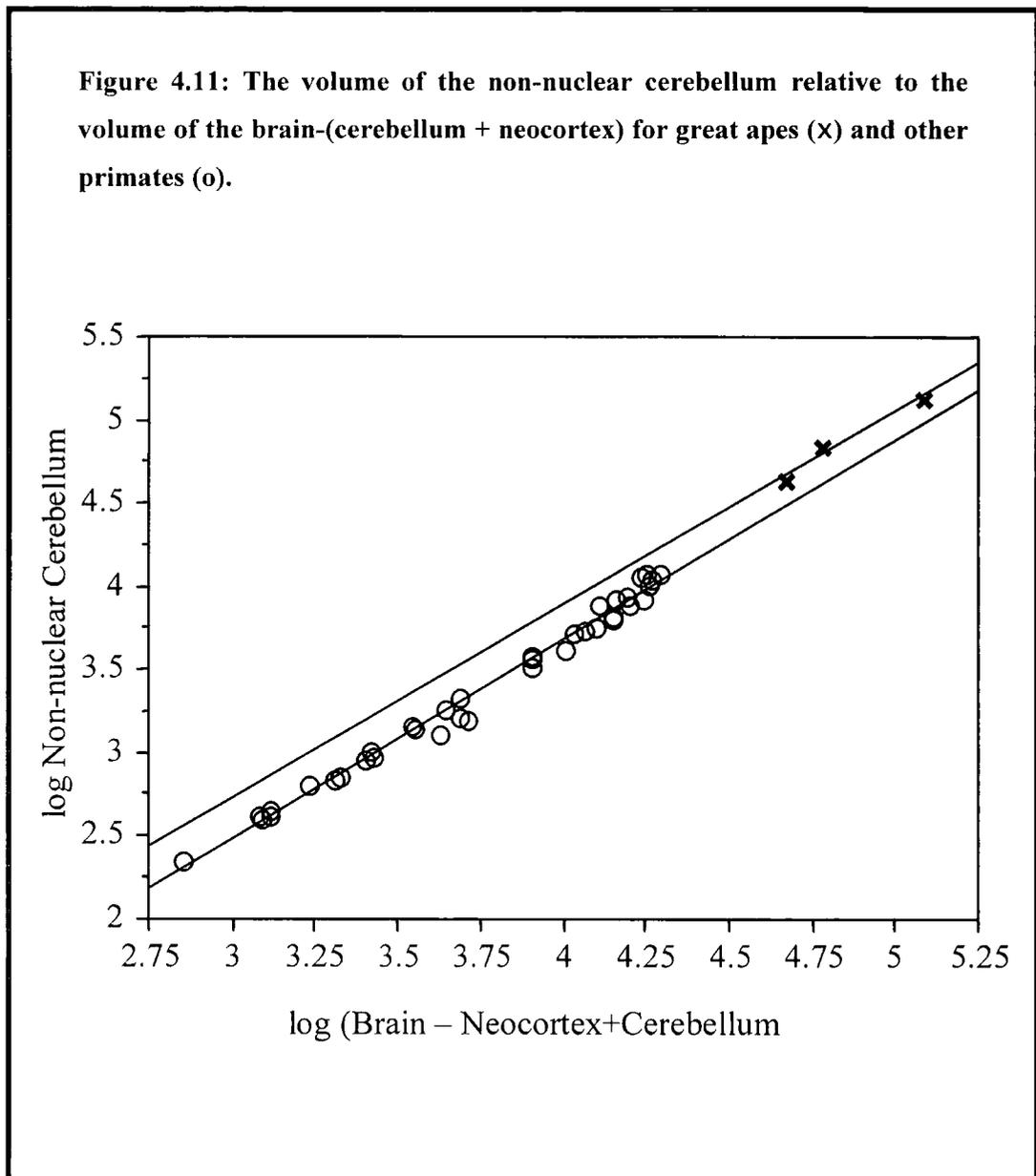
4.5.2 The non-nuclear cerebellum

(i) Primates and insectivores



The slopes of the lines in this figure differ significantly which means that analysis of covariance is not valid. Nevertheless, the graph does indicate that the non-nuclear cerebellum is generally larger in primates.

(ii) Great Apes and other primates



This figure shows that, in line with the finding that the whole cerebellum is unusually large in great apes, the non-nuclear cerebellum is also particularly large in great apes compared to other primates ($p = 0.0001$, $f = 18.207$, $d.f. = 37$).

The tables below show the results of t-tests on residuals produced by independent contrasts analyses on this data to take account of phylogenetic effects. The t-test is

carried out to determine whether the differences between the slopes of the lines for different groups are significant before testing for grade-shifts.

Table F: The probability that the gradient differs for different groups for the cerebellar nuclei regressed against the brain - (neocortex+ cerebellum).

Species	p value	t value	d.f.
Primates/Insectivores	0.8430	-0.199	41
Great apes/others	0.4858	0.705	34

Table G: The probability that the gradient differs for different groups for the non-nuclear cerebellum regressed against the brain - (neocortex+ cerebellum).

Species	p value	t value	d.f.
Primates/Insectivores	0.5808	0.555	74
Great apes/others	0.4933	0.692	34

These results show that for all the comparisons, the slopes for the pairs are not significantly different which means that it is possible to carry out further statistical analyses.

The next step is to determine whether there has been a grade shift for one group compared to the other by looking at whether there are significant differences between the residuals. Tables H and I below shows which pairs are significantly different in the relative size of the cerebellar nuclei and of the non-nuclear cerebellum.

Table H: Statistics for the residuals from independent contrasts analyses which show whether there is a significant difference in relative cerebellar nuclei size between pairs.

Pairwise comparison	Mean of residuals	Standard deviation	Standard error	Value of residual of interest	Significantly different?
Primate / Insectivore	0.025	0.019	0.003	0.046	no
G.A./Other	0.016	0.013	0.002	0.00018	no

Table I: Statistics for the residuals from independent contrasts analyses which show whether there is a significant difference in relative non-nuclear cerebellum size between pairs.

Pairwise comparison	Mean of residuals	Standard deviation	Standard error	Value of residual of interest	Significantly different?
Primate / Insectivore	0.22	0.020	0.002	0.082	yes
G.A./Other	0.012	0.010	0.002	0.019	no

These results show that, after phylogenetic effects have been taken into account, the only significant difference is between the relative size of the non-nuclear cerebellum in primates and insectivores. There is no significant difference between the relative size of the cerebellar nuclei or of the non-nuclear cerebellum in great apes and other primates.



4.6 Discussion (2)

The particular area of the cerebellum that seems to have increased in size in primates is the non-nuclear cerebellum. Although regression analyses also showed the cerebellar nuclei to be relatively larger in primates than insectivores, this difference was not found to be significant.

For great apes, despite the earlier finding that they have an unusually large cerebellum, no significant difference was found in the relative size of the cerebellar nuclei nor of the non-nuclear cerebellum in great apes compared to other primates. This is an unexpected result, because together, the cerebellar nuclei and the non-nuclear cerebellum make up the whole cerebellum. If the whole cerebellum has increased in size in great apes then at least some of its parts must also have increased in size. One possible reason why no significant correlations were found here could be that there is insufficient data. Although measurements of the whole cerebellum are available for 46 primate species, measurements of the cerebellar nuclei (and consequently also the non-nuclear cerebellum) are only available for 40 primates, not including two of the great apes (the bonobo and the orangutan). Without these missing values, it may not be possible to accurately represent the changes that have occurred in the cerebellar nuclei and the non-nuclear cerebellum.

Nevertheless, despite these limitations it is interesting to note that contrary to the prediction, the regression analyses showed that the great ape cerebellar nuclei appeared to be significantly smaller in relative size than those of the other primates. Figure 4.9 shows that the great ape values fall well below the plot for the other primates. This result suggests that it is not an increase in the size of the cerebellar nuclei which is reflected in the large great ape cerebellum, and if it is not the cerebellar nuclei, then it must be the non-nuclear cerebellum which has increased in size in great apes. Preliminary evidence in support of this possibility comes from the regression analyses which showed that the great ape non-nuclear cerebellum appears to be larger in relative size than that of the other primates (see Figure 4.11). As explained above, there may be a good reason for why this difference was not found to be significant once phylogenetic differences had been taken into account. Therefore,

until further work can be carried out, it will be presumed that it is the non-nuclear cerebellum (the input areas) rather than the cerebellar nuclei (the output areas) which has increased in size, and whose size increase is reflected in the large size of the cerebellum as a whole in great apes.

Thus, the results suggest that in primates as a group, and specifically in great apes, it is the non-nuclear cerebellum in particular which has shown significant increases in size over evolutionary time. A possible explanation for this is as follows: It is well known that the cerebellum receives extensive input from numerous different areas (Kandel et al. 2000), this input outweighing the output by a factor of forty. A large proportion of the inputs originate in the cerebral cortex (the motor and prefrontal cortices in particular (Middleton and Strick, 2001)), and there is good evidence for an increase in the volume of these frontal areas in primates over evolutionary time (Pinker, 1997). The argument here is that an increase in the size of the cortical regions which send outputs to the cerebellum resulted in increased numbers of outputs, and thus an increase in the volume of information reaching the cerebellum. In response, the receiving regions of the cerebellum which analyse the input (cerebellar cortex) would have increased in size in order to deal with the increasing volume of new information coming in from the cerebral cortex.

It would be interesting to test this proposal by looking at the relative size of the cortical areas that send output to the cerebellum (the prefrontal cortex, motor and premotor cortex). The prediction would be that these cortical areas would be found to be significantly larger in size in great apes compared to other primates, as the great ape cerebellum (and presumably the non-nuclear areas specifically) are particularly large. Unfortunately, further investigation here is impeded by a lack of data (measurements of the particular regions of the cerebral cortex that send outputs to the cerebellum). The only data that is currently available comes from Brodmann (1912), who provided measurements of the prefrontal cortex in an article on the cytoarchitectonic organization of the cerebral cortex in primates. A very preliminary analysis of the size of the prefrontal cortex in great apes and other primates using Brodmann's data can be found in Appendix A.

Having considered how it might have been possible for the non-nuclear cerebellum to have increased in size, possible explanations for the decrease in the size of the cerebellar nuclei in great apes must also be investigated. It is important to remember that it is not possible to determine the precise nature of evolutionary changes in brain parts. That is to say that the cerebellum may not have increased in size in African great apes, it may just have decreased in size in the other primates, or perhaps it has decreased in all primates, but simply to a lesser degree in the African great apes. Similarly, it cannot be assumed that because the cerebellar nuclei of the great apes have been found to be relatively small compared to other primates, that these nuclei have decreased in size. Because of the uncertainty here, only the most plausible situation will be explained.

A decrease in size, if this is what occurred in the cerebellar nuclei, is just as important an evolutionary change as an increase in size. If the cerebellar nuclei in African great apes have decreased in size, then this could be the result of an increase in the efficiency of these nuclei, where some internal reorganisation resulted in the nuclei simply becoming more able to carry out their individual functions. Preliminary support for this possibility of reorganisation within the dentate nucleus in particular comes from Matano (2001). Matano found that in humans there is an increase in the development of the ventral half of this nucleus compared to the dorsal half. This particular difference was not found in the other great apes and the reason for this reorganisation is as yet unclear. Little is known about the precise functions of the ventral portion of the dentate nucleus, but Matano (2001) suggested that its relative enlargement in humans is associated with its role in fibre connection. The fact that this difference was not found in great apes does not indicate that their cerebellar nuclei did not show any re-organisation, it simply indicates that the dentate nucleus in particular has not been found to have shown changes similar to those that have occurred in the human dentate nucleus. This is not in fact surprising since it is the dentate nucleus that is thought to be involved in cognitive functions and there can be little argument that humans have significantly greater cognitive abilities than great apes. Further work should investigate the other cerebellar nuclei to determine whether there was any re-organisation in these in great apes compared to other primates. If there is no support for this possibility, then it would seem that the cerebellar nuclei in great apes have not decreased in size over evolution, but rather

that the non-nuclear areas have shown such significant increases in size that compared to the rest of the cerebellum, the nuclei appear to be significantly smaller.

Summary

In summary, the results of this Chapter have illustrated that primates have significantly large cerebella compared to insectivores, and that it is the non-nuclear cerebellum in particular that has increased in size. Among primates, great apes were found to have unusually large cerebella, and although they were not found to be significant, the results indicated that this was caused by a particularly large non-nuclear cerebellum.

CHAPTER 5

Environmental Correlates

5.1 Introduction

In the previous two chapters, evidence was presented that elements of the cerebellar-neocortical system have shown correlated size changes in primates, and increases in primates compared to insectivores. Among primates, the African great apes show significant increases in the size of one particular structure in this system: the cerebellum. The aim of the current chapter is to explain general size changes in the primate cerebellum. The focus will be on identifying variables that are associated with changes in cerebellum size and which may be particularly salient for African great apes. Unfortunately, possible reasons for an increase in the size of the cerebellum in primates as a group cannot be directly considered here due to limitations in the data available (there are insufficient measures of environmental variables for insectivores against which primates could be compared). For primates as a group, it will only be possible to look for general patterns of cerebellar correlates.

In attempting to explain the increase in the size of the cerebellum, selected environmental variables will be tested for significant correlations with cerebellum size. Positive correlations will indicate which selection pressures might have affected the size of the cerebellum. In addition to investigating environmental correlates, a developmental explanation will be sought for how the cerebellum could have shown such significant increases in great apes in particular.

The first environmental variables to be considered in looking at the selection pressures affecting cerebellar expansion have been chosen to test the prevailing theories of primate brain evolution: namely the Ecological Hypothesis and the Social

Intelligence Hypothesis (see Section 1.1.3). To this end, correlations of the cerebellum and the following ecological variables will be investigated: home range size, day journey length, percentage fruit in the diet, as well as the 'social variable' (social group size). Although the Social Intelligence Hypothesis has received some support from its ability to account for the expansion of the neocortex in primates, there has been some controversy over the scaling methods used (Deaner et al., 2000). If the same selection pressures were involved in the expansion of both the cerebellum and the neocortex then, if the Social Intelligence Hypothesis is correct, cerebellum size should be significantly correlated with social group size. This will be tested here. (The possibility that different selection pressures acted on the cerebellum and the neocortex is explored further in Chapter 6).

Further variables to be tested here have been chosen on the basis of the well documented role of the cerebellum in motor functions. These variables include locomotor type (in line with work carried out by Matano and Hirazaki, 1997) and fine motor actions (particularly bimanual asymmetric coordination, extractive foraging and tool use - Gibson, 1986 and van Schaik et al. 1999). Fine motor action variables are particularly relevant for great apes, as there is good evidence for high levels of manual dexterity and fine motor abilities in these species (Byrne, 1997) and it is therefore possible that these abilities are associated with the large cerebella in great apes.

It is predicted that cerebellar size will not be found to correlate with any of the ecological variables nor with the social variable. This is because the arguments on which both the Ecological Hypothesis and the Social Intelligence hypotheses are based involve primarily neocortical functions, not cerebellar functions (for example, memory for places and conspecifics). The cerebellum is thought to be primarily involved in motor actions and, on this basis, it is predicted that cerebellum volume will be found to be positively correlated with both locomotor type and measures of fine motor actions. It is important to note, however, that the cerebellum has also been implicated in a number of cognitive functions (see Section 1.3.1.2). If associations are found between cerebellum size and any of the ecological or social variables, then in addition to supporting one of the theories of primate brain evolution, this would also provide evidence for a cognitive dimension to cerebellar function.

Rather than providing direct answers to the question of why the cerebellum became so large in great apes, the aim of the developmental section (Section 5.3.2) is to investigate how it may have been physically possible for the cerebellum to expand. This requires attention to be focussed on the early years of life; the time when the cerebellum is developing and when it is most open to change. The aim is to determine whether great apes as a group differ from other primates in the timing of brain development, and thereby discover whether developmental programming changed in order to accommodate cerebellar expansion in these species. In addition to looking at differences in the timing of development between great apes and other primates, developmental correlates of relative cerebellum size across all primates will also be investigated in order to gain a more general understanding of cerebellar development in primates.

It is already known that, at birth, both human and chimpanzee brains occupy a volume of approximately 350cc, although they differ significantly in their level of maturity. The human brain is far less developed than that of the chimpanzee which only grows to about 450cc in a mature adult, whereas adult human brains grow to about 1300cc (Deacon, 1997). It is physiologically impractical for a human brain to much exceed 350cc at birth, since the human female pelvic opening is not large enough to accommodate a brain of greater volume and humans are therefore born with a relatively small brain (Wills, 1994). After birth, however, the human brain makes up for these restrictions and rapidly increases in size, reaching about 1050cc by the age of four and then gradually expands to its final size of about 1400cc at full maturity (Wills, 1994).

Thus, when chimpanzees are born, their brains are about $\frac{4}{5}$ of the size of the adult chimpanzee brain. This indicates that at least $\frac{1}{5}$ of the chimpanzee brain volume is obtained after birth, and it will be investigated whether post-natal development is similar for other great apes and how this compares with that of other primates. The rationale behind these investigations is that the cerebellum is one of the last brain areas to develop (Wang and Zogbli, 2000). If a species is born with a comparatively undeveloped brain, then it is likely that this late-developing area will undergo at least part of its development outside the womb, when it can be influenced by external stimulation. The possibility that external stimulation was important in the expansion

of the great ape cerebellum will be considered here, which possibility would receive at least some support from a finding that great apes have a longer post-natal developmental period.

5.2 Materials and Methods

5.2.1 Data

The measures of ecological variables (home range, day journey length and percentage fruit in the diet) are taken from Smuts et al. (1987) and Barton (1999). Measures of social group size come from Dunbar (1992). Locomotor data comes from Matano and Hirazaki (1997) and Rowe (1996). The measures of fine motor actions come from van Schaik et al. (1999) (tool use and bimanual asymmetric coordination – (BAC- the ability to perform different but complementary actions with the two hands on a detached object)), and Gibson (1986) (Extractive foraging). The data on neocortical and adult brain volumes used in this investigation comes from Smuts et al. (1987).

5.2.2 Method

Recognising that the results obtained may be influenced by the type of scaling used (Deaner et al, 2000 – see Section 2.1), a number of different measurements will be compared here. Relative cerebellum size will be calculated using the following three control variables:

- (i) Brain – neocortex + cerebellum
- (ii) Medulla
- (iii) Body weight

The residuals of these analyses will be correlated with the ecological, social and motor variables being investigated using simple least square regression plots. In order to determine whether there are any evolutionary relations between the cerebellum and any of these variables, the phylogenetic computer package C.A.I.C. will once again be used. For the continuous variables (home range size, day journey

length, percentage fruit in the diet and social group size), the traditional "CRUNCH" method will be used (Purvis and Rambaut, 1995). For the measures of locomotion and motor actions which are discrete, the "BRUNCH" method (Purvis and Rambaut, 1995). Like the "CRUNCH" algorithm, this "BRUNCH" method looks for any significant correlations between relative cerebellum size and the environmental variables once phylogenetic effects are taken into account. It shows whether there are significant changes in relative cerebellum size each time there is a transition in the independent variable. The difference between the two algorithms is in the nature of the data, that is whether they are continuous or discrete. The results of the "BRUNCH" analyses are tested using a t-test on the mean of the contrasts to determine whether there is a significant correlation between cerebellum size and the various environmental variables under consideration.

In order to look at the development of the cerebellum, neonatal and adult brain volumes will be compared using least square regression analyses and the Purvis grade shift method (Purvis and Rambaut, 1995). The aim is to look for patterns in relative brain size in great apes compared to other primates, in order to gain some idea of how it may have been physically possible for the cerebellum to have shown such significant expansion in these species in particular.

5.3 Results

5.3.1 Environmental Variables

5.3.1.1 Ecological variables

Table J presents the correlation matrix for the three classes of cerebellum residuals and the three different ecological variables. For home range size, body size is taken into account because differences in body size are known to be highly correlated with home range size (Clutton-Brock and Harvey, 1977; Nunn and Barton, 2001).

Table J: Correlations between scaled cerebellar measures and three ecological variables (home range, day journey length and percentage fruit in the diet) as revealed by least square regression analysis on species values

	Residuals of cerebellum and:		
	B - n + c	Medulla	Body weight
Home Range (v. body weight)	p = 0.4478 f = 0.589 r ² = 0.01 d.f. = 37	p = 0.5957 f = 0.287 r ² = 0.008 d.f. = 37	p = 0.0027 f = 10.363 r ² = 0.224 d.f. = 37
Day journey length	p = 0.4179 f = 0.697 r ² = 0.062 d.f. = 15	p = 0.0355 f = 5.412 r ² = 0.279 d.f. = 15	p = 0.4652 f = 0.564 r ² = 0.039 d.f. = 15
Percentage fruit in diet	p = 0.1178 f = 2.583 r ² = 0.075 d.f. = 33	p = 0.2806 f = 1.205 r ² = 0.036 d.f. = 33	p = 0.6164 f = 0.256 r ² = 0.008 d.f. = 33

At the $p < 0.05$ level of significance, there are two significant correlations. The first of these is home range and cerebellum when body weight is taken into account. This indicates that when body weight is partialled out, home range size and cerebellum size are highly correlated. The second significant correlation is between day journey

length and cerebellum relative to medulla size. This indicates that when medulla size is partialled out, cerebellum size is correlated with day journey length.

In order to assess the statistical significance of any correlations between the scaled cerebellar values and the various environmental variables once phylogeny is taken into account, independent contrasts analyses were carried out and the results are presented in Table K.

Table K: Correlated volumetric evolution of the cerebellum (scaled) and three ecological variables (home range, day journey length and percentage fruit in the diet) as revealed by multiple regressions of independent contrasts.

	Residuals of cerebellum and:		
	B – n + c	Medulla	Body weight
Home Range (v. body weight)	p = 0.4031 f = 0.716 r ² = 0.02 d.f. = 36 Negative correlation	p = 0.6335 f = 0.231 r ² = 0.007 d.f. = 36 Positive correlation	p = 0.0884 f = 3.071 r ² = 0.081 d.f. = 36 Positive correlation
Day journey length	p = 0.0852 f = 3.430 r ² = 0.197 d.f. = 15 Negative correlation	p = 0.1303 f = 2.583 r ² = 0.156 d.f. = 15 Positive correlation	p = 0.5003 f = 0.479 r ² = 0.033 d.f. = 15 Positive correlation
Percentage fruit in diet	p = 0.3109 f = 1.060 r ² = 0.032 d.f. = 33 Negative correlation	p = 0.5706 f = 0.328 r ² = 0.01 d.f. = 33 Positive correlation	p = 0.8213 f = 0.052 r ² = 0.002 d.f. = 33 Positive correlation

These results show that once phylogenetic relatedness is taken into account, there are no significant correlations between any of the scaled cerebellum values and any of the ecological variables. Hence, significant correlations in Table J may reflect confounding variables.

5.3.1.2 Group size

The social variable to be investigated here is social group size. Table L presents the correlation matrix for the three classes of cerebellum residuals compared to measures of social group size.

Table L: Correlations between scaled cerebellar measures and social group size as revealed by analysis of variance on least square regression analysis on species values.

	Residuals of cerebellum and:		
	B - n + c	Medulla	Body weight
Group size	<p>p = 0.8712 f = 0.027 $r^2 = 0.001$ d.f. = 42</p>	<p>p = 0.0730 f = 3.386 $r^2 = 0.076$ d.f. = 42</p>	<p>p = 0.1774 f = 1.884 $r^2 = 0.044$ d.f. = 42</p>

These results show that at the $p < 0.05$ level of significance, there is no significant correlation between group size and the various cerebellum residuals.

Table M shows the results of independent contrasts analysis to determine whether any associations exist between the scaled cerebellar values and social group size once phylogenetic relationships are taken into account.

Table M: Correlated volumetric evolution of the cerebellum (scaled) and social group size as revealed by multiple regressions of independent contrasts.

	Residuals of cerebellum and:		
	B - n + c	Medulla	Body weight
Group size	<p>$p = 0.5800$ $f = 0.311$ $r^2 = 0.008$ d.f. = 40</p> <p>Positive correlation</p>	<p>$p = 0.9583$ $f = 0.003$ $r^2 = 0.00007$ d.f. = 40</p> <p>Positive correlation</p>	<p>$p = 0.2074$ $f = 1.644$ $r^2 = 0.04$ d.f. = 40</p> <p>Positive correlation</p>

These results show that there are no significant correlations between group size and any of the scaled cerebellum measures when phylogeny is incorporated in the analysis.

5.3.1.3 Locomotor type

The first of the motor variables to be investigated is locomotor type. The distinction between different types of locomotion used here follows that provided by Matano and Hirazaki (1997). They identified six different locomotor types among primates: arboreal quadrupeds (AQ), modified brachiators (MB), semi-brachiators (SB), specialised bipeds (SPB), true brachiators (TB) and terrestrial quadrupeds (TQ). One

further locomotor type is included in the analyses which follow, this is vertical clingers and leapers (V CandL) and comes from Rowe (1996). Table N below shows the categorisation of primates into locomotor type.

Table N: Classification of the locomotor types of 46 primate species⁴

Species	AQ	V Can dL	MB	SB	SPB	TB	TQ
<i>Alouatta seniculus</i>				1			
<i>Aotus trivirgatus</i>	1						
<i>Ateles geoffroyi</i>				1			
<i>Avahi laniger</i>		1					
<i>Callicebus moloch</i>	1						
<i>Callimico goeldii</i>	1						
<i>Callithrix jacchus</i>	1						
<i>Cebuella pygmaea</i>	1						
<i>Cebus albifrons</i>	1						
<i>Cercocebus albigena</i>	1						
<i>Cercopithecus ascanius</i>	1						
<i>Cercopithecus mitis</i>	1						
<i>Cheirogaleus major</i>	1						
<i>Cheirogaleus medius</i>	1						
<i>Colobus badius</i>				1			
<i>Daubentonia madagascariensis</i>	1						
<i>Erythrocebus patas</i>							1
<i>Galago senegalensis</i>		1					
<i>Galagoides demidoff</i>	1						
<i>Gorilla gorilla</i>			1				
<i>Homo sapiens</i>					1		
<i>Hylobates lar</i>						1	

⁴ The classifications are highly impressionistic as many species fit into more than one category (e.g. orangutans are classified as modified brachiators although they are also quadrupeds and can be bipedal).

Species	AQ	V Can dL	MB	SB	SPB	TB	TQ
Indri indri		1					
Lagothrix lagothricha				1			
Lepilemur mustelinus		1					
Loris tardigradus	1						
Macaca mulatta							1
Microcebus murinus	1						
Miopithecus talapoin	1						
Nasalis larvatus				1			
Nycticebus coucang	1						
Otolemur crassicaudatus	1						
Pan paniscus			1				
Pan troglodytes			1				
Papio cynocephalus							1
Perodicticus potto	1						
Petterus fulvus	1						
Pithecia monachus	1						
Pongo pygmaeus			1				
Propithecus verreauxi		1					
Pygathrix nemaeus				1			
Saguinus midas	1						
Saguinus oedipus	1						
Saimiri sciureus	1						
Tarsius spectrum		1					
Varecia variegata	1						

In order to determine whether cerebellum size correlates with locomotor type, the residuals (taking phylogeny into account by using a C.A.I.C. derived slope – see Purvis and Rambaut, 1995) of the cerebellum against the rest of the brain, against the medulla and against body weight for the different types of locomotion are plotted in Figures 5.1 to 5.3. It is important to note that the residuals predicted from the C.A.I.C. – derived slope do not necessarily average zero. What is important here is the value of the residuals relative to each other.

Figure 5.1: Cerebellum size relative to the brain-(neocortex+cerebellum) for the seven different locomotor types

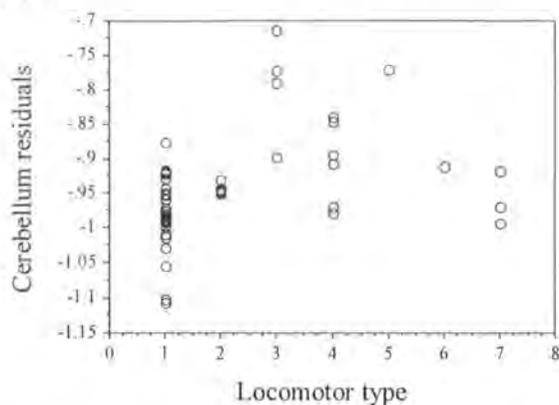
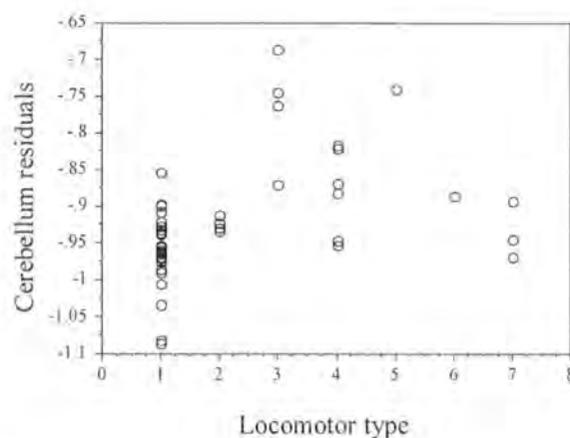


Figure 5.2: Cerebellum size relative to the medulla for the seven different locomotor types



These figures show that within locomotor type, there seems to be much variation in relative cerebellum size, indicating that locomotion may not have driven cerebellum size. There are a number of points which consistently fall above the rest of the points and these are the values for the great apes (locomotor types 3 and 5) which reflect the large size of their cerebella (see Chapter 4). In order to investigate whether there is an association between locomotor type and relative cerebellum size once phylogenetic relatedness has been taken into account, independent contrasts analyses are carried out using the "BRUNCH" algorithm. For this purpose, locomotor types are dichotomised into the following, more general, locomotor groups: quadrupeds (arboreal and terrestrial), brachiators (modified, semi- and true) and vertical clingers and leapers. The specialised biped was not investigated because humans are the only member of this category (i.e. there is only one data point). The results of t-tests on the relative cerebellum size for the groups being considered, are presented in Tables O, P and Q below.

Table O: t-tests of independent contrasts to test for differences in cerebellum size relative to the brain – (neocortex + cerebellum) for three different locomotor types (quadrupeds, brachiators and vertical clingers and leapers).

	p	t	d.f.	mean	-ve contrasts	+ve contrasts
Quadrupeds v. others	0.0038	-4.572	6	-0.013	7	0
Brachiators v. others	0.1633	1.838	3	0.008	1	3
Vertical clingers and leapers v. others	0.1603	1.857	3	0.011	1	3

Table P: t-tests of independent contrasts to test for differences in cerebellum size relative to the medulla for three different locomotor types (quadrupeds, brachiators and vertical clingers and leapers).

	p	t	d.f.	mean	-ve contrasts	+ve contrasts
Quadrupeds v. others	0.0039	-4.536	6	-0.013	7	0
Brachiators v. others	0.1756	1.766	3	0.008	1	3
Vertical clingers and leapers v. others	0.1776	1.755	3	0.011	1	3

Table Q: t-tests of independent contrasts to test for differences in cerebellum size relative to body weight for three different locomotor types (quadrupeds, brachiators and vertical clingers and leapers).

	p	t	d.f.	mean	-ve contrasts	+ve contrasts
Quadrupeds v. others	0.6177	-0.526	6	-0.009	3	4
Brachiators v. others	0.6385	0.521	3	0.018	1	3
Vertical clingers and leapers v. others	0.0890	-2.483	3	-0.033	4	0

The results show that the only significant correlations are between quadrupeds and cerebellum size relative to rest of the brain, and cerebellum size relative to the medulla. There is no significant difference in any of the measures of relative cerebellum size for either brachiators or vertical clingers and leapers. For both of the

significant correlations, all the contrasts in cerebellum size were negative, which indicates that quadrupedalism is negatively correlated with cerebellum size. This means that quadrupedalism can not explain the large size of the primate cerebellum and that the tendency is for non-quadrupeds to have a relatively large cerebellum. Thus it seems that some aspect of locomotor type may be associated with relative cerebellum size, however it is unclear what this aspect may be or how it relates.

5.3.1.4 Fine motor actions

Having so far found no convincing explanation for the large size of the cerebellum in great apes, it is now necessary to look at fine motor actions. The cerebellum plays an important role in fine motor actions and within the cerebellum, the LCN in particular is argued to play a prominent role in the control of these movements (Leiner et al., 1986; Kim et al., 1994). However, levels of proficiency of fine motor actions are extremely hard to measure. There is no clear scale of ability which relates to these high level motor activities and their investigation has been confined to the observation of various behavioural activities thought to involve fine motor action abilities. These behaviours include bimanual asymmetric coordination (BAC), extractive foraging and tool usage. While it is difficult to measure with any degree of accuracy the level of fine motor abilities from such investigations, it is possible to look at more general associations between cerebellum size and the ability of species to carry out these functions. If an association is found then it will be possible to focus attention on the great apes to see whether they have advanced skill levels for that particular function.

The data for BAC and tool usage come from van Schaik et al. (1999). They defined BAC as, "using the hands to perform different but complementary actions on a detached object" and used the example of accessing a fruit by holding it with one hand while peeling it with the other. Van Schaik et al. compiled a database from primary sources, classifying a species as engaging in BAC if it was clearly stated that, "an individual used two hands simultaneously and asymmetrically". In order to overcome the possibility of anomalous results due to the lack of studies which have

been carried out on some species, van Schaik et al. excluded species which had been poorly studied.

The data on tool usage from van Schaik et al. was split into "throwing objects" and "feeding tools" and was compiled from work by Beck (1980), Candland (1987) and Tomasello and Call (1997). For the purpose of the current analyses, those species which show any type of tool use, whether in the wild or in captivity, are classified as tool users.

The third type of fine motor action to be considered is extractive foraging. Data for this measure comes from Gibson (1986) who classified species as being either skilled extractive foragers, specialised extractive foragers, unskilled extractive foragers or non- extractive foragers. All those species which show any type of extractive foraging are classified as extractive foragers in the current analysis. Table P below shows which species carry out which fine motor actions.

Table R: Classification of the fine motor action abilities of 46 primate species

Species	BAC	Tools	E.F.
Alouatta seniculus	0	1	0
Aotus trivirgatus		0	
Ateles geoffroyi	0	1	0
Avahi laniger		0	
Callicebus moloch		0	
Callimico goeldii		0	
Callithrix jacchus	0	0	1
Cebuella pygmaea		0	
Cebus albifrons	1	1	1
Cercocebus albigena	1	1	0
Cercopithecus ascanius	0	1	0
Cercopithecus mitis	0	1	0
Cheirogaleus major		0	
Cheirogaleus medius		0	
Colobus badius	0	1	
Daubentonia madagascariensis	1	0	1

Erythrocebus patas	1	1	0
Galago senegalensis		0	
Galagoides demidoff		0	
Gorilla gorilla	1	1	1
Homo sapiens	1	1	
Hylobates lar	0	1	0
Indri indri		0	
Lagothrix lagothricha		1	1
Lepilemur mustelinus		0	
Loris tardigradus		0	
Macaca mulatta	1	1	1
Microcebus murinus		0	
Miopithecus talapoin		0	
Nasalis larvatus		1	0
Nycticebus coucang		0	
Otolemur crassicaudatus		0	
Pan paniscus	1	1	1
Pan troglodytes	1	1	1
Papio cynocephalus	1	1	1
Perodicticus potto		0	
Petterus fulvus		0	
Pithecia monachus		1	0
Pongo pygmaeus	1	1	1
Propithecus verreauxi		0	
Pygathrix nemaus		0	
Saguinus midas	0	0	0
Saguinus oedipus	0	0	0
Saimiri sciureus	0	1	1
Tarsius spectrum		0	
Varecia variegata	0	0	

For the blank boxes data is not available, for the “0s”, species have not been observed carrying out the action in question. In order to determine whether relative cerebellum size correlates with any of the measures of fine motor ability, the residuals (determined using a C.A.I.C.-derived slope) of the cerebellum against the rest of the brain, against the medulla and against body weight for the three measures of fine motor ability are plotted in Figures 5.4 – 5.12 below.

Figure 5.4: Cerebellum size relative to the brain - (neocortex+cerebellum) in primates which are (1) and are not (0) able to carry out bimanual asymmetric coordination (BAC)

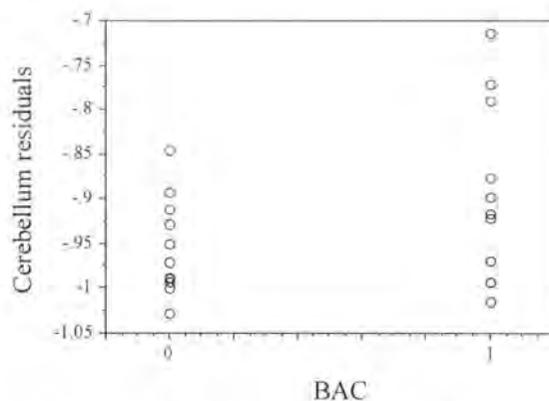


Figure 5.5: Cerebellum size relative to the medulla in primates which are (1) and are not (0) able to carry out bimanual asymmetric coordination (BAC)

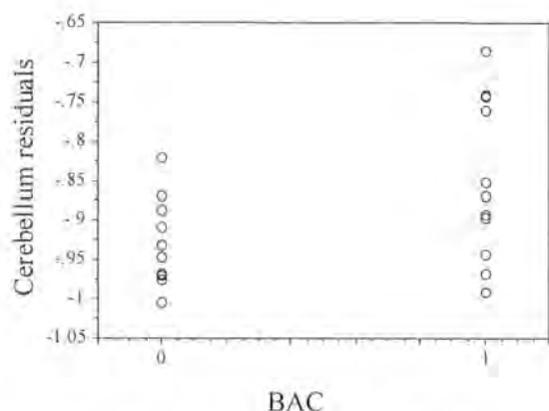
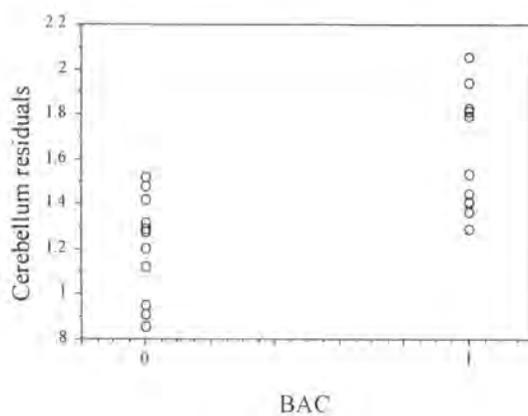


Figure 5.6: Cerebellum size relative to body weight in primates which are (1) and are not (0) able to carry out bimanual asymmetric coordination (BAC)



These figures indicate that there is overlap in the spread of the species which can and which cannot carry out bimanual asymmetric coordination (BAC) and it is therefore unlikely that a significant positive correlation will be found between any of the measures of relative cerebellum size and BAC.

Figure 5.7: Cerebellum size relative to the brain – (neocortex+cerebellum) in primates which do (1) and do not (0) use tools

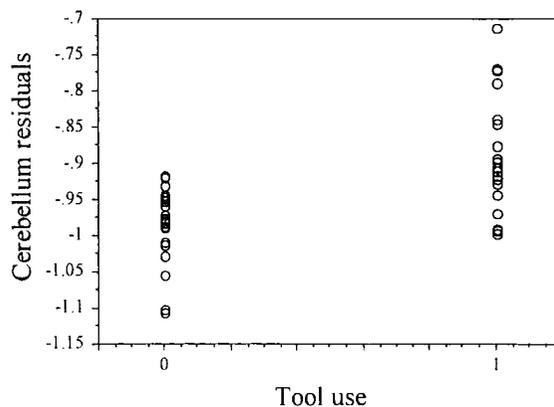


Figure 5.8: Cerebellum size relative to the medulla in primates which do (1) and do not (0) use tools

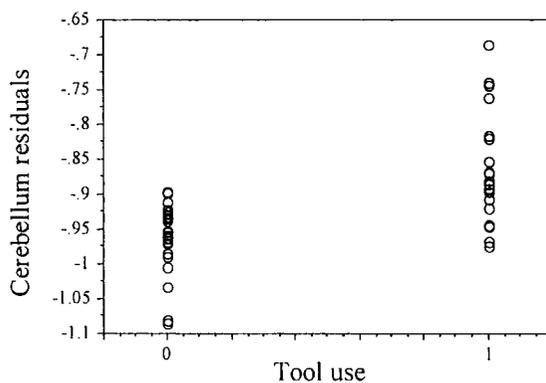
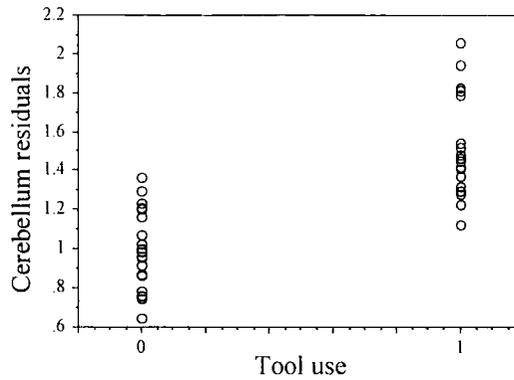


Figure 5.9: Cerebellum size relative to the body size in primates which do (1) and do not (0) use tools



These figures show that, although there is overlap in the relative cerebellum size of species which do and do not use tools, there is a tendency for tool-users to have a relatively larger cerebellum size in all three figures. This indicates that a significant correlation may be found between relative cerebellum size and the ability to use tools.

Figure 5.10: Cerebellum size relative to the brain – (neocortex+cerebellum) in primates which do (1) and do not (0) carry out extractive foraging.

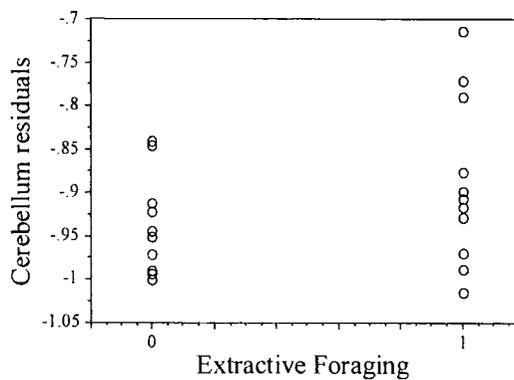


Figure 5.11: Cerebellum size relative to the medulla in primates which do (1) and do not (0) carry out extractive foraging.

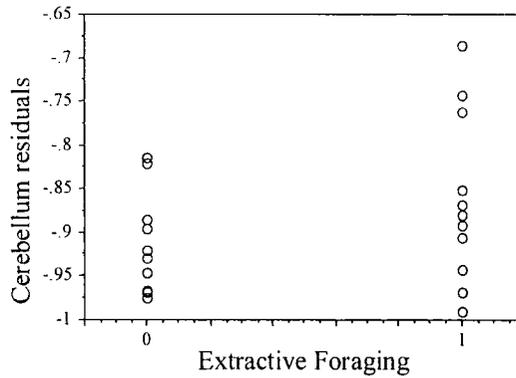
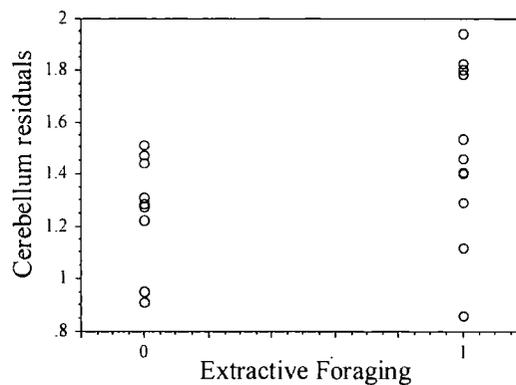


Figure 5.12: Cerebellum size relative to body size in primates which do (1) and do not (0) carry out extractive foraging.



From these figures there does not appear to be a very large difference between relative cerebellum size in the species which do and do not carry out extractive foraging. It is therefore unlikely that a significant correlation will be found between extractive foraging and any of the measures of relative cerebellum volume.

In order to assess the statistical significance of these analyses, t-tests on independent contrasts are carried out to determine whether relative cerebellum size differs

significantly in species which do and do not carry out the various different measures of fine motor actions. The results are shown in Tables Q, R and S.

Table S: t-tests on independent contrasts to test for significant differences in cerebellum size relative to the brain – (neocortex+cerebellum) for three measures of fine motor actions (BAC, tool use and extractive foraging)

	p	t	d.f.	mean	-ve contrasts	+ve contrasts
BAC	0.9474	0.070	4	-0.0003	2	3
Tool use	0.3032	1.181	4	0.011	2	3
E.F.	0.7569	-0.324	6	-0.002	4	3

Table T: t-tests on independent contrasts to test for significant differences in cerebellum size relative to the medulla for three measures of fine motor actions (BAC, tool use and extractive foraging)

	p	t	d.f.	mean	-ve contrasts	+ve contrasts
BAC	0.9448	0.074	4	0.001	2	3
Tool use	0.8347	0.223	4	0.002	1	4
E.F.	0.7707	-0.305	6	-0.003	2	5

Table U: t-tests on independent contrasts to test for significant differences in cerebellum size relative to body weight for three measures of fine motor actions (BAC, tool use and extractive foraging)

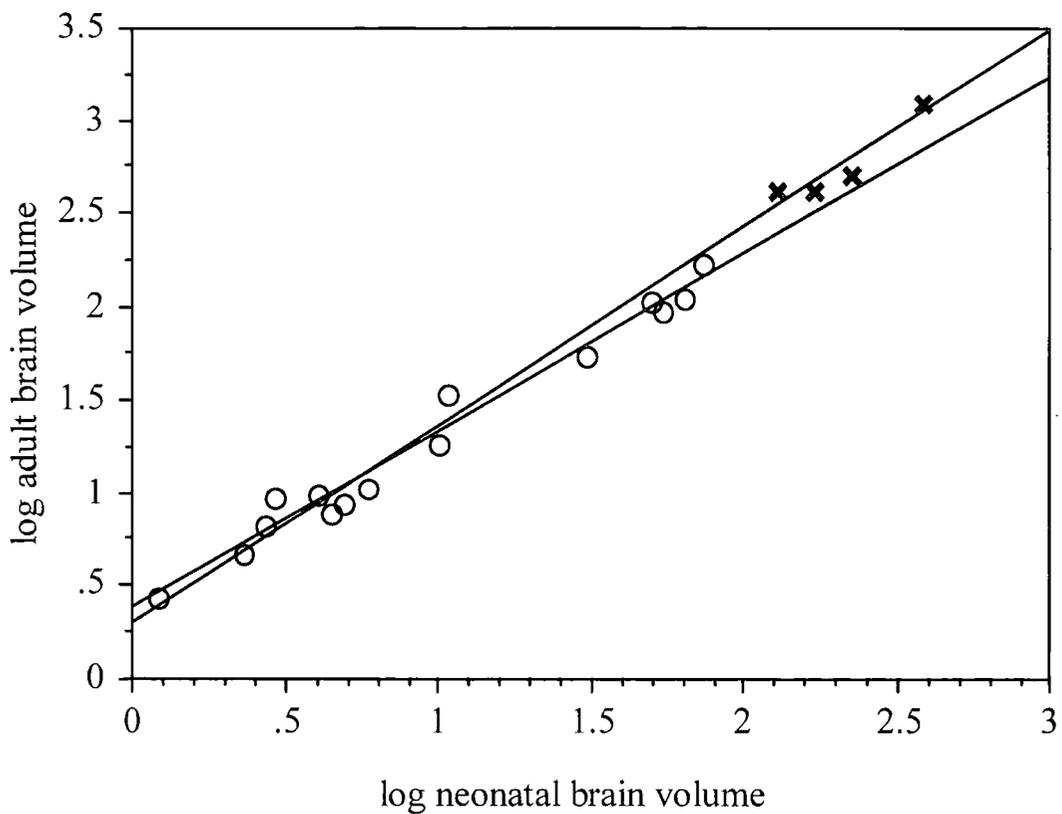
	p	t	d.f.	mean	-ve contrasts	+ve contrasts
BAC	0.9760	-0.032	4	-0.0003	3	2
Tool use	0.5568	-0.064	4	-0.012	2	3
E.F.	0.9713	-0.037	6	-0.0004	4	3

These results show that, after phylogenetic effects have been taken into account, there are no significant correlations between the relative measures of cerebellum size and any of the measures of fine motor actions. This is a surprising result, as the cerebellum is known to play an important role in fine motor actions (Matano and Hirasaki, 1997). However, there are a number of reasons why cerebellum size may still be correlated with fine motor actions despite these findings. These reasons, which will be discussed later (see Sections 5.4 and 6.1 (iii)), include the fact that only a very small sample size was used in the analysis and that the nature of the “BRUNCH” algorithm is such that small numbers of evolutionary transitions in the fine motor variables would mean that no significant correlations would be found. In addition, the correlation tested for was between cerebellum size and presence or absence of the different fine motor actions, rather than the degree of use or qualitative type of use. Finally, primates were not compared with other mammals here, and in such a comparison a significant result would be expected (Cartmill, 1974a).

5.3.2 Development of the cerebellum

In order to investigate whether great apes have a longer post-natal brain development period than other primates, neonatal brain volume is plotted against adult brain volume (Figure 5.13).

Figure 5.13: Neonatal brain volume plotted against adult brain volume for great apes (X) and other primates (O).



This figure shows that great apes are at the upper end of the distribution for adult brain size relative to neonatal brain size. The percentages of the neonatal brain compared to the adult brain (from Harvey, Martin and Clutton-Brock, 1987) are given in Table V:

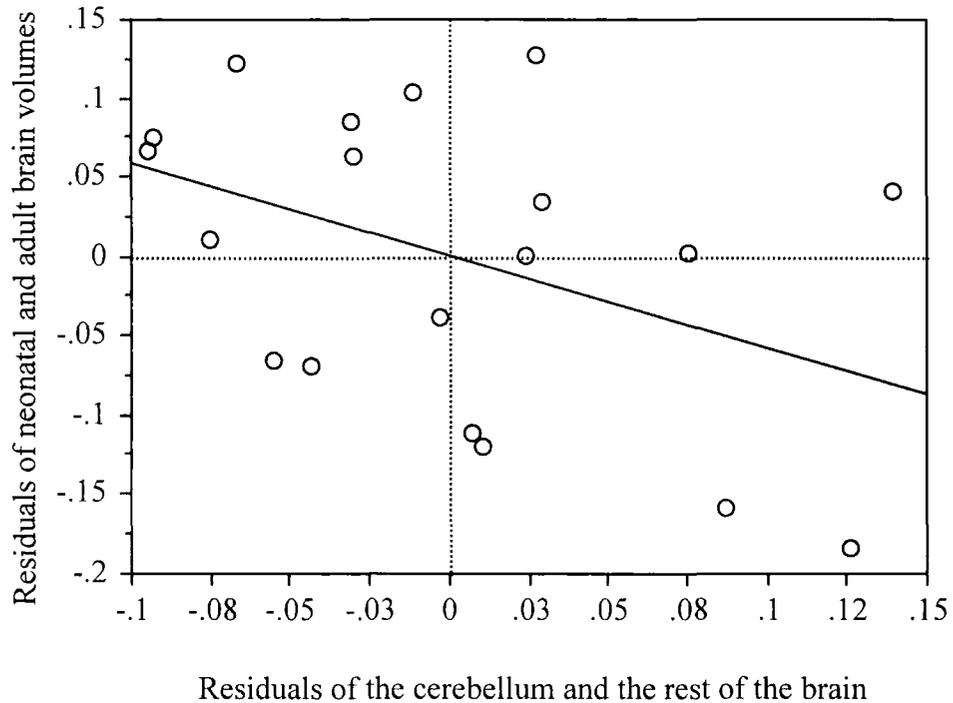
Table V: Neonatal brain volume as a proportion of adult brain volume in 19 primate species

Species	Neonatal brain volume as a proportion of adult brain volume
Alouatta palliata	0.559
Aotus trivirgatus	0.555
Ateles geoffroyi	0.577
Callimico goeldii	0.537
Callithrix jacchus	0.557
Galago senegalensis	0.479
Galagoides demidoff	0.444
Gorilla gorilla	0.449
Homo Sapiens	0.307
Hylobates lar	0.465
Lepilemur mustelinus	0.305
Loris tardigradus	0.403
Macaca mulatta	0.573
Nycticebus coucang	0.400
Pan troglodytes	0.312
Papio cynocephalus	0.435
Pongo pygmaeus	0.412
Saguinus oedipus oedipus	0.544
Varecia variegatus	0.310

These results provide preliminary support for the possibility that great ape brains undergo longer periods of postnatal development than do the brains of the other primates. As the cerebellum is one of the last brain areas to develop, the great ape cerebellum will cover most of its developmental stages postnatally. This will not be the case for other primates which undergo very little postnatal brain growth.

In order to test whether "late-developers" (species which reach maturity in brain size relatively late) have a large cerebellum, cerebellum size relative to the rest of the brain is plotted against neonatal brain size relative to adult brain size (Figure 5.14).

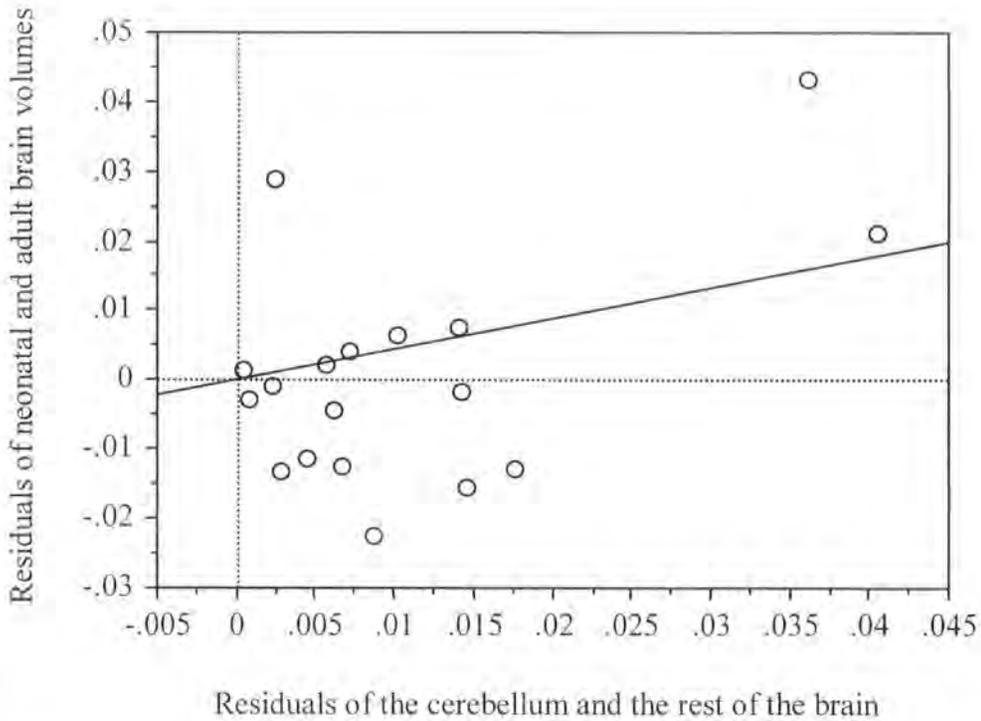
Figure 5.14: Neonatal brain volume relative to adult brain volume plotted against cerebellum volume relative to the rest of the brain.



This Figure indicates that late developers show a tendency towards having a larger cerebellum than earlier developers, however this is only supported at the $p = 0.10$ level of significance ($p = 0.0705$, $F = 3.724$, $d.f. = 18$).

Figure 5.15 shows the results of independent contrasts analyses which were carried out in order to determine whether there is a significant correlation between relative neonatal brain volume and relative cerebellum size once phylogenetic relationships are taken into account.

Figure 5.15: Regression plot after independent contrast analysis to show the correlation between cerebellum size relative to the rest of the brain, and neonatal brain volume relative to adult brain volume.



Analysis of covariance showed that when phylogeny is incorporated in the analysis, the correlation between relative neonatal brain volume and relative cerebellum size is not significant at $p = 0.05$, but is significant at $p = 0.10$.

5.4 Discussion

The results show that once phylogenetic relatedness has been taken into account, no significant correlations exist between scaled measures of the cerebellum and any of the ecological variables, the social variable (group size) or fine motor actions. The

only significant correlations were between scaled cerebellum measures and quadrupedalism. However, these were negative correlations, and quadrupedalism can therefore not explain the expansion of the primate cerebellum. The finding that there was no significant correlation between scaled cerebellar measures and any of the fine motor actions was particularly unexpected as the cerebellum is known to play an important role in such actions. Nevertheless, it is still possible that motor actions did influence the expansion of the cerebellum and that significant correlations were not found here because this investigation is beyond the scope of comparative methods. In the current analyses, correlations between relative cerebellum size and the presence or absence of various motor actions were investigated. It was, however, not possible to test for cerebellar correlates of differing levels of proficiency or mechanisms of execution of the fine motor actions, and it is very possible that it is in these respects that primates differ from one another. Furthermore, although the fine motor action abilities of primates and insectivores were not compared here, the fact that primates are able to carry out these actions, but insectivores are not, points to a difference between these two groups which is very possibly related to the difference in their relative cerebellum sizes. Thus, while no significant correlations were found between relative cerebellum size and measures of fine motor actions in the current investigations, it is still very possible that cerebellum size is associated with fine motor action abilities, but that in order to uncover this association, it is necessary to look at more intricate differences between primates in the way in which fine motor actions are carried out.

In the developmental investigation, the results showed firstly that the cerebellum of great apes has completed a smaller proportion of its development at birth, and secondly that those species that reach maturity in brain size relatively late (the "late-developers") tend to be the ones that have large cerebella. These results indicate that great apes have a longer postnatal brain development period than other primates, and that this might be associated with the large size of the cerebellum in these species. Because of the immaturity of this structure at birth, the great ape cerebellum will benefit from the experience of external stimulation throughout a large proportion of its development. The benefits for a motor structure of an animal being able to experiment with motor actions as it is developing are very strong. Imagine the advantage of being able to experience actions such as fine manipulation of the digits

in the environment in which the animal will spend the whole of its life. The level of acuity must far exceed that gained by other species whose only experience of motor actions are inter-uterine when they will be impeded by the presence of amniotic fluid.

It is important to note that whether the cerebellum is developing intra- or extra-uterine, the sequence of its development is similar among species. This means that for the 'premature' brains, the connections formed in cerebellar development will be more applicable to everyday life. This solid foundation will then be reinforced, strengthening connections as more and more experiences with motor components are gained. For the species whose brain is already well developed at birth, the experience of movements in the outside world may well not fit into their established cerebellar networks. Rather than strengthening cerebellar connections, the experience of movement in the outside world might instead mean that the connections formed within the womb need to be adapted or replaced.

Thus, as far as movement is concerned, the species who are born with an under-developed cerebellum will have a distinct advantage over other species in training the neural circuits underlying certain motor abilities. Whether this relates to all aspects of movement remains to be seen.

Support for the possibility that the cerebellum is strongly affected by external stimulation during its postnatal development comes from the observation that although the majority of the brain develops from the prosencephalon and mesencephalon, the cerebellum develops from the rhombencephalon (Rilling and Insel, 1998). This means that cerebellar development is not closely tied to the development of the rest of the brain, and that it is likely that, in response to external stimulation, it can change in size more readily than many other brain regions. This might go some way towards explaining how it was physically possible for the cerebellum to have shown such significant evolutionary increases in size both in primates as a group, and in great apes in particular due to their extended postnatal period of brain development.

Summary

To summarize, the aim of this Chapter was to find explanations for why and how the cerebellum expanded over primate evolution. Although the results showed no significant positive correlations between relative cerebellum size and any of the environmental variables tested (ecological variables, social group size and motor variables), it was argued that it is likely that, in line with its functions, cerebellum size is significantly correlated with fine motor actions. It was suggested that the reason why such an association was not found here is that the measures of fine motor actions were too general, they did not allow for variation in the level of proficiency or nature of the action among primates. The investigation of the development of the cerebellum showed that late developers tend to have a larger cerebellum than earlier developers. In addition, great apes seem to be born relatively prematurely compared to other primates, and the cerebellum, which is one of the last areas to develop, therefore undergoes much of its development postnatally when it can be affected by external stimulation. This can go some way towards explaining why the cerebellum could have shown such significant increases in size over great ape evolution and the fact that the cerebellum develops from a distinct precursor to the brain (rhombencephalon), could explain why the cerebellum was so prone to change in the evolution of the primate brain.

CHAPTER 6

Discussion and Conclusions

In summary, the results obtained from the empirical investigations (Chapters 3-5) showed that primates have an unusually large relative cerebellum size compared to insectivores, indicating that it was not only relative neocortex size that has increased in primate brain evolution. In addition, support was found for the co-evolution of the cerebellum and the neocortex. Furthermore, almost all of the structures and sub-structures of the cerebellar-neocortical system were found to exhibit correlated evolutionary size changes, thereby supporting the concept of mosaic evolution. When different groups of primates were compared, great apes were found to have unusually large cerebella. For both primates as a group, and great apes in particular, it appears that it is the non-nuclear cerebellum that has shown the most significant increases in size. Investigations into why the primate cerebellum showed such expansion over evolution found no significant positive correlations between any of the selection pressures tested and any of the measures of relative cerebellum size, although it was argued that cerebellum size is still likely to be correlated with measures of fine motor action abilities. Cerebellar expansion was also investigated from a developmental perspective, and it was found that great apes have an extended postnatal brain development period, and so the additional external stimulation received during that time may have affected its size.

The discussion of these findings that follows is split into two main sections. The first of these (6.1) will look at how the current results concerning the cerebellum and cerebellar-neocortical system fit in with previous work on primate brain evolution. The second (6.2) will look in detail at great apes in an attempt to identify the specific pressures which might have selected for an increase in the size of the cerebellum in great apes in particular and in primates in general.

6.1 Implications of the findings of the present study for previous theories of primate brain evolution.

The major theories purporting to explain the evolution of the primate brain are the Ecological Hypothesis and the Social Intelligence Hypothesis. These were outlined in Chapter 1, where it was concluded that although the Social Intelligence Hypothesis appears to best account for the current data, modifications would be necessary before either hypothesis could be accepted. It is now time to return to these hypotheses in order to determine whether they can account for the new findings and if they cannot, whether a new theory or a modified existing theory proves more promising.

(i) The Ecological Hypothesis

The finding that none of the three ecological variables tested (home range size, day journey length and percentage of fruit in the diet) were significantly correlated with cerebellum size when phylogeny was taken into account, suggests that they cannot explain increases in cerebellum size in primates. However, as it is not the cerebellum alone, but the whole of the cerebellar-neocortical system that has expanded during primate evolution, it is possible that the Ecological Hypothesis can partly account for overall brain expansion: it may be able to explain the expansion of the neocortex. Previous investigations of this possibility have not provided consistent results. For example, although Dunbar (1992, 1995) found no significant association between a number of ecological variables and neocortex size, Deaner et al. (2000) reported significant associations between neocortex size and home range size. Clearly, further investigation is needed here in order to determine whether or not neocortex size is significantly correlated with any ecological variables and thus whether such variables can explain the expansion of the neocortex over primate evolution.

(ii) The Social Intelligence Hypothesis (and the Machiavellian Intelligence Hypothesis)

The main support for the Social Intelligence Hypothesis comes from the finding that social group size is significantly correlated with neocortex size (Dunbar, 1992, 1995). However, Dunbar's findings are again questioned by those of Deaner et al. (2000) who did not consistently find significant correlations between group size and scaled neocortex measures.

In the present study, no significant correlation was found between social group size and cerebellum size, and so large social groups cannot be accepted as an explanation for the evolution of the large size of the cerebellum in primates. However, as was the case for the Ecological Hypothesis, the Social Intelligence Hypothesis may still explain the evolution of the neocortex. This depends on whether there should prove to be a significant correlation between social group size and neocortex size, a question that requires further investigation in the light of the controversy surrounding it.

Thus, although either ecological variables or social group size might be able to explain the expansion of the primate neocortex, they cannot explain the expansion of the other major structure in the cerebellar-neocortical system: the cerebellum.

(iii) Modifications of theories of primate brain evolution based on motor abilities

The findings of no significant associations between ecological and social variables and relative cerebellum size indicate that there were other influences affecting primate brain evolution. If either the Ecological Hypothesis or the Social Intelligence Hypothesis is to be accepted as an explanation of the evolution of the primate brain, they must be combined with other theories in order to be able to account for all the influences. This is not, however, an easy task as it is far from clear what these other influences might have been, or how they might have interacted. The most likely candidates are fine motor actions, as the cerebellum is known to play an important

role in these actions (Matano and Hirasaki, 1997). Although in the current investigations relative cerebellum size was not found to show significant correlations with any of the motor variables tested, it is still possible that cerebellum size correlates significantly with fine motor action ability. There are two main possible reasons why this association did not come to light here:

- a) **Limitations of the data:** The measures of fine motor actions used in the current analyses were very general in that merely the presence or absence of such actions was tested for significant correlation with relative cerebellum volume. What is far more likely is that it is particular aspects of fine motor actions that are associated with cerebellum size changes, such as the precision and complexity of the fine motor actions. This point is particularly important in the case of the great apes, which have demonstrated increased abilities in fine motor actions, arguably associated with advanced mental representation abilities (Byrne, 1997). This will be considered in some detail in Section 6.2 (i), but what must be noted here is that differences in the way in which fine motor actions are carried out by great apes, which could well be associated with their large cerebella, could not be tested in the current analyses.

- b) **Primates as a group:** In the current analyses, the focus was on uncovering patterns of cerebellar correlates *within* primates, rather than investigating why the cerebellum in primates as a group might have expanded. In order to investigate this using comparative methods, it would be necessary to look for correlations of relative cerebellum size in primates and other mammalian groups. Although these investigations are not within the scope of the current investigation, it is predicted that very strong correlations would be found between relative cerebellum size and measures of fine motor actions if primates and insectivores were included in the analyses. This is because it is well known that primates are very competent at motor actions and have high levels of hand-eye coordination (Cartmill, 1974a). As primates were found to have a significantly larger relative cerebellum size than insectivores, and as they appear to have superior fine motor action abilities (Cartmill, 1974a), it is likely that a correlation exists between relative cerebellum size and measures of fine motor actions. It is important to note, however, that such a correlation does not necessarily imply causation.

Nevertheless the well-established role of the cerebellum in fine motor actions would allow an implication of a causative link to be confidently made from a significant positive correlation.

These limitations of the current analyses mean that it is still very possible that the evolutionary changes in the primate cerebellum are associated with fine motor action abilities. Clearly further work is required here both to produce higher-level classifications of fine motor actions, and to look at cerebellar correlates in primates as a group.

Thus, it is argued here that while it is unclear what the precise nature of the influences were that affected the expansion of the primate cerebellum, it is likely that they were motor-related. It is proposed that in the evolution of the primate brain, different influences affected different parts of the cerebellar-neocortical system: whilst motor action variables may have affected both cerebellum size and neocortex size (as a system), social or ecological variables may have primarily influenced neocortex size. This would mean that there would be much variation in the size of the cerebellum and neocortex in different species.

Having considered possible explanations for the expansion of the cerebellum in primates as a group, the next section will consider the distinctive expansion of the cerebellum in great apes in an attempt to further investigate the possibility that fine motor actions (or some aspect of these) influenced the increase in the size of the cerebellum in primates as a group and possibly also in great apes in particular.

6.2 Explaining the large great ape cerebellum

Fine motor actions appear to have been the most likely reason for the large cerebellum in primates. However, it is important to remember that the cerebellum has been implicated in a number of cognitive functions, leaving open the possibility of cognitive explanations for its expansion. Such explanations in great apes in

particular receive support from the evidence presented in Chapter 1 for a cognitive difference between great apes and other primates (Byrne, 1995).

(i) Motor abilities and the Technical Intelligence Hypothesis revisited

It is not currently possible to accurately test whether great apes are more competent than other primates at fine motor actions which might be predicted if cerebellum size is associated with the ability to carry out fine motor actions as is argued here. However, the possibility that these are abilities in which great apes show advanced skill does seem to be in line with Byrne's Technical Intelligence Hypothesis detailed in Section 1.1.5.1 (v). Byrne (1997) claimed that compared to other primates, great apes have advanced mental representational abilities that enable them to plan and organise activities into goal-oriented sequences of actions. Tool use is a clear example of a goal-oriented action sequence. Chimpanzees, for example, use a variety of different sticks to probe termite nests in order to extract these insects which they then swiftly remove with the other hand and put into their mouths (an example of BAC) (McGrew, 1992b). In this example, chimpanzees direct their actions towards a food goal and the action sequence is the use of different sized sticks in the correct order to gain access to the termites. BAC, while not being a goal-oriented action sequence in itself, is however strongly involved in such sequences. One of the best examples of the importance of BAC in goal oriented sequences is in extractive foraging to access complex food items. Great apes need to feed on low-fibre foods because of their simple digestive tracts and as there is much competition over such foods, they have evolved the ability to access plant parts protected from other herbivores, such as those with hard or spiky casings (Byrne, 1997). Accessing these foods requires a number of fine motor actions to be put together in the correct order to form complex sequences of actions.

Relating these examples back to the Technical Intelligence Hypothesis, they seem to evidence the need to be able to mentally represent final goals in order for great apes to spend the time and energy carrying out these action sequences. The extent to which mental representations are important in the production of the action sequence, however, is unclear. Taking the protected food example, the sequences followed to

access these foods are generally carried out in precisely the same order time and time again (Byrne, 1997). This suggests that, while representations might be needed for the first few repetitions, sequences are likely to become learned over time so that representations become less important and sequences become habit. Nevertheless, however important representations might prove to be once sequences become learned, the fact remains that these sequences could not be learnt in the first place without the ability to produce mental representations. The Technical Intelligence Hypothesis is therefore viable as an explanation based on the acquisition of motor skills.

To summarize, whilst great ape competence at fine motor actions cannot, at present, be tested, the Technical Intelligence Hypothesis lends support to the idea that these activities are related to cerebellar expansion. This is because fine motor actions (BAC, tools use and extractive foraging in particular) are examples of activities which involve goal-oriented action sequences and it is therefore possible that the large size of the cerebellum in great apes is related to their ability to use mental representations to produce these complex action sequences.

In order to assess the validity of this argument, it is necessary to look within the cerebellum at precisely which areas have changed in size. It was noted in Chapter 1 that the cerebellum is made up of numerous different functional regions. By looking at the function of the regions that appear to have expanded in great apes, it should be possible to gain a better idea of the reason for the expansion.

(ii) A more detailed look at cerebellar expansion in the great apes

Within the cerebellum, it was demonstrated that the non-nuclear regions seem to have shown the greatest increase in size in great apes (the cerebellar nuclei were found to be particularly small in relative size). The non-nuclear areas include the cerebellar cortex (the major input structure of the cerebellum) as well as the sub-cortical white matter. The cerebellar cortex receives all the information coming into the cerebellum, projecting relevant information to the cerebellar nuclei and is clearly an important component of the cerebellum. In order to investigate why the cerebellar cortex might have expanded in great apes, it is necessary to look at its particular functions and to

determine whether these might be associated with the complex motor sequences considered above.

The primary function of the cerebellar cortex is the learning of motor skills (Marr, 1969; Jenkins and Frackowiak, 1993; Schweighofer et al. 1998). In order to investigate whether the cerebellar cortex could also be important for learning particular complex sequences such as those used by great apes and identified by Byrne (1997), it is necessary to go back to Marr's original theory of the functions of the cerebellar cortex. Marr (1969) argued that the one-to-one nature of connections between olivary cells and the purkinje cells of the cerebellar cortex is important. He claimed that each olivary cell is concerned with a particular movement (an "elemental movement") and that as a result of instruction received from the neocortex, different patterns of olivary cells fire. The output of these cells passes to the purkinje cells (via the climbing fibres) which then initiate the movement that is associated with the particular olivary cells from which the impulse was received. At the same time as they are receiving information from the olivary cells, Marr claimed that the purkinje cells are also receiving information about the context in which that cell fired, by means of mossy fibre input. He argued that purkinje cells are capable of learning these contexts so that when a movement has been repeated enough to become learned, context alone can cause purkinje cells to fire and produce the elemental movements. That is, in the absence of input from the neocortex to the olivary cell or from the olivary cell to the purkinje cell, particular movements can still be executed through context recognition. The cerebellar cortex thus learns to produce motor actions. (See Houk et al. (1996) for a recent review of models of the cerebellar cortex).

But, can this explain the complex motor abilities of great apes? An increase in the size of the great ape cerebellar cortex would suggest an increase in the number of cells within this area. This would include an increase in the number of purkinje cells, indicating that there would be an increase in the quantity or quality of information processing. Therefore, it seems very possible that the increase in the size of the cerebellar cortex in great apes could be associated with the performance of complex motor actions such as BAC, tool use or extractive foraging, which would require higher level information processing abilities. However, there is as yet no direct evidence that the cerebellar cortex is involved in the ordering of actions *per se* which

is a significant part of these complex motor sequences. This means that, while there is good evidence that the cerebellar cortex is involved in learning motor actions, it is not clear whether or not this area of the cerebellum is involved in ordering these actions into complex sequences.

It is in fact very possible that another area of the cerebellum is involved in the ordering of learned motor actions. The prime candidate for this function would be the lateral cerebellum, the area of the cerebellum which has consistently been implicated in the planning of motor actions (Allen and Tsukahara, 1975; Eccles, 1977; Smith et al. 1993; Timmann et al., 1999). The lateral cerebellum includes the lateral cerebellar cortex, the dentate nucleus and the white matter in between and the reason why the planning abilities of these regions are important here is that the ability to order motor actions into complex sequences clearly implies the ability to plan. This is because planning requires there to be some awareness of the intended outcome and so the order in which actions need to be carried out. As the ordering of actions into sequences is an ability argued to be possessed by great apes but not by other primates, it would be predicted that the lateral cerebellum is significantly larger in great apes. The lateral cerebellum includes the dentate nucleus and this is the nucleus which Matano (2001) found to have shown internal re-organisation in humans. If the lateral cerebellum is the area which has expanded in great apes, then it is likely that although the dentate nucleus as a whole did not expand (see Section 4.5.1 (ii)), different areas within the great ape dentate nucleus changed in size – i.e. there was internal reorganisation. Unfortunately a lack of available data means that it is not currently possible to test this prediction (although the current results suggest that the cerebellar cortex, which includes the lateral cerebellar cortex, has expanded in great apes).

To summarize, the area of the cerebellum which has probably shown the greatest increase in size in great apes is the cerebellar cortex. The primary function of the cerebellar cortex is the learning of motor actions. In addition to learning motor actions, great apes are thought to be able to order actions into sequences and evidence suggests that the lateral cerebellum is involved in this activity. This would indicate that the lateral cerebellum should be larger in great apes, but a lack of data means that it is not currently possible to test this prediction. Thus, it is argued that because of

their large cerebellar cortex, great apes can learn motor actions and once these actions are learned, they can be ordered into complex sequences by the lateral cerebellum.

(iii) Consolidation of Discussion: Theories of cerebellar expansion in great apes

It is clear that further investigation is needed to determine exactly which areas of the cerebellum have expanded in great apes. However, on the basis of the current data, it is possible to propose a number of hypotheses as to why the African great ape cerebellum showed such a significant expansion over evolution:

Hypothesis 1: The large size of the great ape cerebellum is a reflection of the large size of the cerebellar cortex. Great apes have a large cerebellar cortex because they have an increased need for learning more complex motor actions in order to deal with the increasing degrees of freedom presented by their extending habitats (as indexed, for example, by their need for fine motor actions to access hostile foods).

Hypothesis 2: The area of the cerebellum that has shown the most significant increase in size is not the cerebellar cortex, but rather it is the lateral zone. Great apes have a large lateral cerebellum because they have an increased need for planning complex motor actions (such as preparing tools for future use). The lateral cerebellum is known to be implicated in planning.

Individually, neither of these hypotheses can adequately account for the advanced abilities of great apes. This suggests either that both accounts together might be correct, or that they should be combined into one as in Hypothesis 3 below:

Hypothesis 3: The lateral cerebellar cortex is the area of the cerebellum that has shown the most significant increase in size in great apes and which is reflected in the large size of the cerebellum as a whole in these species. The lateral cerebellar cortex includes areas for motor learning and for more cognitive skills such as motor planning. It is the only area of the cerebellum to receive direct information from the

neocortex, which supports findings that it is strongly involved in the cognitive functions of the cerebellum, including mental imagery (Ryding et al., 1993).

In line with the Technical Intelligence Hypothesis, it is argued that a large lateral cerebellar cortex allows great apes to plan and order complex sequences of motor actions using mental representations of the relevant goals. The lateral cerebellar cortex theory links the special selection pressures argued to act on great apes by the Technical Intelligence Hypothesis (complex motor actions) with the finding of which particular brain areas have increased in size in these species (the cerebellar cortex – possibly the lateral areas in particular). It is granted that this is somewhat hypothetical as it relies on the correct identification of the selection pressure (complex motor actions) plus the correct understanding of what is involved in such complex motor actions, and hence what part of the brain might be responsible. Nevertheless, the increasing evidence of a cerebellar role in cognition (coming mainly from work carried out on humans) and the finding that the cognitive cerebellar areas are likely to have enlarged in great apes, suggests that the prime explanation for cerebellar expansion in these species is a particular type of cognition. As this cognition seems to be mainly linked to motor actions (the established function of the cerebellum), this function will be called ‘Motor Cognition’, which may well be wider in some respects than the function of technical intelligence that was referred to earlier. To summarize, this theory argues that the large size of the great ape cerebellum is in fact a reflection of the large size of the lateral cerebellar cortex which has expanded due to the need for cognitive abilities related to complex motor actions, that is, the need for motor cognition.

Out of these three theories, the third one certainly seems to be the most plausible as it can account for the advanced abilities which set great apes apart from other primates. It would be easy to test this theory by looking at whether it is the lateral cerebellar cortex in particular which has increased in size in great apes. Unfortunately, current data limitations mean that this will have to wait until more volumetric measurements are available.

(iv) Explaining the large cerebellum in primates as a group

Having looked at the expansion of the great ape cerebellum in such detail, it is important to relate these findings back to theories of brain evolution in primates as a group. Support was found for the idea that, despite their general tendency to evolve together, different selection pressures may have acted on the neocortex and the cerebellum, as it was argued that the increase in the size of the cerebellum in great apes is associated with a need for increased motor learning and planning abilities. This means that it is likely that, although the cerebellar-neocortical system tended to evolve as a whole in primates, particular selection pressures acted on the neocortex and cerebellum to different degrees in different lineages. Thus, ecological or social pressures could have been the prime cause of an increase in neocortex size, while improved motor abilities would have been associated with the large cerebellum.

One important question that remains unanswered here is which aspect of the motor abilities that were associated with an increase in the size of the cerebellum in primates as a group meant that they acted as selection pressures? The theory proposed here, which appears to best account for the large size of the great ape cerebellum, asserts that the great ape difference is due to advanced cognitive abilities related to motor action, that is motor cognition. These particular abilities cannot be present in all other primates, or else they too would have cerebella as large as those of the great apes. It is argued here that although other primates are capable of motor learning, what they lack is this motor cognition – they do not possess the same level of cognitive abilities as great apes which enable them to plan and manipulate fine motor actions to very high levels of proficiency. Thus the aspect of fine motor actions that is likely to be associated with the increase in the size of the *primate* cerebellum is that they are prone to being learnt; through practice primates become very competent at fine motor actions which are important in their everyday lives because of the large size of their cerebella.

Thus, the difference between primates and most other mammals is that primates are capable of advanced motor learning, which is what selected for their large cerebellum. It is predicted that it is the cerebellar cortex in particular that has expanded in primates, as this is the area for motor learning. This possibility receives

support from the earlier finding that it is the non-nuclear cerebellum in particular that has expanded in primates compared to insectivores. Furthermore, the difference which sets great apes apart from other primates, and the reason why great apes have an unusually large cerebellum, is that great apes possess advanced abilities which have here been called motor cognition.

6.3 Conclusions

The evolution of the primate brain involved an increase in the whole of the cerebellar-neocortical system. Within this system, the expansion of the cerebellum is argued to be associated with increased motor learning abilities in primates, whereas the expansion of the neocortex, although still somewhat controversial, is likely to be associated with the increasing complexity of social relations. It is argued that because different selection pressures acted on the cerebellum and neocortex, these changed in size to different degrees depending on the particular selection pressures acting on individual species, resulting in a continuum of cerebellum and neocortex size amongst different species. Within primates, African great apes were shown to have a particularly large cerebellum and it is argued that this is due to more than just increased abilities in motor learning. It is claimed that, in line with Byrne's Technical Intelligence Hypothesis, great apes have certain cognitive abilities not present in other primates and which are directly related to motor actions. These abilities together are termed motor cognition, and it is argued that the large size of the great ape cerebellum is associated with a need for motor cognition.

6.3 Future directions

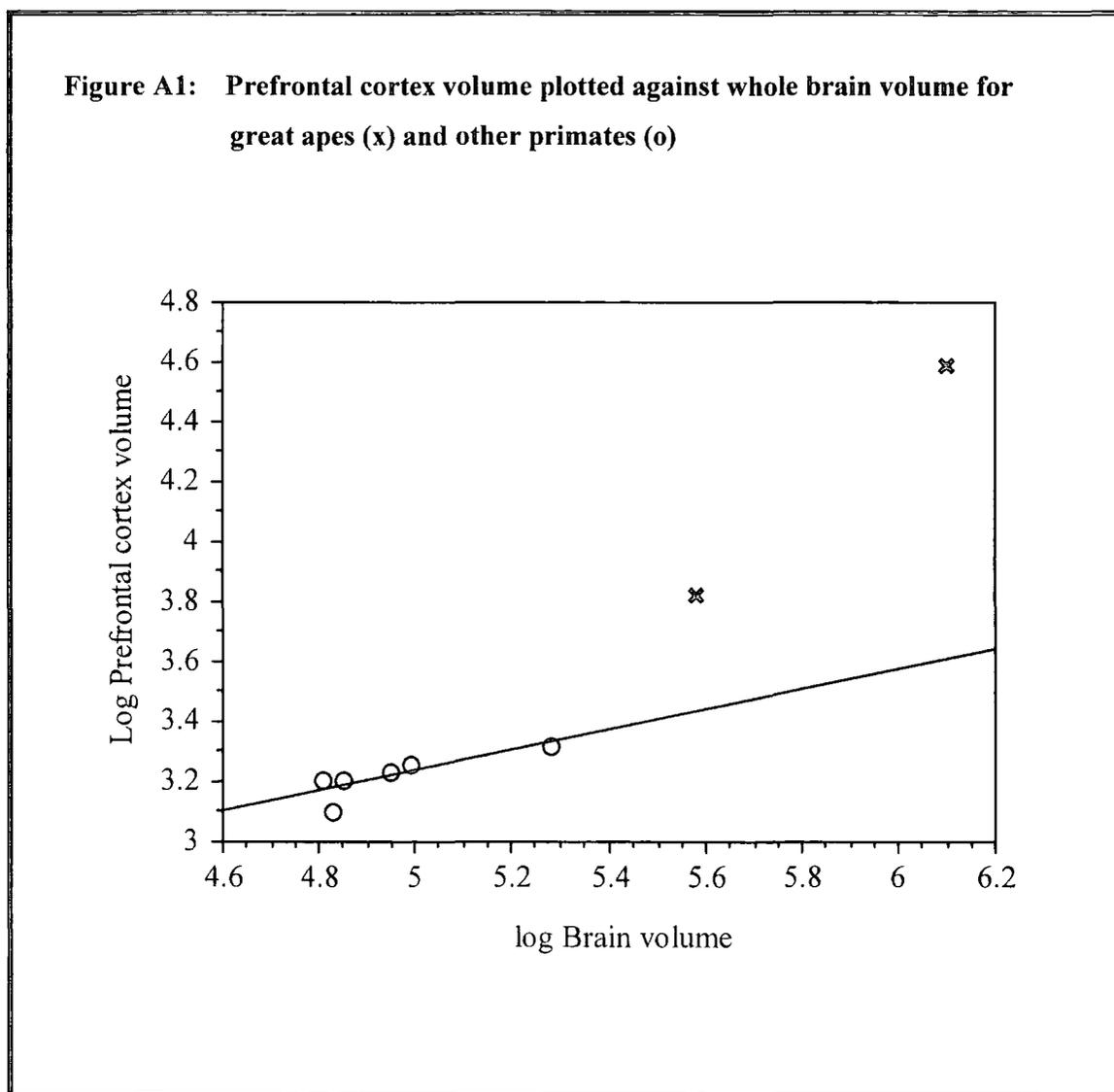
- (i) **Neuronal density:** An important investigation that needs to be carried out is the assessment of the variation in cell size and number in different brain structures and in different species. The use of volumetric measurements depends upon the assumption of a similar concentration of neurons within a particular area, however a lack of studies means that there has as yet been no test of the validity of this assumption.

- (ii) **Volumetric measurements:** In order for investigations into primate brain evolution to advance, work is needed to calculate volumetric measurements of the following:
 - a) **Brain structures:** There is a need for more data on the volumes of brain structures both at the species and individual level. This is particularly true for great apes, for whom there is a relative paucity of brain volume data currently available.
 - b) **Particular regions within brain structures:** In addition to a general need for more data on brain structures, it is important to have more specific measurements of particular brain areas. Areas for which volumetric measurements would be particularly useful in the light of the current investigations include: the motor, premotor and prefrontal cortices; individual thalamic nuclei; the cerebellar cortex and the lateral cerebellum.

- (iii) **Fine motor actions:** In order to be able to test whether there is a significant correlation between relative cerebellum size and proficiency at fine motor actions, higher-level classifications of fine motor action abilities are needed. Such classification would relate to the precision and complexity of types of motor action, and the relative proficiency of the various primates. These studies should also take in other mammalian groups such as insectivores in order to provide a comparison for primate studies.

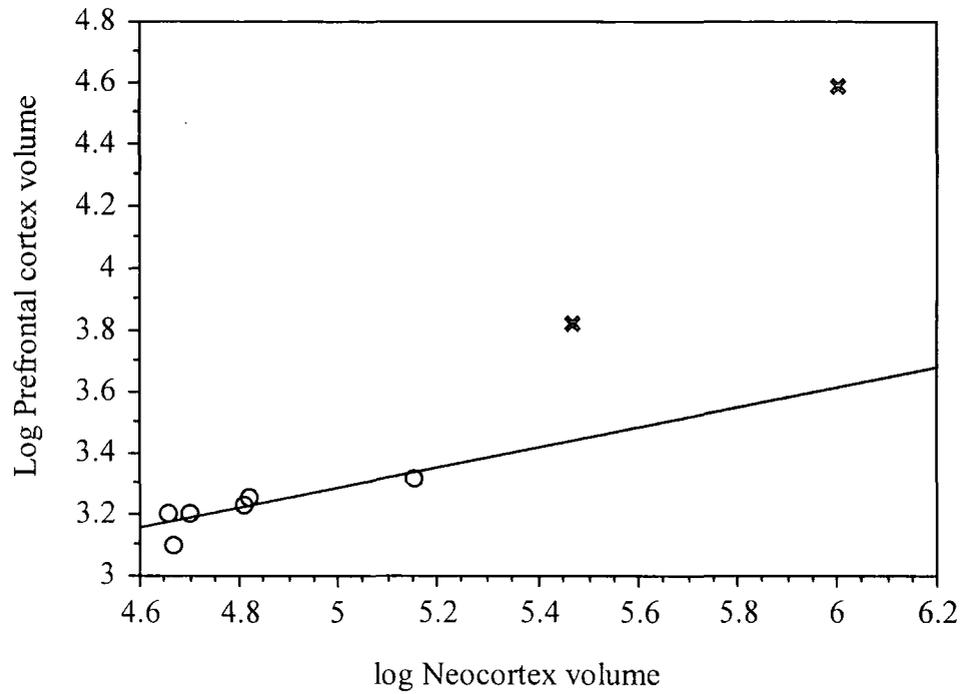
Appendix A

Figures A1-A3 are included here to provide very preliminary evidence that the prefrontal cortex, which has strong connections with the cerebellum (Middleton and Strick, 2001) is also unusually large in great apes. The data on the "Regio frontalis" (prefrontal cortex) comes from Brodmann (1912). There are only two great ape measurements available - *Homo sapiens* and *Pan troglodytes*.



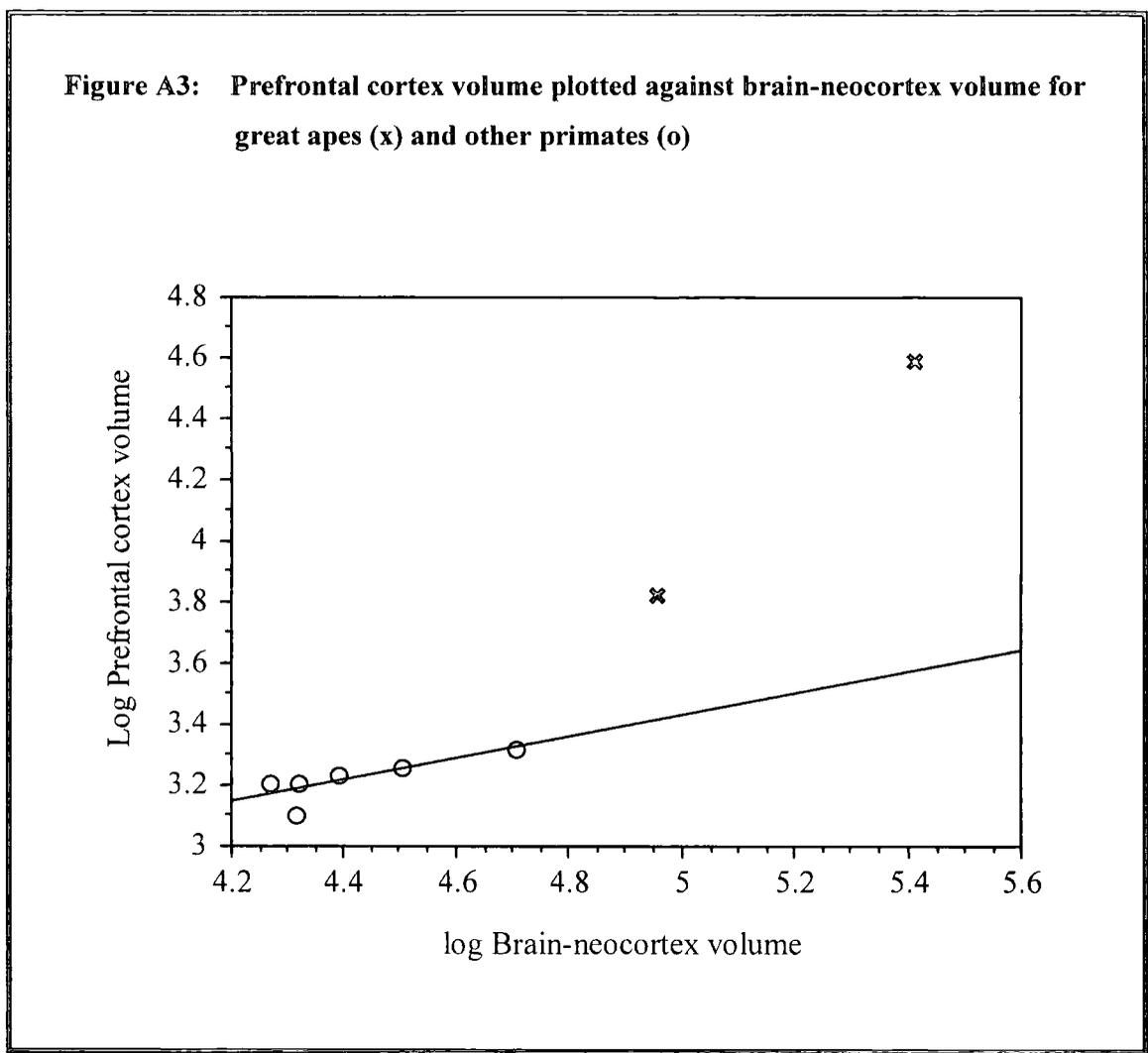
The great ape prefrontal cortex appears to be larger than that of other primates compared to the volume whole of the brain.

Figure A2: Prefrontal cortex volume plotted against neocortex volume for great apes (x) and other primates (o)



Even compared to the neocortex, the great ape prefrontal cortex appears to be unusually large compared to that of other primates.

Figure A3: Prefrontal cortex volume plotted against brain-neocortex volume for great apes (x) and other primates (o)



Relative to non-cortical brain size, the prefrontal cortex is unusually large in great apes.

These preliminary results thus indicate that it is likely that great apes have particularly large prefrontal cortices in line with the large size of the great ape cerebella with which it has strong connections. Clearly there is a need for more measurements of prefrontal cortex volume in more species and further investigations into relative prefrontal cortex volume in primates will have to wait until such data is available.

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