

SIZE AND SHAPE OF THE CEREBELLUM IN CATARRHINE PRIMATES AND
PLIO-PLEISTOCENE FOSSIL HOMININS: A PALEONEUROLOGICAL
ANALYSIS OF ENDOCRANIAL CASTS

by

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ABSTRACT

Size and Shape of the Cerebellum in Catarrhine Primates and Plio-Pleistocene Fossil Hominins: A Paleoneurological Analysis of Endocranial Casts

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Over the past several decades, neuroscientists have expanded scientific understanding of the function of the primate cerebellum. Experimental and clinical evidence has revealed that the cerebellum plays a role in both motor and cognitive functions. The strong link between the cerebellum and neocortical areas associated with higher cognitive functions makes this structure an important piece in the puzzle of human brain evolution.

This dissertation utilizes endocranial casts of five primate species (*Macaca*, *Hylobates*, *Pongo*, *Gorilla*, and *Pan*) and eight Plio-Pleistocene fossil hominins (*Australopithecus*, *Paranthropus*, *Homo*) to examine the evolution of cerebellum size and shape through time. Linear and geometric morphometric techniques are employed to quantify the size and shape of the posterior cranial fossae (representing the cerebellum) and endo-basiscranial surfaces of catarrhine and fossil endocasts.

Three general questions are tested in this dissertation. 1) Do cerebellum size and shape show grade level differences in this sample of catarrhine primate endocasts? 2) Are cerebellum size and shape laterally asymmetrical? 3) Are cerebellum size and shape sexually dimorphic?

The major empirical findings of this work are: 1) analysis of linear cerebellar measurements reveals no statistically significant lateralization or dimorphism in the total catarrhine sample; 2) linear measurements indicate that macaque males are significantly larger than females in cerebral length, cerebellar breadth, and cerebellar length, 3) absolute measurements of cerebellum size appear to parallel cognitive advancements in catarrhine evolution more closely than relative or index measures, 4) cerebellum shape appears to differ between grades of primates, 5) *Macaca* cerebellum shape and basicrania as determined by landmarks and geometric morphometric techniques are lateralized and sexually dimorphic; 6) principal components analyses of cerebellum landmarks alone and in conjunction with other basicranial landmarks reveal an antero-posterior foreshortening and a medio-lateral expansion in cerebellum and basicranial shape from monkeys to hominoids; 7) hominins and apes differ mainly in the position of the landmark representing the location of the foramen magnum.

DEDICATION

This dissertation is dedicated with love and affection to my parents, John and Carolyn White. Thank you for your constant support and faith in my abilities.

*

A EKA

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PART 1: INTRODUCTION

In the past two decades, great leaps have been made in the field of cognitive neuroscience based extensively on recent technological achievements in medical neuroimaging (Raichle, 1998). These technological leaps have provided a new means with which to observe and explore the seemingly limitless complexity of the human mind. Procedures such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have provided researchers with an extraordinary opportunity to create detailed functional maps of the living human brain (Friston, 1998). These procedures have also enabled neuroscientists to effectively re-evaluate conventional knowledge of brain function, verifying and in some cases modifying previous beliefs. One area in which these innovations have inspired significant reassessment is the study of cerebellar function (Schmahmann, 1997).

To appreciate the improvements made in our general understanding of the cerebellum we must begin with the standard “classical” definition of cerebellar function. One introductory neuroanatomy text provided this definition:

“Although the cerebellum has an abundant input from sensory receptors it is essentially a motor part of the brain, functioning in the maintenance of equilibrium and the coordination of muscle action in both stereotyped and nonstereotyped movements. The cerebellum makes a special contribution to synergy of muscle action (i.e., to the synchronization of muscles that make up a functional group), ensuring that there is contraction of the proper muscles at the appropriate time, each with the correct force (Barr and Kiernan, 1993:160).” [Emphasis added]

This simple, clear definition of cerebellar function can be found in any introductory anatomy text from as early as 1906 up to the present. The concept of

cerebellum as motor coordinator and muscle synchronizer has been tested and supported in numerous animal species (Babinski, 1902; Bolk, 1906; Dow and Moruzzi, 1958; Eccles et al., 1967; Ferrier and Turner, 1893; Holmes, 1917; Ito, 1984; Sherrington, 1906). Research conducted in the past 20 years, however, shows that this definition tells only part of the story.

Neuroimaging studies of humans with both normal and pathological cerebellums have revealed that the synchronizing, coordinating role of the cerebellum may be involved not only in motor but also non-motor (i.e. cognitive) functions. These functions include activities such as the generation of verbs, synonyms, rhymes (Martin et al., 1995; Petersen et al., 1988; Raichle et al., 1994), translating (Klein et al., 1995), working memory (Fiez et al., 1996; Fiez and Raichle, 1997), planning behavior (Schmahmann and Pandya, 1997), musical ability (Falk, 2000; Hutchinson et al. 2003) and abstract reasoning (Leiner et al., 1986; 1989; 1991; 1995). This research has done nothing less than revolutionize our thinking about the relative importance of the cerebellum in the study of brain function, psychology and paleoanthropology.

For most of this century brain researchers interested in the cerebellum have wondered about the phylogenetic and functional implications of the enlarged lateral cerebellar hemispheres in *Homo sapiens* (Dow, 1942,1974; Leiner et al., 1989; Passingham, 1975). It has been hypothesized that a phylogenetically new structure, the ventrolateral dentate nucleus, developed in humans in relation to lateral cerebellar hemispheres. This simultaneous enlargement of the dentate and the cerebellar hemispheres has traditionally been explained by the processing power needed to perform fine motor skills and maintain equilibrium while walking erect (Matano et al.,

1985a,b). However, a new theory of cerebellar function suggests that this relatively large increase in cerebellar and dentate size may be a consequence of processing both motor and non-motor (cognitive) information (Leiner et al., 1986). Although there is some debate (MacLeod, 2000), most current neuroimaging research has supported these claims and changed the perception of the cerebellum in the scientific community. Fortunately, as paleoneurologists we have the ability to approach the study of human cerebellar evolution directly from the fossil hominin record, and it is therefore possible to re-interpret the rarely considered fossil evidence of cerebellar morphology (Weaver, 2005).

In this dissertation, I utilize linear measurements and geometric morphometric techniques on endocranial casts (endocasts) of catarrhine primates and Plio-Pleistocene fossil hominins in order to quantify the size and shape of the area that represents the cerebellum. This is the first study to employ geometric morphometrics to study primate and fossil hominid cerebellum from endocasts.

Chapter 1 focuses on the development of our understanding of cerebellar function and how it has changed dramatically through time. Chapter 2 introduces the basic biology of the the cerebellum as well as the clinical and experimental evidence that make up our current understanding of this important brain sub-structure. Chapters 3 through 5 provide the results of my analysis of catarrhine and fossil endocasts. Chapter 3 is a study of the linear size of the catarrhine posterior cranial fossa. Chapter 4 is a geometric morphometric analysis of the size and shape of the posterior cranial fossa and Chapter 5 is a geometric morphometric analysis of the endo-basicranium of these endocasts.

CHAPTER 1: A BRIEF HISTORY OF CEREBELLAR RESEARCH

In order to thoroughly understand the sweeping changes in cerebellar research and its implications on human brain evolution it is important to examine the historical ideas, which led to our current state of knowledge. The main objective of this chapter is to explore the historical theories and developments that led to the classical and quite recent modern definitions of cerebellar function (Table 1-1). Due to the exponential growth of recent research, these developments will be separated into two parts. The first part this chapter will deal with the first advances in cerebellar research spanning a period of approximately 2500 years and proceed chronologically to the present. The second part of this chapter will focus on the last 50 years of animal, clinical and medical neuroimager research, which has provided a new way of approaching cerebellar function and evolution. Finally, the importance of these advances will be discussed relative to our understanding of human brain evolution and the hominin¹ fossil record.

¹The term “hominin” -based on Tribe *Hominini* -is preferred to the more familiar term “hominid” because it reflects the understanding from molecular phylogenetics that *Pan*, *Gorilla*, and *Homo* are more closely related to each other than any of the three are related to *Pongo*. In this dissertation, hominin refers to modern humans and all direct fossil ancestors of modern *Homo sapiens* since the split with the common ancestor of modern *Pan* and modern *Homo* (Wood and Richmond, 2000).

TABLE 1-1 Selected theories of cerebellar function throughout history

Author	Year	Theory
Galen	ca A.D. 200	Source of motor nerves and the origin of the spinal cord.
da Saliceto	ca 1200	Origin of involuntary and vital movements
Vesalius	1543	Memory
Varolio	1573	Hearing and taste
Willis	1664	Involuntary motor functions
Malacarne	1776	Intelligence
Foville and Pinel	ca 1800	Sensation
Walker and Grohmann	ca 1800	Cerebellum and will
Von Walther	ca 1800	Animal instincts
Gall	ca 1800	Sexual excitation
Rolando	1809	Motor production
Magendi	1823	Forward motion and equilibrium
Flourens	1824	Motor coordination
Gowers	1888	Psychical processes
Luciani	1891	Coordination of muscles
Babinski	1902	Coordination of smooth movements
Sherrington	1906	Proprioception and coordinated movement
Bolk	1906	Coordination and functional localization
Dow	1942	Higher cognitive abilities

Developing a definition of cerebellar function

The Hellenistic period

The Greeks provided modern biology with three fundamental traditions of scientific thought that formed the essential foundation for the development of modern biological thinking. The first tradition comes from the interest that the ancient Greeks showed for observing the natural world. They catalogued hundreds of varieties of plants and animals and documented their utility for society. This tradition, called natural history, provided two essential ingredients in modern scientific research; careful observation and the comparative approach to problems (Mayr, 1982).

The second tradition passed down from the ancient Greeks came from the Ionian school of thought and provided an important step away from mystical or supernatural explanations of natural phenomena. The philosophers of the Ionian school sought to explain their observations of natural events with natural causes. They observed basic physiological functions such as reproduction and perception and tried to find real world explanations. Unlike today, the early Greek philosophers did not use experimentation to seek solutions to biological problems. Instead, they believed that concentration and cogitation could provide logical, natural solutions to every question (Clarke and O'Malley, 1968; Mayr, 1982).

In the sixth century, the center of philosophical thought moved from Greece to the Greek colonies in southern Italy. There, philosophers such as Pythagoras and Empedocles endeavored to find universal explanations for natural events. Empedocles, in particular, linked everything in the natural world to four basic elements- earth, air,

water, and fire (Clarke and O'Malley, 1968). This concept deeply influenced the perception of the natural world and the understanding of human biology well into the Renaissance period.

It was during the sixth century that Alcamaeon of Crotona, Italy and Anaxagoras (500 - 428 B.C.) first proposed the brain as the essential organ of sensation and thought. This earliest proposal was probably based on observations of injured or sick animals, although the primary sources no longer exist. Nonetheless, centering sensation and thought in the brain was a clear breaking point with the strong cardiocentric localization of "mind" (discussed below) (Clarke and O'Malley, 1968).

The third essential tradition developed by the Greeks was the study of biomedicine. This tradition focused essentially on the understanding of basic anatomy and physiology. The first empirically developed study of human anatomy and disease was developed by the Greek physicians of the Hippocratic school (Mayr, 1982).

Hippocratic Writers

Hippocrates (460 - 370 B.C.) was a clinician, scientist, and teacher who, through his school, extensively documented clinical observations of human disease and trauma. The major contribution of the Hippocratic School is a multivolume work called the *Corpus Hippocraticum*. In this work, the Hippocratic writers linked the symptoms they observed in patients with seizure disorders and paralysis to the dysfunction of the brain. Consequently, they regarded the brain as the central organ of sensation, thought, and emotion. This belief however, was difficult to justify for two main reasons. Firstly, early physicians astutely recognized that people with traumatic head injuries sometimes exhibited similar symptoms to patients with non-injury related disorders such as

epilepsy or stroke. Unfortunately, the physical and/or behavioral manifestations of brain pathology could not be clearly linked to their actual anatomical sources because both human and animal dissection was proscribed during the Hellenistic period (Finger, 1994).

The second reason concerns the prevailing idea that the heart (not the brain) was the center of sentient and emotional activity. This belief has been traced historically as far back as the ancient Egyptian world where, at death, the life of the individual was evaluated by literally weighing the heart. The Book of the Dead shows the god of the dead, Anubis (jackal-god) measuring the heart of the deceased against the feather of the goddess Maat (truth) in order to determine the persons worthiness to enter Paradise. If the individual lived a good moral life the heart was not heavy with sin and balanced on the scales of truth. In this case a blissful afterlife was assured. If the heart was heavier than the feather of truth, the monster Ammit (the Gobbler) devoured the heart and soul of the deceased leading to eternal suffering. It was for this crucial ceremony that the ancient Egyptians preserved the heart inside the body during the mummification process while all the other organs, including the brain, were removed. Some organs, (liver, lungs, stomach, and intestines) were preserved in special canopic jars representing the four sons of Horus, while the brain was normally discarded (El Mahdy, 1989; Finger, 1994). Remnants of this tradition, as reported by later Greek writers, probably infiltrated the Greek belief system.

This traditional belief greatly influenced and retarded the understanding of the brain well into the Middle Ages. Aristotle, one of the most prominent figures in the

history of biological thought, was greatly influenced by the traditional cardiocentric localization of intellect and emotion.

Aristotle

Our earliest references differentiating the cerebrum and the cerebellum appeared in the fourth century B.C. writings of the Greek natural philosopher Aristotle (384 - 322 B.C.) (Clarke and O'Malley, 1968; Finger, 1994; Mayr, 1982). Aristotle was keenly interested in comparative anatomy and is, in fact, credited with founding the comparative approach in biology (Mayr, 1982). Aristotle was a devoted empiricist and his investigations included the dissection of at least 49 species of animals (Clarke and O'Malley, 1968; Finger, 1994). Despite his extensive observation of anatomy he was not convinced by the Hippocratic physician's position that the brain was the seat of intelligence. Although a devoted disciple of Plato (c. 429 - 348 B.C.) who believed the brain was the organ of intellect, Aristotle was quite conservative in his approach to physiology and maintained that the heart was the center of intellect and emotion (Finger, 1994; Mayr, 1982). Unlike previous philosophers and scholars, Aristotle sought to explain this established belief through observation and reasoning. Thus, he observed that the brain was highly vascularized and appeared to be "cool" and motionless compared to the beating "hot" heart. He hypothesized that the brain was like a radiator that served to temper the excesses of the emotional, irrational heart (Finger, 1994). Although Aristotle was the first to formally recognize the separation of the major divisions of the brain, in reality, his conservative notions of anatomy and physiology greatly hindered the understanding of brain function.

Eventually, with the impetus created by the early Greek philosophers, several centers of learning developed throughout the Greek and Egyptian world in the second and first centuries B.C. (Clarke and O'Malley, 1968; Finger, 1994). One of these first "university" centers, located in Alexandria, Egypt, saw the birth of human anatomical research. Sanctioned by the Egyptian State, the once banned practice of anatomical dissection of human cadavers became accepted. Moreover, the acceptance was so complete that the Egyptian government supplied captured criminals for live experimentation and vivisection. Scholars began proposing functions for various organs based on better, albeit gruesome, empirical evidence (*ibid.*).

Erasistratus

One of these Alexandrian scholars, Erasistratus (c. 310 - 250 B.C.), was the first to suggest that the cerebellum and cerebrum were involved in the higher cognitive abilities found in humans. Although his writings were unfortunately lost to science, his remarks have been preserved in the works of later scholars such as Celsus (25 B.C. - A.D. 50) and Galen (A.D. 130 - 200). Erasistratus believed that the extensive gyrification he saw in the human cerebellum and cerebrum explained the greater intellectual abilities found in humans. Galen quoting Erasistratus in his *On the opinions of Hippocrates and Plato*, VII, 3 wrote;

"the cerebellum was set off by itself, as well as the cerebrum, and was like the jejunum and very much folded. The cerebrum was constructed from even more and differing foldings. From this the observer may learn that as in those animals that surpass the others in speed of running, such as the stag and hare, well constructed with muscles and nerves useful for this, so also, since man greatly surpasses other beings in intelligence, his brain was greatly convoluted (Clarke and O'Malley, 1968:p. 12)."

To his credit, Erasistratus detected differences in neuroanatomical complexity and foldedness between humans and other mammals and linked these differences to behavioral characteristics. Interestingly, Galen took this quote, which is very vague about the role of the cerebellum in higher cognitive functions, and used it to disparage Erasistratus's interpretations of brain function (discussed below).

The Roman Period

The Roman period in medical history was, in general, an extension of the Greek tradition begun in Alexandria. Many Greek physicians fled the declining Greek Empire for the relative security of *Pax Romani*. These physicians were called upon to teach Roman students and attend to Roman Emperors but were often mistrusted and feared. It took until 46 B.C. before these expatriate scholars were granted full Roman citizenship (Finger, 1994). The most prolific and respected of these Greek physicians in the Roman world was certainly Galen.

Galen of Pergamon

Galen of Pergamon (A.D. 129 – 199) produced the largest collection of medical writings in the ancient world (Clarke and O'Malley, 1968). It is mainly through his voluminous corpus of over 500 pieces of writing that we have evidence of earlier Alexandrian medical and philosophical thought. Galen greatly admired Hippocrates and Aristotle but when his views were opposed to theirs, he did not blanch at the prospect of criticizing his mentors. Galen was the most highly respected physician of his time and served as personal physician to four Roman Emperors (Finger, 1994). His work was so well esteemed that it became the foundation of later medieval medical knowledge (Clarke and O'Malley, 1968).

Galen, like his predecessor Hippocrates, believed that the brain was the seat of intellect (Finger, 1994). He also admired Aristotle greatly but he found his hypothesis of brain function illogical. Galen argued that Nature would not have situated the brain so far from the heart if its purpose were merely to temper the heart's irrationality. He believed that if the brain were indeed an organ of emotional restraint that it would be found more logically in the thoracic cavity and not far off in the cranium (Clarke and O'Malley, 1968; Finger, 1994).

In order to better understand the functions of the brain, Galen used bovine brains as models for human brains (Finger, 1994). He dissected the nerve tracts in these experimental animals differentiating between motor and sensory nerves. Although previous anatomists had already described these two pathways, Galen took this observation one step further, localizing the origin of the sensory nerves in the cerebrum and the motor nerves in the cerebellum. He proposed this theory of cerebellar function based on his observations of the texture and density of the cerebrum and cerebellum. To Galen, the sensory nerves were soft, allowing them to carry the fine sensory input to the soft cerebrum. Conversely, the cerebellum being denser and harder was logically related to the hard motor nerves.

"In substance the encephalon is very like the nerves, of which it was meant to be the source, except that it is softer, and this was proper for a part that was to receive all sensations, form all images, and apprehend all ideas. For a substance easily altered is most suitable for such actions and affections, and a softer substance is always more easily altered than one that is harder. This is the reason why the encephalon is softer than the nerves, but since there must be two kinds of nerves, as I have said before, the encephalon itself was also given a twofold nature, that is, the anterior part is softer than the remaining hard part, which is called *enocranium* and *parencephalis* by anatomists. Now...the posterior part had to be harder,

being the source of the hard nerves distributed to the whole body (Galen quoted from Finger, 1994; p. 16).”

Galen also criticized Erasistratus’s observations on cerebral and cerebellar complexity. He wrote in *De usu partium*:

“Erasistratus demonstrates very well that the *epenkranis* (as he calls the cerebellum) is of a more varied composition than the cerebrum; but when he claims that the cerebellum, and with it the cerebrum, is more complex in man than in other animals, because these latter do not have an intelligence like that of man, it does not appear to me that he is reasoning correctly, since even asses have a very complicated cerebellum although their imbecile character demands a very simple and unvariegated cerebrum (Galen’s *De usu partium* quoted in Clarke and O’Malley, 1968; p. 631).”

Galen’s criticism of Erasistratus however is confusing based on his quotation of Erasistratus from above (see **Erasistratus**). In *On the opinions of Hippocrates and Plato* Erasistratus does not relate the intellectual abilities of humans merely to cerebellar complexity but both cerebellar and cerebral complexity. He states quite clearly, contrary to Galen’s remark, that the cerebrum is “constructed from even more and differing foldings” than the cerebellum. Therefore, it appears that Erasistratus clearly noticed the regularity of the mammalian cerebellum and the relative differentiation of the cerebrum. There are at least three possible explanations for this discrepancy. 1) Galen, having access to Erasistratus’s works, may have found contradictory statements in the original writings and chose to exploit these contradictions in order to disparage Erasistratus’s work [a practice not unknown to Galen (Finger, 1994)]. 2) Galen simply misunderstood or reinterpreted Erasistratus’s original statement. 3) An error may have been made in translation from Greek to Latin

(or later French and English) which transformed Erasistratus's word *epenkranis* to *encephalon* effectively inverting the meaning.

When dealing with ancient historical documents that have been translated and re-translated many times, it is not obvious where the root of the trouble began. Finger (1994) plainly illustrates this point by making the same type of mistake. He wrote the following concerning Galen's critique of Erasistratus:

"Galen did not believe that the convolutions of the brain were associated with intelligence, as had been maintained by Erasistratus. He pointed out that donkeys have exceedingly complex cerebrums, even though they are remarkably stupid animals (Finger, 1994;p.16)." [Emphasis added]

As one can see from Galen's work quoted above, he stated that "asses have a very complicated cerebellum although their imbecile character demands a very simple and unvariegated cerebrum". In this case a modern historian of neuroscience misrepresented both Galen and Erasistratus.

In reality, neither Galen nor his contemporaries spent much time investigating the cerebellum. Most of Galen's interest in the cerebellum concentrated on the cerebellar vermis and he seems to have ignored the subtle differences appreciated by Erasistratus (Clarke and O'Malley, 1968). Galen believed that the vermis was the valve that regulated the "animal spirits" passing to and from the cerebral ventricles. These spirits were the essential forces, which modified memory, intellect, and imagination. In the following centuries this basic idea would be elaborated to produce a "ventricular localization theory," in which higher cognitive functions, were localized to specific ventricles in the brain (Finger, 1994).

Nemesius

Nemesius (c. 390) of Syria was one of the first scholars to combine Galen's work and Church doctrine to localize higher cognitive functions in the brain (Finger, 1994). Nemesius wrote that the perceptual senses were confined to the anterior (lateral) ventricles due to their proximity to the organs of sense. He located intellect in the middle part of the brain or third ventricle probably because Galen's writings suggested that some frontal lobe damage did not injure intellectual proficiency. Finally, memory was thought to be found in the posterior or fourth ventricle of the brain due to anecdotal evidence of head trauma as demonstrated in Nemesius's own words:

"If it is the cerebellum that is damaged, only loss of memory follows, while sensation and thought take no harm. But if the middle of the brain and the cerebellum share in the damage, in addition to the front ventricles, sensation, thought, and memory all founder together, with the result that the living subject is in danger of death (Clarke and O'Malley, p. 465)."

It is interesting to note that brain tissue did not play a part in higher cognitive functions. Instead, the essential "animal spirits", bounded by the ventricular spaces, executed the duties of cognition and sensation (Finger, 1994).

The Middle Ages

The end of the Roman period brought several centuries of relative scientific stagnation in Europe. The Roman Empire slowly collapsed while the Roman Church quickly gained power. *Pax Romani* evolved into decentralized vernacular societies. Lay scholars with their knowledge of Greek and Latin gradually disappeared, canalizing classical erudition to the central Roman Church (Hollister, 1990). The Christian explanation for the creation of the world effectively answered all earlier speculation about nature and the physical world. The almighty God created the natural world containing all living creatures in exactly six days. From that point onward the natural world was fixed in place and with it scholarly endeavor. Independent thinking was no longer necessary nor encouraged (*ibid.*).

As the ecclesiastical leader of the Church, the Pope yielded considerable power over the state of knowledge during the Middle Ages and long after. One example of this power was the ban on autopsy decreed by Pope Boniface VIII in the tenth century. The ban probably derived from a long held Church edict forbidding representatives of the Church to shed blood (Finger, 1994). This effectively removed the practice of surgery and human anatomy from the educated clergy and placed it in the hands of barber surgeons and itinerant charlatans. Medical research suffered tremendously, and forced those few remaining scholars of anatomy to work almost clandestinely (*ibid.*).

da Saliceto

Before discussing the “rebirth” of scientific endeavor in the Renaissance period, it is worth noting briefly the work of one 13th century medical scholar from the School of Bologna, Italy. Schools of higher learning were quite progressive in northern Italy

and provided a relatively safe haven for intellectual development (Hollister, 1990). Guglielmo da Saliceto (1210 - 1280), a surgeon, surmised that the cerebrum controlled voluntary movements in the body while the cerebellum controlled what he called “natural and necessary” movements (Finger, 1994:193). Saliceto’s work, once again, based on anecdotal evidence of head trauma, provided the first erroneous indication that the cerebellum might be involved in what would in the 17th century be defined as involuntary and vital movements (Clarke and O’Malley, 1968; Finger, 1994).

The Renaissance

The Renaissance period saw a resurgence of interest in the study of anatomy, physiology, and natural history. Although the study of anatomy did exist in the Middle Ages in northern Italy and France, anatomy courses essentially reiterated the works of the Roman physician Galen (Hollister, 1990). An average anatomy course consisted of a professor lecturing about his opinion on Galen’s observations while his assistant demonstrated the lesson on a cadaver. Students found themselves packed into amphitheaters with little or no chance of seeing or touching the relevant anatomical structures. Frustrated with this pedagogical method, Andreas Vesalius (1514 -1564), a young Belgian-born medical student in Paris, jumped at the occasion to study anatomy at the progressive medical school in Padua, Italy. There he found an institution which could provide adequate dissection subjects and professors willing to challenge anatomical dogma (Mayr, 1982).

Vesalius

Vesalius is best known for his extraordinary work *De Humani Corporis Fabrica* published in 1543. In this work he corrected many mistakes made by Galen and provided excellent drawings of human cadavers. Vesalius also described the external morphology of the cerebellum and noted that it was only about one-tenth the size of the cerebrum (Finger, 1994; Mayr, 1982). Additionally, he mentioned the cerebellum's connection to memory but he did not have much confidence in this hypothesis (Finger, 1994). Vesalius and his contemporaries provided an important break with the rigid medieval past by re-establishing the tradition of observation and empiricism. These scholars were no longer content to read Galen and watch dissections, they wanted to get their hands dirty and see for themselves. Although the intellectual break with medieval scholarship was crucial in later periods, Renaissance scholars contributed little more than descriptive improvements to the understanding of human anatomy.

Two of Vesalius's contemporaries, Estienne (1503 - 1564) and Varolio (1543 - 1575), are worth mentioning for their contributions to the understanding of the cerebellum. Estienne provided one of the first accurate illustrations of cerebellar folia, while Varolio described and named the pons (often called *pons Varolii* or "bridge of Varolio").

Varolio

Varolio also popularized the technique of removing the brain from the cranium and dissecting from the base. This technique allowed him to identify the pons as well as the vestibulocochlear and facial nerves passing through it. Varolio believed that the pons and the cerebellum were part of the same anatomical structure, the cerebellum.

This unfortunate coupling caused him to confuse sensory information passing through the pons with true cerebellar functions. Thus, he shrewdly, yet wrongly, hypothesized that the cerebellum was involved in audition and gustation (Finger, 1994).

The 17th Century

The 17th century is best characterized as a period of considerable growth in the physical sciences and mathematics based on the contributions of Newton, Descartes and Kepler. This period also saw the development of scientific instruments such as the telescope, barometer and microscope. In comparison, neuroscientific advances were much less momentous (Finger, 1994). The brain was described and illustrated in much better detail during this time but only one scholar, Thomas Willis, truly advanced the study of neurology.

Thomas Willis

The renowned Oxford physician and anatomist, Thomas Willis (1621 - 1675), presented the most important post-Galenic hypothesis of cerebellar function (Finger, 1994). Willis in his dedicated brain volume *Cerebri anatome*, published in 1664, postulated that the cerebellum was neither the organ of memory nor sensation but the organ that controlled involuntary movements in the body. Willis expressed his ideas quite clearly in the following passage:

“When some time ago I gave careful and serious consideration to the function of the cerebellum and revolved in my mind various things concerning it, finally as the result of analogy and much thought about the matter, I arrived at this (as I believe) true and genuine use of it; that is, that the cerebellum is a special fountain of animal spirits that are designed for certain tasks, wholly distinct from the cerebrum. Imagination, memory, discourse, and other superior acts of the animal function are performed within the

cerebrum; furthermore, animal spirits flow from it into the nervous order, by which all spontaneous movements, that is, those of which we are conscious and which we direct, are performed. The duty of the cerebellum, however, seems to be to supply animal spirits to certain nerves by which involuntary actions take place (such as the heartbeat, normal respiration, concoction of aliment, production of chyme, and many others); that is those of which we are unaware or we are unaware of their constant activity (Willis quoted from Clarke and O'Malley, 1968; p. 638)."

Willis came to this realization through dissecting and observing the brains of many types of animals. Like his predecessor Varolio, he believed that the pons with its associated cranial nerves was an integral part of the cerebellum. Willis stated:

"I was led finally to this conjecture regarding the use of the cerebellum by a thread of reasoning to which anatomical study later contributed and clearly confirmed me in my opinion, for in the frequent dissections of the heads of different kinds of animals I made certain observations that seem to put this matter beyond doubt. That is to say, first I observed that the pairs of nerves which serve the functions normally performed by instinct of nature or by force of passions rather than by the judgment of the will depend so directly from the cerebellum that the influx of animal spirits into their origins seems able to be derived only from there (Willis quoted from Clarke and O'Malley, 1968; p. 638)."

He also noticed, like Galen fourteen centuries before, that the cerebellum seemed to remain quite convoluted in whatever animal was investigated, yet the cerebral hemispheres varied greatly. Thus, he sought a functional "common denominator" in these experimental animals and incorrectly concluded that the involuntary autonomic processes of the heart and respiration were controlled by the cerebellum.

"And so in the second place we notice that the cerebellum has a special conformation, that is, that its mass is composed of folds or little circles in a distinct series, methodically and appropriately disposed at regular intervals. . . I observed, in addition, that in whatever animals, no matter how much they differ in

appearance and form, nevertheless the shape of the cerebellum is always very similar or wholly the same . . . (Willis quoted from Clarke and O'Malley, 1968; p. 639)."

Willis also derived evidence for his hypothesis by comparing pathological and normal brains. He observed somatic disturbances in patients and experimental animals with occipital damage or cerebellar lesions (Clarke and O'Malley, 1968). Stimulated by Willis's work, researchers in France and Switzerland supported Willis's hypotheses in their laboratories. Bonet (1620 - 1689) and Vieussens (1641 - 1716) both showed that cerebellar (that is cerebellar and pontine) damage caused circulatory and respiratory arrest and even death (Finger, 1994). Although not all experimental evidence supported Willis's claims, his hypothesis would influence students of cerebellar function into the next century.

The 18th Century

The eighteenth century saw a greater emphasis on good experimental technique in brain research. The experimental evidence of Willis and his supporters was strongly challenged by Haller (1707 - 1777), Zimmerman (1728 - 1795) and Zinn (1727 - 1759) who claimed that the surgical procedures of these earlier workers confounded their results (Finger, 1994). Contrary to Willis's opinion, these later researchers suggested that cerebellar ablation and even excision was, in fact, survivable for at least a short period of time in experimental animals. Similarly, in two important and complementary works, two French physiologists, Lorry (1726 – 1783) and Legallois (1770 – 1840), showed that the involuntary action of respiration was in fact localized to the medulla oblongata region and not the cerebellum (Finger, 1994). This revelation helped

researchers to understand the paradoxical survival of decerebellate animals and also helped to instigate the functional separation of the cerebellum from the rest of midbrain structures (Clarke and O'Malley, 1968; Finger, 1994).

This century also produced the first monograph dedicated exclusively to the cerebellum. The monograph, entitled *Nuova esposizione della struttura del cervelletto umano*, was written in 1776 by Michele Malacarne (1744 - 1816) an Italian anatomist and surgeon. In this work, Malacarne described both the external and internal structure of the cerebellum in detail and suggested that the number of cerebellar laminae in a species reflected its intellectual capacity (Clarke and O'Malley, 1968).

The 19th Century

The 19th century proved to be a watershed period for neurological research. Along with the innovative research conducted on the cerebellum leading to our modern classical definition of cerebellar function (discussed below), several important discoveries influenced neuroscience as a whole. On the microscopic level, Jan Purkyne (1787 - 1869) in 1837 first described the neurons in the cerebellum, which would bear his name. Two years later Schwann (1810 - 1882) introduced “cell theory”, giving biology the basic building blocks of living organisms (Finger, 1994). In 1861, Paul Broca (1824 -1880) demonstrated the link between the frontal cortex and the ability to produce articulate, fluent speech which sparked further research into functional localization of the cerebral cortex (Gould, 1981). Sir David Ferrier (1843 -1928) began mapping the motor cortex of the monkey, while Richard Caton (1842 - 1926) pioneered the study of electrical activity in the brain. The century ended with a more thorough

understanding of nervous tissue through the staining innovations of Golgi (1843 - 1926) and Ramon y Cajal (1852 - 1934) (Finger, 1994).

Paleoneurology in the 19th Century

The nineteenth century also witnessed the first descriptions of fossil endocranial casts (endocasts) beginning with Cuvier's description of the fossilized natural endocast of an extinct form of horse, *Paleotherium medium*, an event that marked the beginning of the formal study of paleoneurology (Cuvier, 1804; Edinger, 1975).

In 1863, Hermann Schaaffhausen produced the first description of a hominin endocast in essence beginning the formal study of human paleoneurology. The cast was a plaster model taken from the Neandertal type specimen discovered in 1856 near Dusseldorf, Germany. The first description was a brief metric comparison of the Neandertal endocast with the brains of an Australian and a European (Edinger, 1975). Schaaffhausen noted what he believed to be primitive characteristics reproduced on the fossil endocast, such as a sloping frontal region, an uncomplicated pattern of cerebral convolution and a simplified meningeal vessel pattern. To his credit, however, these "primitive" characteristics did not hinder his proposition that the skeleton from Dusseldorf represented the fossil remains of a human species (Kochetkova, 1978; Trinkaus and Shipman, 1993).

Shortly after Schaaffhausen's description of the Neandertal fossil Charles Darwin and Alfred Russel Wallace presented their theory of the origin of species by natural selection at the Linnean Society in London in 1858. Interestingly, their presentations made no real mark on the scientific community until a more detailed picture was assembled by Darwin a year later. Darwin's essay "On the origin of species by means

of natural selection” was published in December 1859 and became an immediate retail success going through six editions in 12 years (Desmond and Moore, 1991; Mayr, 1982). During this time the scientific community throughout the world had the opportunity to discover and digest what Darwin’s proposals meant for the study of biology and human origins. A whole new generation of scientific workers was inspired by these new evolutionary proposals to go out and look for scientific evidence.

Steeped in the writings of Darwin, Wallace, and Haeckel, a young Dutch physician and anatomist, Eugène Dubois set off for the Dutch East Indies in search of fossil hominin remains. Dubois’ decision to go to the Dutch East Indies were fourfold: he had the opportunity to work as an Army physician; he believed that human evolution began in the tropics; he knew that one of our closest cousins, the orangutan, was indigenous to the region; and lastly, fossil hominoids had already been found in Asia. Miraculously, his explorations were fruitful and in 1891 on the island of Java, Dubois’ team found the relatively complete skull of “*Pithecanthropus erectus*” (*Homo erectus*) (Theunissen, 1989). It took eight years for Dubois to finally describe the endocast of *Pithecanthropus I*, helping to both legitimize the study of endocasts and bring it to the international level (Dubois, 1899; Kochetkova, 1978). Dubois’ analysis, like later discussions in the early twentieth century, focused on the size and shape of the endocast. In fact, Dubois’ was one of the first researchers to note that allometric scaling must be accounted for when comparing brain weight and volume data. Unfortunately, both the Neandertal and the *Pithecanthropus* specimens were missing their cranial bases, effectively barring any analysis of the cerebellar morphology (Johanson and Edgar, 1996). The first discussion of the cerebellar morphology of a

fossil hominin endocast would not come until the next century with Boule's thorough analysis of the La Chapelle-aux-Saints adult Neandertal from the Dordogne Valley in France.

Neurological research in the 19th Century

Among the important scientific minds representing the nineteenth century, three researchers stand out for their contributions to the understanding of cerebellar functions. Rolando (1773 - 1831), Flourens (1794 - 1867), and Luciani (1840 -1919) helped to establish the foundations of our modern understanding of the cerebellum.

Rolando

Luigi Rolando, an Italian surgeon, was the first to show ipsilateral motor deficiency in experimental animals with ablated cerebellums. The modern "classical" understanding of cerebellar function derives in part from his early experiments. In one experiment, Rolando eliminated the right cerebellar hemisphere in a chicken and produced severe muscular deficiency in the right leg and wing. He specified that; "the animal never became drowsy or fell into a stupor; it kept its eyes open and observed all objects; but it was in vain that it attempted to execute any movement through means of the muscles dependent on the locomotive faculty (Rolando translated by Clarke and O'Malley, 1968: p. 654)."

Rolando also demonstrated that major cerebellar damage produced major motor deficiencies while minor damage produced temporary and often reversible motor impairment.

"When I suddenly lacerated, impaired, or removed this organ, the animal was always completely paralyzed, but if I injured it only slightly, after several hours it regained the faculty of movement (Rolando translated by Clarke and O'Malley, 1968: p. 654)."

Thus Rolando believed that the paralysis he observed in his experimental animals was due to the disruption of the motor production center of the brain. Although, this interpretation of cerebellar function would be modified and improved 15 years later by the French physiologist Pierre Flourens, Rolando's efforts were crucial to our modern understanding of cerebellar function (Finger, 1994).

Flourens

Flourens, a contemporary and colleague of Cuvier, is considered to be one of the founders of the French school of experimental physiology (Clarke and O'Malley, 1968). His experiments on the cerebrum and cerebellum in birds represent some of the classic first steps in modern brain theory. Similar to the excision experiments of Rolando, Flourens removed layer after layer of cerebellar tissue to observe the post-operative effects in his experimental animals. His experimental technique and knowledge of cerebellar anatomy, although still crude by today's standards, were greatly improved over the earlier experiments of Rolando. In his 1824 monograph entitled *Recherches experimentales sur les propriétés et les fonctions du système nerveux dans les animaux vertébrés*, Flourens described his ablation technique and observations:

"I removed the cerebellum from a pigeon slice by slice. During the removal of the first slices, only slight weakness and lack of coordination of movement appeared.

With the middle slices, an almost universal restlessness was manifested although there was no sign of convulsion; the animal performed sudden and disordered movement; it heard and saw. ...On the removal of the last slices, the animal, in which the faculty of jumping, flying, walking, and of maintaining an erect posture had become more and more disturbed by the preceding mutilations, lost this faculty altogether (Translated in Clarke and O'Malley: p. 657)."

Flourens realized from his experiments that the cerebellum was not, as Rolando concluded, a center of motor production but rather a center for motor regulation and coordination. His description from above continued:

“Placed on its back it was not able to rise. Far from remaining calm and steady as in pigeons deprived of the cerebral lobes, it became vainly and almost continually agitated, but it never moved in a steady and firm manner....For example, becoming aware of a threatened blow and wishing to avoid it, it made a thousand efforts to do so but without success. When placed on its back, it did not wish to stay there and exhausted itself in vain attempts to get up, but in the end remained in the same position despite its efforts....Finally, volition, sensation, and perception persisted; the ability to carry out general movements also persisted; but the coordination of these movements in an orderly and determined manner was lost (Translated in Clarke and O’Malley: p. 657). [Emphasis added]”

Flourens repeated this experiment in other types of birds, dogs, and pigs with similar conclusions. He remarked that subtotal cerebellar lesions produced muscle coordination difficulties and caused these animals to appear drunk while moving. Despite the questions raised by the rather vague experimental methods and the use of birds and quadrupeds as models for the human condition, these conclusions were accepted quite rapidly (Finger, 1994).

Interestingly, Finger (1994), discussing Flourens contributions to the modern understanding of cerebellar function, stated:

“These experiments were important in finally laying to rest at least four old ideas: 1) that the cerebellum was the organ of sensation, 2) that it played a role in intellectual functions, 3) that it was the center for memory, and 4) that it was responsible for the vital functions essential to life (Finger, 1994:212).”

At least one of these “old ideas”, i.e., that the cerebellum plays a role in intellectual functions, will be discussed in greater detail in the second part of this section.

Luciani

Luigi Luciani contributed greatly to our understanding of postoperative behavior in decerebellate animals. The introduction of aseptic surgical techniques allowed Luciani to study his experimental animals for periods of up to a year after ablation of the cerebellum (Clarke and O’Malley, 1968). In his 1891 publication, *Il cervelletto. Nuovi studi de fisiologia normale e patologica*, Luciani detailed the deficits he observed in these animals. Of greatest importance was his observation that dogs with surgically removed cerebellums experienced three main physiological symptoms: atonia (loss of muscular tension), asthenia (reduced muscle strength), and astasia (inability to stand or sit erect due to motor incoordination). These three pathological deficiencies soon became the foundation of our modern definition of cerebellar function (Clarke and O’Malley, 1968; Finger, 1994).

Furthermore, Luciani claimed that although anatomical evidence showed the cerebellum was comprised of two different hemispheres it actually functioned as a single unit. He found no evidence in his experimental work to suggest that the cerebellum had somotopically localized divisions that controlled different parts or systems of the body. This theory, known as the Unitary theory of cerebellar function, was well accepted by most researchers in the twentieth century (Clarke and O’Malley, 1968).

The Early 20th Century

At the start of the twentieth century the ideas of Rolando, Flourens, and Luciani were quite well received. Neuroscientists accepted the idea that the cerebellum was a motor coordination center that was essential for smooth efficient movement. It was also believed that the two hemispheres of the cerebellum, although divided, worked as a single unit. From this base, workers such as Sherrington (1857 – 1952), Babinski (1857 – 1932), and Holmes (1876 – 1965) began the task of testing and refining the findings of their predecessors.

Neurological research in the Early 20th Century

Sherrington

Charles Sherrington, the London-born physician and physiologist, best known for his groundbreaking insight into the theory of integrative nervous function also provided one of the clearest definitions of cerebellar function in the early twentieth century. He wrote the following in his 1906 book *The integrative action of the nervous system*:

“Knowledge is not ripe as yet for an adequate definition of the function of the cerebellum. Many authorities have defined it as the centre for the maintenance of the mechanical equilibrium of the body. Others regard it as the organ for coordination of volitional movement. Spencer suggested that it was the organ of coordination of bodily action in regard to space, the cerebrum he suggested being the organ of coordination of bodily action in respect of time. Lewandowski considers it the central organ for the “muscular sense.” Luciani, the universally acknowledged authority on the physiology of the cerebellum, describes it as the organ which by unconscious processes exerts a continual reinforcing action on the activity of all other nerve-centres.

It is instructive to note how all these separate pronouncements harmonize with the supposition that the organ is the chief coordinative centre or rather group of centres of the reflex system of proprioception. The cerebellum may indeed be described as the head-ganglion of the proprioceptive system, and the head ganglion here, as in other systems, is the main ganglion (Clarke and O'Malley, 1968:673).”
[Emphasis added]

We can clearly see that this definition bears a striking resemblance to our modern definition, which recapitulates the themes of equilibrium, coordination, and muscle synchronization. While some of Sherrington's contemporaries supported and modified his definition, it saw its first major revisions only at the end of the twentieth century.

Sherrington also commented on the unitary theory of cerebellar function. That is, the idea that the cerebellum functioned as a single unit and not a series of localized functional areas such as in the cerebrum.

“The division into hemispheres and middle lobe is founded merely upon gross anatomy. The organ commonly, probably always, “functions” as a whole. Luciani is right to insist on this, and the reason that it “functions” as a whole seems clearly because it is so largely a piece of mechanism that deals with the innervation, not of this or that piece of musculature, but of the musculature of the body as a whole. The earlier observers, Flourens, Bouilland [sic], etc. stated this when they spoke of the cerebellum as an organ of “equilibration” (Clarke and O'Malley, 1968:674).”

Sherrington's prolific French colleague Joseph Babinski also held this point of view.

Babinski

Babinski's major contribution to the understanding of cerebellar functions comes from his direct observations of clinical patients. His most famous observation concerned the inability in cerebellar patients to perform rapid successive voluntary

movements. In light of these observations, Babinski coined the term “diadokokinesia” (meaning “successive movements” in Greek) and thus “adiadokokinesia” to denote the inability to perform these actions. He observed that when he asked a patient suffering from cerebellar lesion or injury to perform a simple movement such as turning the head from side to side, the patient was able to accomplish the task. But when the patient was asked to perform the same task multiple times or to change directions, the task became arduous and much slower (Clarke and O’Malley, 1968, Finger, 1994).

Babinski also clarified how cerebellar injury effected equilibrium. He noted that the standard definitions of his time did not distinguish between static equilibrium (the ability to hold oneself erect in a stationary position) and kinetic equilibrium (the ability to perform smooth coordinated intentional movements). Babinski realized that his patients with cerebellar damage actually had normal or even improved static equilibrium, while their kinetic equilibrium was impaired to varying degrees. This impairment in modern clinical terminology is now called intention tremors.

Holmes

Babinski’s contemporary, the British neurologist GM Holmes, is best known for his fascinating clinical work with World War I gunshot victims. Holmes’s clinical observations contributed substantially to our understanding of human cerebellar function and dysfunction. Most notably, in his 1917 article dedicated to cerebellar dysfunction, Holmes confirmed Luciani’s “triad” of cerebellar deficiency with his observation that atonia, asthenia, and astasia existed in human gunshot victims. His discourse concerning the triad was clear and concise, beginning with the primary involuntary dysfunction of atonia:

“*Atonia*, or diminution of that slight constant tension which is characteristic of healthy muscle, is such a constant and striking feature of all early injuries, and persists for such long periods when the wounds are large, that it is obviously a primary and direct result of the [cerebellar] lesion...Clinical experience...fully confirms the statements of Luciani and other physiologists that atonia is a constant, important and striking result of acute cerebellar destruction. It diminishes gradually in time, and may, like all other symptoms, disappear, at least if the lesion is not very extensive (Clarke and O'Malley, 1968:678).”

Subsequently, Holmes tackled intentional deficiencies remarking:

“It has been shown that when a man with a cerebellar lesion attempts to grasp the observer’s two hands simultaneously: (1) the power exerted by the affected limb is defective; (2) the initiation and the execution of muscular contractions and relaxations are slower than on the normal side; (3) the grasp is often intermittent and irregularly maintained; and (4) the affected limb tires more quickly than its fellow (Clarke and O'Malley, 1968:681).”

To describe these deficiencies in voluntary motions, Luciani coined the terms *asthenia* and *astasia*. Holmes validated their existence in modern cerebellar patients and commented on their relative importance. He noted that *asthenia* (“diminished functional energy of the affected limb”), like *atonia*, was “a primary and immediate symptom of cerebellar injury” (Clarke and O’Malley, 1968:678).” *Astasia*, in his opinion was not “a prominent symptom in most local lesions of the cerebellum in man as it is in animals after experimental destruction, though it varies in degree in different cases” (*ibid.*).

Bolk

The Dutch anatomist Lodewijk Bolk was the first researcher to propose a basic organizational plan of the mammalian cerebellum. Bolk studied the cerebellar morphology of 69 species of mammals and created a cerebellar blueprint dividing the

cerebellum into four principal regions, the anterior lobe, the posterior vermis, and the two cerebellar hemispheres. Within each region he named and mapped each group of cerebellar lobules (consisting of folia). He argued that a basic morphological plan for the cerebellum across mammalian species persisted although the number of folia and the relative size of the principal divisions varied depending on the animal. Through this organizational plan and his ideas about the nature of movement, Bolk was able to approach the question of cerebellar function by comparing the differences and similarities between species (Glickstein and Voogd, 1995).

Like his contemporaries, Bolk believed that the cerebellum was involved in the coordination of voluntary movements but, contrary to Luciani, he did not believe that the cerebellum worked as a single unit. Instead he claimed that the cerebellum possessed a somatomotor localization that coincided with specific muscular systems. Bolk inferred from embryological evidence that the cerebellum had four major growth centers: anterior, posterior, postero-medial and postero-lateral. These growth centers appeared to coincide with the major somatomotor regions of the body (i.e. limbs, trunk, head, and neck). From this base, Bolk began to link behavioral characteristics of the animals he studied with the size of specific cerebellar lobules in their brains. He reasoned that if an animal demonstrated fine coordinated movements in a particular muscular system that ability would be represented by an enlargement in the appropriate cerebellar lobule. Two examples of this come from the spider monkey and the giraffe. Bolk found that the spider monkey had a relatively elongated flocculus (postero-lateral lobe) which he linked to its agile prehensile tail (Clarke and O'Malley, 1968). The giraffe possessed an unusually large posterior lobe (lobulus simplex) which Bolk

related to fine coordinated neck movements (Clarke and O'Malley, 1968; Glickstein and Voogd, 1995). He hypothesized that there were two main types of voluntary movement: 1) movements that required the cooperation of muscles across the midline and 2) movements that involved muscles on one side of the body. This idea, along with his comparative neurological data, led Bolk to conclude that the anterior lobe was the site for coordinating muscles in the head. He also concluded that the vermis in the posterior lobe was the site for coordinating muscles of the trunk, and the lateral cerebellar lobes were the sites for coordinating the muscles in the arms and legs. Although Bolk's somatotopic plan was over-simplified and incorrect in some aspects, parts of his analyses still remain valid (Glickstein and Voogd, 1995).

Paleoneurology in the Early 20th Century

Just as the classic definition of cerebellar function was being honed in physiological and clinical studies, anthropologists and archeologists (both amateur and professional) throughout Asia, Europe and Africa were discovering the remains of our ancient hominin ancestors. Each new discovery was like finding a piece to a puzzle that had been scattered from space to settle on three different continents. Always fragmentary and often poorly excavated, these early finds provided the impetus for challenging old ideas and developing new theories of human origins. As fate would have it, these fossilized skeletons also often included the remains of the cranium and thus the braincase. As mentioned above, endocasts had been made and briefly described as early as 1804, but these crucial pieces of evidence begin to be effectively studied only in the twentieth century.

The paleoneurological reports from the first half of the twentieth century were mainly descriptive (Falk, 1982; Holloway, 1997). The field of paleoanthropology was in its infancy and the amount of comparative fossil evidence was considerably less than is the case today. During the first forty years of the twentieth century, fossil finds from Western Europe (Neandertal and Cro Magnon type) and Asia (*Homo erectus*) were given the most scholarly attention. The major contributors in this period such as Boule (1911), Dart (1925), Dubois (1933), Weidenreich (1936), Elliot-Smith (1928), McCown and Keith (1939), and Ariëns Kappers (1929) were greatly interested in the size and shape of endocasts as well as the convolutional and meningeal patterns they reproduced (Falk, 1982).

Almost all comparative neuroanatomical research focused on the cerebrum and what it could tell about the evolution of the human brain. It is well documented that the human cerebral cortex increased tremendously in size and complexity throughout evolutionary history (Changeux and Chavillon, 1995; Tobias, 1971). This size increase coupled with the ability to assign functional behavioral significance to its surface anatomy made the study of the neocortex in humans and fossil endocasts a fruitful endeavor. The analysis of the cerebellar hemispheres of fossil endocasts, on the other hand, rarely received more than a passing descriptive comment.

This bias is reflected in the scholarly writings of paleoanthropologists throughout the twentieth century. It is, however, an understandable bias when we consider the fragmentary nature of the fossil record and the fact that the classical definition of cerebellar function does not say very much about behavior. It was simply assumed that the cerebellum synchronized voluntary movements in fossil hominins, as

was assumed for modern animals. The cerebellum was essentially as interesting anthropologically as the medulla oblongata or spinal cord, although it was second only to the cerebral cortex in phylogenetic growth. The following examples from three major monographs demonstrate the attention given the cerebellum from the beginning of the twentieth century to the present.

Boule

At the beginning of the twentieth century a series of scientific reports was published concerning the endocast of the classic Neandertal specimen from La Chapelle-aux-Saints, France. This relatively complete adult Neandertal specimen was first described by Marcellin Boule in 1908 and quickly became the “psychological” and popular type specimen for all earlier and later Neandertals (Trinkaus and Shipman, 1993). Boule’s anatomical description of the skeleton and endocast of this severely arthritic and traumatized individual had long standing repercussions on the way Neandertals were perceived in both the lay and scientific communities. In general, Boule’s anatomical descriptions were beyond reproach but his interpretations of these anatomical facts presented Neandertals as lumbering neophyte bipeds with primitive skulls and bodies. In spite of Boule’s *a priori* conclusions that the “Old Man” of La Chapelle-aux-Saints was clearly more “apelike” than “humanlike,” his account of the voluminous plaster endocast gives a slightly less prejudiced portrayal.

In Chapter VI of his 1912 monograph, Boule considers the cranial capacity of the La Chapelle-aux-Saints specimen and provides a volume measurement of 1626 cubic centimeters. Faced with such a large cranial capacity in what he believed to be a very primitive hominin, Boule wrote:

“The relative enormity of this number may be surprising to those who consider cranial capacity to be a zoological and anthropological character of first order, in close relationship to the development of intellectual faculties. Our fossil man presents many inferior morphological characteristics that reduce the vast space that separate the human group from the group that makes up the anthropoid apes, and yet he enters here squarely in the human series (Boule, 1912:169).” [my translation]

Boule does not indicate explicitly that he is or is not a member of this group of scientists that considers cranial capacity an essential indicator of intellect but he does concede that for all of the other primitive qualities he perceives, the size of the La Chapelle-aux-Saints endocast puts it firmly on the human end of the the ape-human continuum. He also noticed that the endocast appeared to be lateralized and possessed relatively well developed sensory regions although deficient in prefrontal association area (Boule and Anthony, 1911; Kocetkova, 1978). In a modern reanalysis of Neandertal endocasts, Holloway (1985) stated convincingly that when aspects of size, gyrification, and asymmetry are taken together, Neandertal endocasts do not show primitive characteristics. Boule’s *a priori* interpretations of the skeleton clearly influenced his interpretation of the endocast.

Out of this series of reports came the first description of a fossil hominin cerebellum. Boule compared the cerebellar lobes of the “Old Man” to modern casts of “primitive” Australians, “civilized” Europeans, and nonhuman primates. As with many of his other comparisons, Boule chose to emphasize the similarities between the Neandertal morphology and that of nonhuman primates. His short treatment of the cerebellum as it appeared in the 1912 edition of the *Annales de Paléontologie* was as follows:

“On the casts of Australians which we have examined, the two cerebellar lobes are less jutting than in Men of our race; their internal borders move away from each other, the space which separates them becomes larger, and thus the vermis is usually revealed. The cast A 3828 is particularly remarkable in this regard. In the anthropoid apes, the cerebellar lobes are still generally slightly jutting, but their separation, much less prominent, is evident above all, in the inferior portion of the cerebellum; the medial lobe of the cerebellum is revealed and the dura mater spreads over its surface. This morphology is even more prominent in the lower primates....The Man of La Chapelle-aux-Saints resembles, in this regard, the anthropoid apes and presents a less pronounced jutting of the lateral cerebellar lobes. ...There is no doubt that in this specimen the vermis was exposed like that of the living apes and that the dura mater was in the same position as well (Boule, 1912:190).” [my translation]

This brief descriptive section of Boule’s *Mémoire* is indicative of the treatment accorded the cerebellum throughout the century. In fact, given the early publication date of this analysis, it is commendable that the cerebellum was even considered. (Ariëns Kappers makes no mention of the cerebellum or cerebellar morphology in his 1929 comparative analysis of Pithecanthropus I, Broken Hill, La Chapelle, La Quina, Combe Capelle, and Predmost). Boule’s 1912 *Mémoire* also presented two of the three traditional indicators of cerebellar progression in paleoneurological reports: 1) the amount of vermal exposure and 2) size and projection of lateral cerebellar hemispheres. The third indicator, 3) the amount of *surplombement* or the extent to which the occipital lobe overhung the cerebellum in fossil hominin endocasts, was actually first mentioned a year earlier in 1911 (Boule and Anthony, 1911). These traits were normally measured on the ape to human continuum with fossil hominins occupying a multitude of points in between.

McCown and Keith

Approximately, thirty years after the publication of Boule's description of the La Chapelle Neandertal, Theodore McCown and Arthur Keith analyzed the skeletal and endocranial remains of the Skhul hominins found at Mt. Carmel in Israel. The endocranial discussion focused on the Skhul I and Skhul V specimens, representing a child and an adult respectively. The analysis was organized into sections and discussed the major divisions of the brain separately (frontal, temporal, parietal, and occipital) as well as the venous sinuses and meningeal vessel patterns. The following comments were made about the cerebellar morphology of Skhul I and Skhul V:

"The lateral lobes of the cerebellum [of Skhul I] take a larger share in forming the lower lateral walls of the cast than is the case in casts taken from either Neanthropic or Neanderthal skulls. We have already noted the rounded backward projection of the cerebellar lobes. The prominence of the lateral lobes of the cerebellum, both in a lateral and in a posterior direction is a character we meet with in the endocranial casts from chimpanzee and gorilla skulls. This must be counted a primitive or anthropoid feature in the Carmel cast (McCown and Keith, 1939:351). ...The cerebellar lobes [of Skhul I and Skhul V] were placed widely apart and projected backwards more prominently than is usual in modern skulls (McCown and Keith, 1939:357)." [Emphasis added].

The themes revealed by Boule reappear quite clearly in McCown and Keith's discussion. The prominent, backward projecting and widely spaced lateral cerebellar lobes plainly demonstrated the primitive anthropoid position of the cerebellar hemispheres and the vermis. To their credit McCown and Keith also provided metric information about the cerebellar lobes, although they did not try to interpret their significance. This practice was continued in later works like that of Tobias (1967).

Tobias

Tobias dedicated a chapter in his substantial monograph describing the morphology of Olduvai Hominid 5 (OH 5) to its endocast. As in the previous study by McCown and Keith (1939), Tobias compared the size and shape of the entire endocast with the comparative material available at the time. His thorough analysis focused most importantly on the cranial volume and allometry, encephalometric measurements and the vascular anatomy reproduced on fossil hominin endocasts. Tobias wrote the following concerning the cerebellar morphology of “Zinj”:

“The large size of the cerebellum of *Zinjanthropus*, to which reference has been made in the account of the posterior cranial fossa, is brought out both by the absolute measurements and by the cerebellar indices. The cerebellum seems to have been better developed in *Zinjanthropus* than in any of the other australopithecine brains (Tobias, 1967:92).”

Once again, metric data were provided with no interpretation to explain the functional relationship between the size of the cerebellum and behavior.

Grimaud-Hervé

In a superbly illustrated study of the evolution of the brain in *Homo erectus* and *Homo sapiens*, Dominique Grimaud-Hervé is concerned mainly with gyrification and cranial blood flow data reproduced on ~70 endocasts of extant and fossil hominins. A short summary accompanies each fossil endocast, which recapitulates the same types of observations made by Boule almost one hundred years earlier. In the author’s final analysis a rather conservative explanation for the relatively enlarged neocerebellum found in *Homo erectus* and early *Homo sapiens* is ventured. Grimaud-Hervé states:

“We can reasonably presume that this increase in volume is due to the enlargement of the neocerebellum, which is responsible for the automatic control of voluntary and semi voluntary movement. This may

have some connection with the balance in newly bipedal creatures (Grimaud-Hervé, 1997:370)” [my translation]

The consideration given the cerebellum in this 1997 monograph on brain evolution is reflective of the limited understanding of cerebellar function that has characterized paleoanthropology.

Kochetkova

One paleoneurological work however stands out in its treatment of the cerebellum in human evolution. The Russian paleoanthropologist Veronika Kochetkova was well aware of the progress that had been made toward understanding the hominoid cerebellum during the 1950’s, 1960’s, and early 1970’s. In the chapter dedicated to the occipital region and cerebellum of her important 1978 monograph *Paleoneurology*, Kochetkova explained the future of cerebellar research in paleoneurology:

“The progressive evolution of the cerebellum throughout a considerable period, including the period of existence of archanthropines, paleanthropines, and in most respects of neanthropines as well, was apparently, characterized by the formation of the newest connections of the cerebellum with the cerebral cortex, especially of the system of descending connections, linking the prefrontal region to the cerebellum. Developing later than others, the *tractus cortico-cerebellaris*, apparently was formed directly during the anthropogenesis, since it connects the cerebellum with regions strongly developed only in man. Therefore even the evolutionary changes in the cerebellum are characterized by the kind of progressive development associated with the development of specifically human regions of the brain (Kochetkova, 1978:229).”

This concise and astute statement expresses a hypothesis that 20 years of medical neuroimaging has only just begun to support.

Modern concept of cerebellar function

Significance for Paleoanthropology

Two goals of paleoanthropology are to determine the timing of phylogenetic changes in the human fossil record and to deduce the behavioral abilities of extinct hominin species. It is with these goals in mind that we examine recent exciting discoveries of neuroscience.

The fossil record provides evidence of the external structure and shape of the brains of extinct hominins. The evidence is often fragmentary but in certain rare cases the external morphology of the lateral cerebellar hemispheres is preserved. As we have seen, this fact has been known since the late nineteenth century but very little critical analysis of the cerebellum in human evolution has been attempted. The work of Weaver (2005) and MacLeod (2000) are two recent exceptions. It is now clear that the cerebellum can provide paleoanthropologists with important information about the timing of cerebral and cerebellar reorganization, and possibly some behavior abilities of extinct hominins.

Summary

Although, it is clear that the cerebellum has been underestimated throughout history, scientific research in the last two decades has done a great deal to improve our understanding. As paleoanthropologists we now have the opportunity to better exploit the precious few remains that we possess. In Chapter 2, I will examine cerebellar anatomy and circuitry in greater detail. I will also assess the available clinical and

neuroimagery data in order to determine how far paleoanthropological interpretation can lead us.

CHAPTER 2: CEREBELLAR ANATOMY AND FUNCTION

The object of this chapter is to succinctly present findings from modern neuroscientific research regarding the anatomy, cytoarchitecture, and functioning of the human cerebellum. A great deal of relatively new research has revitalized scientific interest in this once underestimated organ and has shown that it plays a much greater role in higher cognitive functions than had ever been suspected before.

To better understand the important innovations made in the study of cerebellar function and evolution, it is necessary to provide a basic outline of cerebellar ontogeny, cytoarchitecture, and gross anatomy. The first section of this chapter provides details about each of these areas that will enable the reader to comprehend the experimental and clinical research findings presented in later sections. Also included in the first part is information about the size, volume and surface area of the primate cerebellum.

The second section details the neural circuitry that has been shown to connect the cerebellum to association areas in the cerebral neocortex of experimental animals and humans. This dynamic input / output system may have played a crucial role in the phylogenetic development of the human neocerebellum.

The next three sections cover the evidence gained from medical neuroimaging and clinical research performed on humans. This research has shed light on the functioning of the normal human cerebellum as well as deficiencies caused by cerebellar pathology. Future paleoneurological contributions to our understanding of human neocerebellar evolution are discussed in the last section.

Human cerebellar anatomy

Development of the cerebellum

The human cerebellum forms from cells in one of the three primary brain vesicles of the developing embryo called the rhombencephalon. The rhombencephalon (hindbrain), prosencephalon (forebrain) and mesencephalon (midbrain) make up the majority of the developing embryo and are clearly visible at about 5 weeks postmenstrual (Figure 2-1).

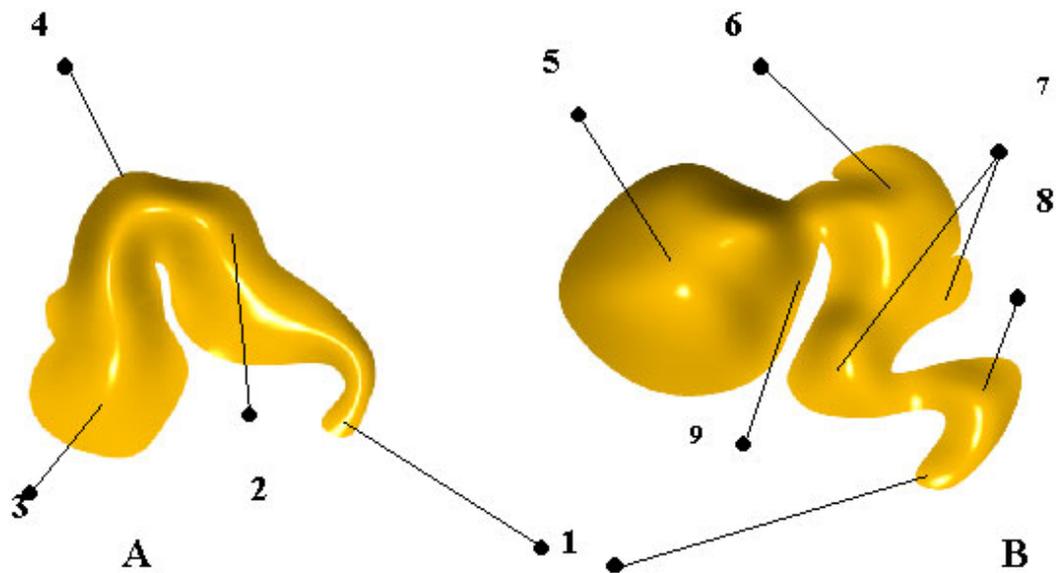


Fig. 2-1 Human embryogenesis. A) 5 weeks postmenstrual B) 7 weeks postmenstrual. 1=Spinal cord, 2=Rhombencephalon, 3=Prosencephalon, 4=Mesencephalon, 5=Telencephalon, 6=Mesencephalon, 7=Metencephalon, 8=Myelencephalon, 9=Diencephalon (after Barr and Kiernan, 1988).

This period of embryonic development lasts only about two weeks due to the rapid cell division and differentiation of the developing embryo. At about 7 weeks

postmenstrual, the rhombencephalon separates into two secondary divisions called the metencephalon and myelencephalon. The metencephalon becomes the pons and the cerebellum while the medulla oblongata forms out of the myelencephalon. (As noted above the pons and cerebellum were once thought to be the same organ.) At this stage of development it is clear that different regions of the embryonic brain grow at different tempos. Beginning at 13 and continuing through 30 postmenstrual weeks, the head breadth (a measure of brain growth) of the developing human fetus grows at peak velocity. Interestingly, head circumference growth, which better accounts for cerebellar growth, begins to increase in velocity slightly later than head breadth (Tanner, 1990). This variation in tempo shows that the cerebellum has a relatively delayed peak growth velocity compared to the cerebral hemispheres. Finlay and Darlington (1995) and Finlay et al. (1998) hypothesized in their phylogenetic analysis of brain allometry that prolonged periods of neurogenesis can vastly increase the number of neurons produced in a brain structure. They postulate that “progressive” structures such as the cerebrum and cerebellum produce more precursor cells during their relatively longer neurogenesis, which leads to an exponential growth of the nerve cells during ontogeny.

At birth the cerebellum represents only about three to five percent of neonatal brain volume, while the cerebrum (including the corpus callosum, basal ganglia, and diencephalon) represents approximately 92 percent. After birth, cerebellar growth velocity picks up rapidly and eventually peaks at about 10-11 percent of total brain volume at 2 years postnatal (Jeffrey, 2003; Tanner, 1990). Adult size however, is not attained until late in adolescence (Ellis, 1920). Actual neuronal division in the cerebellum ceases several months prior to achieving the adult ratio of cerebellar to total

brain volume, while neuronal division in the forebrain continues slightly longer. This continued neuronal growth might explain the slightly greater allometric growth of the human forebrain compared to the cerebellum when compared to great apes. At this point the cerebellum contains over half as much DNA in its densely packed cortex as the eight times more voluminous cerebrum (Brasel and Gruen, 1986). A more recent study by Andersen et al. (1992) suggests that the adult human cerebellum actually contain more nerve cells than the rest of the central nervous system combined.

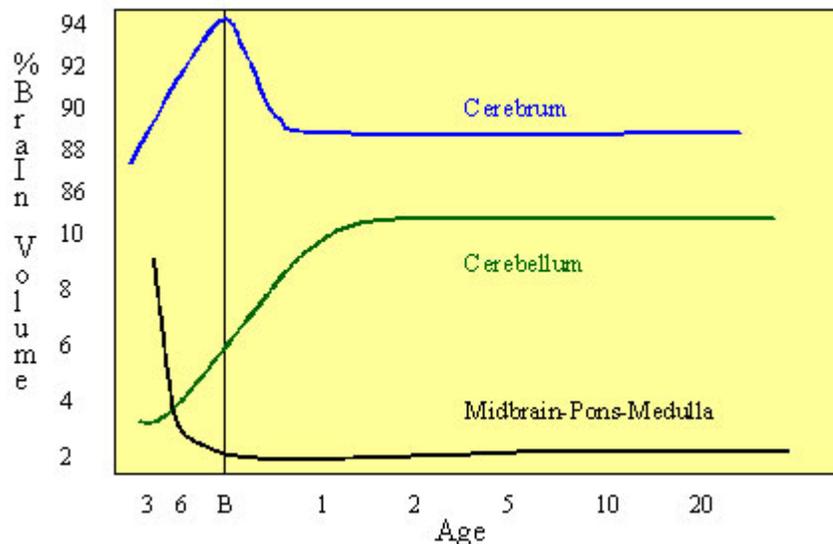


Fig. 2-2 Human brain growth curve (Tanner, 1990)

Gross Anatomy

The human cerebellum is located in the posterior cranial fossa inferior to the two large cerebral hemispheres. Between the cerebral hemispheres and the cerebellum is a tentlike layer of protective tissue, the tentorium cerebelli, which attaches posteriorly to the superior ridges of the posterior cranial fossa and encloses the transverse venous sinuses (Figure 2-3). Anteriorly, the tentorium cerebelli attaches to the superior

margins of the two petrous temporal bones and terminates on the bilateral anterior and posterior clinoid processes of the sphenoid bone (Gray, 1901). This extension of the protective dura mater serves to displace the downward force of the large cerebral lobes so as not to crush the underlying cerebellum nor herniate it through the foramen magnum [as seen in clinical cases of basilar impression (Dow and Moruzzi, 1958)].

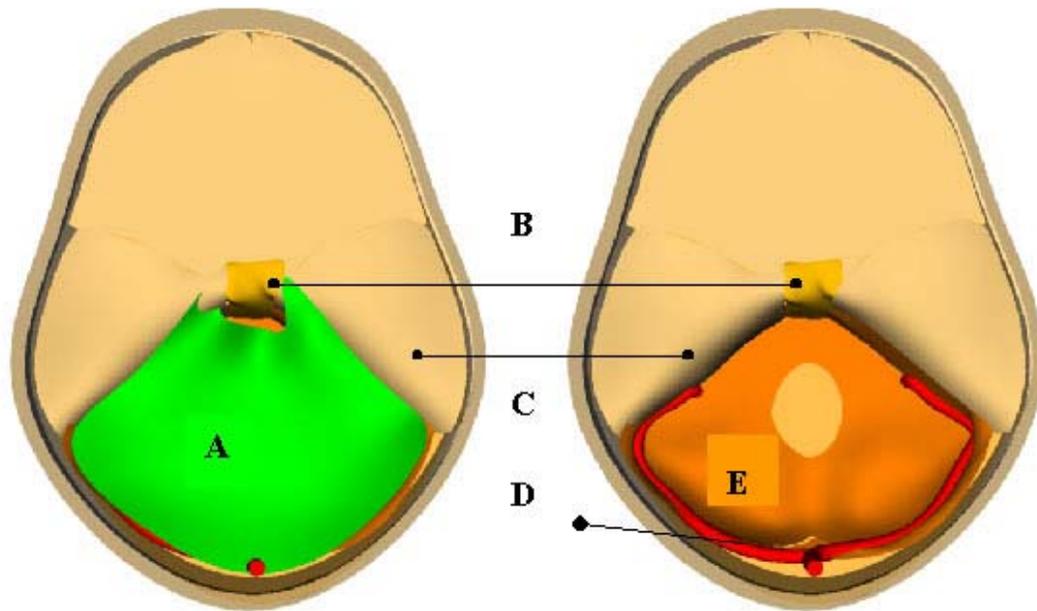


Fig. 2-3 Superior view of basicranium. A=Tentorium cerebelli, B=Clivus, C=Petrous temporal bone, D=Venous sinuses, E=Posterior cranial fossa.

The study of cerebellar morphology is often quite confusing due to the array of anatomical nomenclature used to represent its various parts. The cerebellum has been traditionally divided in two planes of orientation, sagittal and coronal, based on comparative anatomical research. Early in this century Bolk developed a general mammalian plan of cerebellar morphology that was based on the morphology of *Lemur albifrons* (Glickstein and Voogd, 1995). This plan, modified and improved by Larsell (1970), provides the general divisions and nomenclature that are accepted by most neurological researchers (Figure 2-4). The basic divisions that are used in this analysis are discussed below.

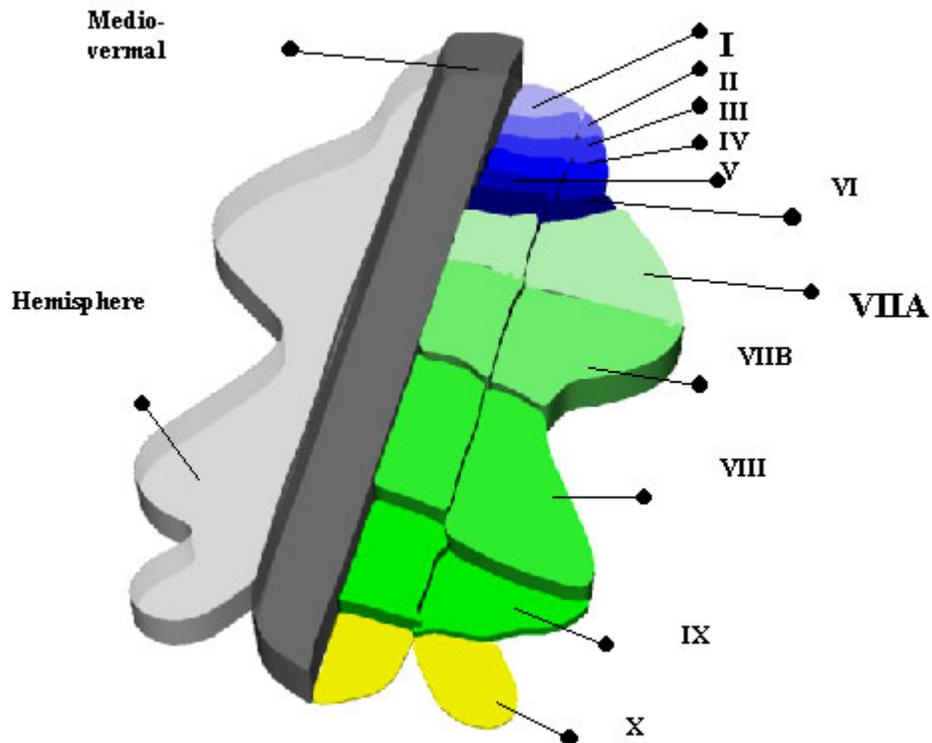


Fig. 2-4 Larsell's (1970) generalized plan of the mammalian cerebellum folded out in one plane. The Roman numerals signify the parallel concentric folia (lobules) which make up most mammalian cerebellums. The numbers run from anterior to posterior beginning in the anterior lobe. This plan is not significantly different from the plan developed by Bolk (1906). The anterior lobe is thought to encompass lobules I-VI, the posterior VIIA – IX, and the flocculonodular lobule X.

The mature human cerebellum is composed of three primary lobes: flocculonodular, anterior, and posterior (Figures 2-5 and 2-6). In the unfolded cerebellum, these divisions run antero-posteriorly in the sagittal plane and also serve to roughly delineate the three major phylogenetic divisions of the primate cerebellum: archicerebellum, paleocerebellum, and neocerebellum (Figure 2-4). Transversely, the cerebellum can be divided into two lateral cerebellar hemispheres encompassing both

anterior and posterior lobes and a medial region called the vermis (meaning wormlike) (Figure 2-6). Information passing in and out of the cerebellum is routed through four deep cerebellar nuclei which are linked functionally to the medial, intermediate, and lateral divisions of the cerebellar cortex (Matano et al., 1985a). These nuclei are the fastigial (medial), globose, emboliform (intermediate), and dentate (lateral).

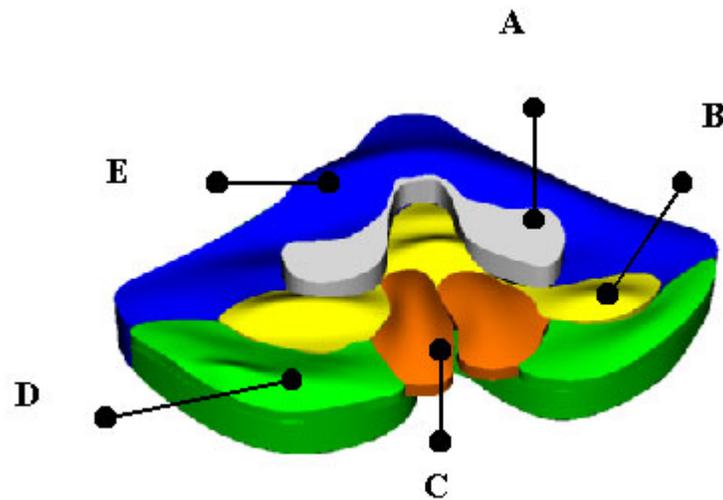


Fig. 2-5 Anterior view of cerebellum. A=Cerebellar peduncles, B=Flocculonodular lobe (Archicerebellum), C=Tonsil, D=Posterior lobe (Neocerebellum), E=Anterior lobe (Paleocerebellum).

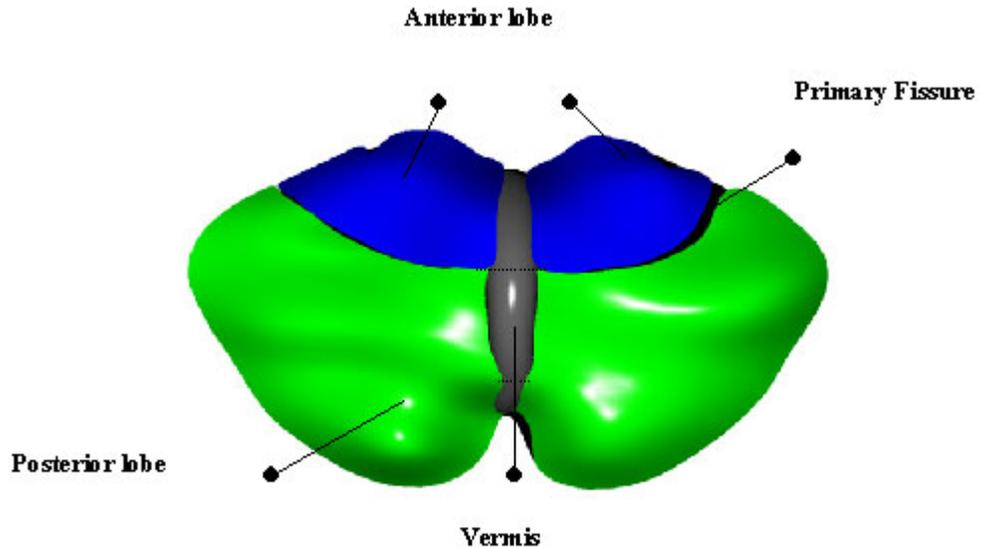


Fig. 2-6 Superior view showing the transverse divisions and lobes of the cerebellum. Lateral cerebellar hemispheres= green and blue areas; Vermis= gray area; Anterior lobe= blue areas including superior vermis; posterior lobe= green areas including inferior vermis.

Flocculonodular lobe

The flocculonodular lobe is found in the center of the cerebellum enveloped by the anterior and posterior lobes (Figure 2-5). Of the three primary lobes of the cerebellum the flocculonodular is phylogenetically the oldest. This subdivision of the cerebellum is the smallest of the three primary lobes and contains the smallest amount of total and concealed surface area. Although few data exist concerning the size of this lobe, Blinkov and Glezer (1968) provide data from Kreuzfuchs (1902) that show that the flocculonodular lobe possesses only one percent of the total surface area of the human cerebellum. The flocculonodular lobe, which contains part of the inferior vermis in the midline, is also called the archicerebellum because it receives afferent fibers from the vestibular nerve and nuclei. The archicerebellum plays a crucial role in

the phylogenetically old vestibular system and can be found in lower order fish and amphibians as well as higher order mammals. Afferent vestibular fibers enter the inferior cerebellar peduncle and terminate in the fastigial nucleus, one of the four paired nuclei of the cerebellum. Efferent information is then routed out of the same nucleus to terminate in the brain stem, the vestibular nuclear complex, and the reticular nuclei. This pathway serves to control body tone and equilibrium (Barr and Kiernan, 1988).

The flocculonodular lobe with its connections to the limbic lobe also appears to modify some aspects of emotion such as aggression and fear (Schmahmann, 1997). Heath (1977) showed, from clinical electrophysiological studies of dysfunctional patients, that afferent fibers from the limbic system activated cells in the fastigial nucleus when patients experienced anger or fear. In addition, Berman et al. (1978) showed that aggression was modified in macaque monkeys with lesions in the flocculus region.

Fastigial nucleus

The fastigial nuclei are the most medially oriented and the least progressive (most phylogenetically primitive) deep cerebellar nuclei in prosimians and primates. In humans, the volume of all the deep cerebellar nuclei combined, measures $\sim 1,500 \text{ mm}^3$ and the fastigial nuclei make up only one tenth of this total (Matano et al., 1985b). In fact, these nuclei are smaller in humans than would be expected for a prosimians of equal body weight (Blinkov and Glezer, 1968; Matano et al., 1985b; Matano and Hirasaki, 1997).

Activation of the fastigial nuclei in experimental animals has also clearly linked this structure to aggression regulation. In cats and monkeys fastigial ablation produced

states of constant arousal and hyperactivity as well as disrupted sleep-wake cycles. Overstimulation of the nucleus caused aggressive predatory behaviors in laboratory animals such as sham rage in cats. (Sham rage is a spontaneous hissing fit which is thought to be caused by the hypothalamus and is generally inhibited by fastigial activation (Dow and Moruzzi, 1958; Schmammann, 1997)).

In addition to its connection with the vestibular and limbic systems, the fastigial nucleus also receives information from portions of the autonomic nervous system. Experiments with laboratory animals have shown that fastigial activation produces changes in pupil diameter in monkeys and cats, as well as inhibitory effects on vasomotor tone (i.e. lowering blood pressure) (Dow and Moruzzi, 1958; Schmammann, 1997). These vestibular and limbic connections clearly mark the archicerebellum and its nuclei as a phylogenetically old structure that has been retained in higher mammalian phylogenies.

Anterior lobe

The anterior lobe of the cerebellum is located on the antero-superior portion of the human cerebellum. This lobe encompasses cortex and white matter in the two lateral cerebellar hemispheres as well as portions of the superior and inferior vermis (Figures 2-5 and 2-6). The anterior lobe receives fibers from spinocerebellar, cuneocerebellar, reticular and trigeminal tracts that convey sensory (proprioceptive) information to the emboliform and globose nuclei of the cerebellum. This proprioceptive information is processed in the ipsilateral cerebellar cortex in order to regulate coordinated muscle movements, tone and proprioception. The medial (vermal)

portion of the anterior lobe corresponds to the phylogenetically old paleocerebellum found in amphibians, reptiles and birds (Barr and Kiernan, 1988; Larsell, 1970). Parts of the paleocerebellum are also found in the posterior lobe of the cerebellum.

Emboliform and Globose nucleus (interpositus nucleus)

Situated between the fastigial and dentate nuclei in great apes and humans, the emboliform and globose nuclei often form a single interpositus nucleus on each side of the midline in lower primates and mammals. Like the fastigial nuclei, the emboliform and globose nuclei are not progressive and no clear increase in relative size was detected by Matano et al. (1985b) in their study of 56 species of mammals. The interpositus nuclei in *Homo sapiens* make up approximately 13 percent of total cerebellar nuclei volume, which is about two percent less than *Pan troglodytes* and 19 percent less than *Macaca mulatta*. These figures are easily explained by the dramatic increase in the most lateral cerebellar nuclei in *Homo sapiens* and great apes relative to the other nuclei (Table 2-1).

TABLE 2-1 Size of deep cerebellar nuclei in primates (mm³)

Specimen ¹	Fastigial	Interpositus	Dentate	Total	% Dentate / Total
<i>Macaca mulatta</i>	53.24	75.13	106.94	235.31	45%
<i>Hylobates lar</i>	35.41	65.6	141.08	242.09	58%
<i>Pan troglodytes</i>	58.32	87.27	455.83	601.42	76%
<i>Gorilla gorilla</i>	93.44	112.36	534.6	740.4	72%
<i>Homo sapiens</i>	156.4	190.48	1166.9	1513.78	77%

¹Data from Matano et al (1985b).

Dorsal and ventral spinocerebellar fibers carrying mainly proprioceptive information from the peripheral nervous system pass through the inferior and superior cerebellar peduncles, the interpositus nuclei and finally to the cerebellar cortex. Although the cerebellum does not possess a clear somesthetic map due to the extensive interconnections in the cortex, spinocerebellar fibers from the trunk project mainly to vermal and paravermal cortex, while fibers carrying information from the limbs are projected to the lateral cortex (Thach, 1997).

Posterior lobe

The posterior lobe of the human cerebellum is the largest of the three primary subdivisions and encompasses the majority of the lateral cerebellar hemispheres and the tonsil. (The human lateral cerebellar hemispheres actually contain 88-89% of total cerebellar volume (Eccles, 1982; Matano et al., 1985a,b).) It is delineated from the anterior lobe by the deep primary fissure and from the flocculonodular lobe by the hidden posterolateral fissure. This lobe is considered to be the most progressive and newest phylogenetic structure in the cerebellum. Lobules in this part of the cerebellum (specifically the superior and inferior semilunar) seem to have expanded extensively

throughout hominin evolution (Leiner et al., 1986; Matano et al., 1985a,b). These lobules along with the gracile, anterior and posterior quadrangular lobules make up the phylogenetically important neocerebellum (Table 2-2, Figure 2-3).

TABLE 2-2 Lobes and lobules of the human cerebellum (Larsell and Jansen, 1972)

Vermis Lobule	Name	Phylogeny
I	Lingula	Paleocerebellum
II	Centralis	Paleocerebellum
III	Centralis	Paleocerebellum
IV	Culmen	Paleocerebellum
V	Culmen	Paleocerebellum
VI	Declive	Neocerebellum
VIIA	Folium	Neocerebellum
VIIIB	Tuber	Neocerebellum
VIII	Pyramis	Paleocerebellum
IX	Uvula	Paleocerebellum
X	Nodulus	Archicerebellum
Hemisphere Lobule	Name	Phylogeny
HI		
HII		
HIII		
HIV	Anterior Quadrangular	Neocerebellum
HV	Anterior Quadrangular	Neocerebellum
HVI	Posterior Quadrangular	Neocerebellum
HVIIA	Semilunar	Neocerebellum
HVIIIB	Gracile	Neocerebellum
HVIII	Biventer	Paleocerebellum
HIX	Tonsil	Paleocerebellum
HX	Flocculus	Archicerebellum

The posterior lobe of the cerebellum has become an important structure to neurologists and anthropologists because of its extensive connections to motor, sensory and particularly association areas of the cerebral neocortex. Until quite recently most neuroscientists believed that the large neocerebellum bestowed on hominoids a unique motor benefit (Leiner et al., 1991). An earlier theory of cerebellar evolution suggested that neocerebellar expansion was linked to fine manipulation of objects and specialized

locomotor adaptations seen in hominoids. However, this theory has been refuted by more recent neuroimaging research (Gao et al., 1996, discussed below).

Research has shown that an enormous quantity (~20,000,000) of afferent fibers originating in sensory, motor, and association areas of the cerebral neocortex are projected to the pontine nuclei of the ventral pons. These nuclei subsequently send fibers to the cortex of the lateral cerebellar hemispheres. The vast amount of neocortical information transmitted through these afferent fibers is processed in the contralateral cerebellar hemisphere and sent back to the cerebral neocortex via the dentate nucleus and the ventrolateral thalamus.

Dentate nucleus

The dentate nucleus is the largest and most laterally oriented of the four deep cerebellar nuclei (Table 2-1). In *Homo sapiens*, the dentate nuclei are approximately 4.5 times more voluminous than what would be expected for a prosimian of equivalent body size (Matano et al., 1985b). Morphological, embryological, histochemical and pathological research has shown that the hominoid dentate nucleus is composed of two phylogenetically separate regions with distinct histological compositions (Dow, 1942, 1974; Leiner et al. 1986). The phylogenetically older portion, the dorsomedial dentate (DMD), is microgyric (small gyri) and magnocellular (large cells) while the newer ventrolateral portion (VLD) is macrogyric (large gyri) and parvicellular (small cells) (Demole, 1927; Dow, 1942). The dorsomedial dentate has been shown to be homologous to the dentate nuclei in lower primates and mammals while the ventrolateral dentate exists uniquely in great apes and humans (Leiner et al., 1986, 1989, 1991).

Ventrolateral dentate nucleus

Leiner et al. (1989, 1991, 1993, 1995) have hypothesized that this phylogenetically new portion of the dentate nucleus found in great apes and humans accounts for the drastic enlargement in the absolute size of the dentate in these species. They postulate that this new phylogenetic structure is not only anatomically distinct from the DMD but also functionally distinct. Neurosurgical evidence from stereotaxic lesions of the dentate demonstrates that, unlike in the DMD, destruction of the VLD does not cause classic motor dysfunction (ataxia, atonia, etc.) (Leiner et al., 1989).

However, there is not complete unanimity among cerebellar researchers that there exists a true bipartite dentate nucleus. MacLeod (2000) points out correctly that the extensive study of the human dentate performed by Demole (1927) and cited by Dow (1942) as evidence for the DM and VL distinction is based entirely on a qualitative analysis. Demole (1927) does not provide quantitative evidence of cell size differences, cell type frequencies and gyrification patterns in the ventral and dorsal regions of the dentate. Matano (2001) has provided preliminary volume measurements of the VL and DM portions of two *Gorilla*, 1 *Pan*, and 2 *Homo sapiens* specimens (Table 2-3) but this analysis does not address whether the distinction between the two parts is scientifically sound.

TABLE 2-3 Volume (mm^3) of the dentate nucleus from Matano (2001)

	<i>Gorilla</i>	<i>Pan</i>	Humans
Ventral dentate	331.33	284.47	791.69
Dorsal dentate	203.27	171.36	375.21
Total	534.6	455.83	1,166.90

A relatively clear visual distinction can be made between the microgyric DM and the macrogyric VL when viewed from both two-dimensional serial sections and three-dimensional reconstructions (Yamaguchi and Goto, 1997). Cell size and frequency in the VLD and DMD has not been investigated rigorously enough to determine if the parvicellular/ magnocellular dichotomy is a worthy distinction. MacLeod (2000), whose work provides the largest and most diverse data set to date, demonstrates that the dentate nuclei in primates appears to scale most closely with brain volume (minus cerebellum) not with lateral cerebellar hemisphere volume as predicted by Leiner et al. (1989). However, it is clear that the human cerebellum and cerebellar hemispheres are larger (~2.9 times) than expected in a similarly sized ape brain (MacLeod, 2000; Rilling and Insel, 1998).

Thus, it appears that the neocerebellum (and perhaps the phylogenetically new VLD) developed concomitant with the reorganization and expansion of the cerebral association areas throughout primate evolution (Weaver, 2005). In other words, the cerebellum is much more than just a coordinator of muscles. It may also be a coordinator of language, thought, planning and a host of other nonmotor higher cognitive functions. This hypothesis has obvious implications for the study of hominin brain evolution. The remainder of this section is dedicated to presenting the clinical, experimental and theoretical evidence that supports the evolutionary connection

between the neocerebellum and higher cognition, and how this information can help paleoneurologists interpret the timing and functional capabilities of our fossil hominin ancestors.

Cytoarchitecture

Although the size and shape of the cerebellar cortex appear to have been transformed through phylogenetic evolution, its essential molecular components have remained the same through time. The conservative nature of the cerebellar cortex has facilitated a considerable amount of research and subsequent insight into cerebellar connectivity and molecular function (Dow and Moruzzi, 1958; Ito, 1984, 1997; Llinas, 1975; Massion and Sasaki, 1979; Palay and Chan-Palay; 1982). This section presents an overview of the essential components and their interactions in the vertebrate cerebellum.

There are three distinct cytoarchitectural layers contained in the vertebrate cerebellar cortex. The deepest layer is called the granule layer, the middle layer is called the Purkinje cell layer, and the surface layer is called the molecular layer (Figure 2-7). Arranged in these layers are seven types of nerve cells, which can be placed into three categories based on the functions they perform: afferent, interneuron, and efferent. The afferent system, bringing information to the cerebellum is composed of two types of cells, climbing fibers and mossy fibers while the efferent system utilizes only one cell type; Purkinje cells (pronounced “purkine”). Four types of cells make up the cerebellar interneurons: granule cells, Golgi cells, basket cells and stellate cells. The cells or neurons in each of these groups have the same basic structural elements as all

nerve cells. They all possess nucleated cell bodies, dendrites, and axons that carry electrical action potentials and release chemical neurotransmitters. Each group will be discussed separately beginning with the Purkinje cells, which were one of the first neurons to be described in 1837 by the Czech physiologist, Johannes E. Purkinje (Finger, 1994).

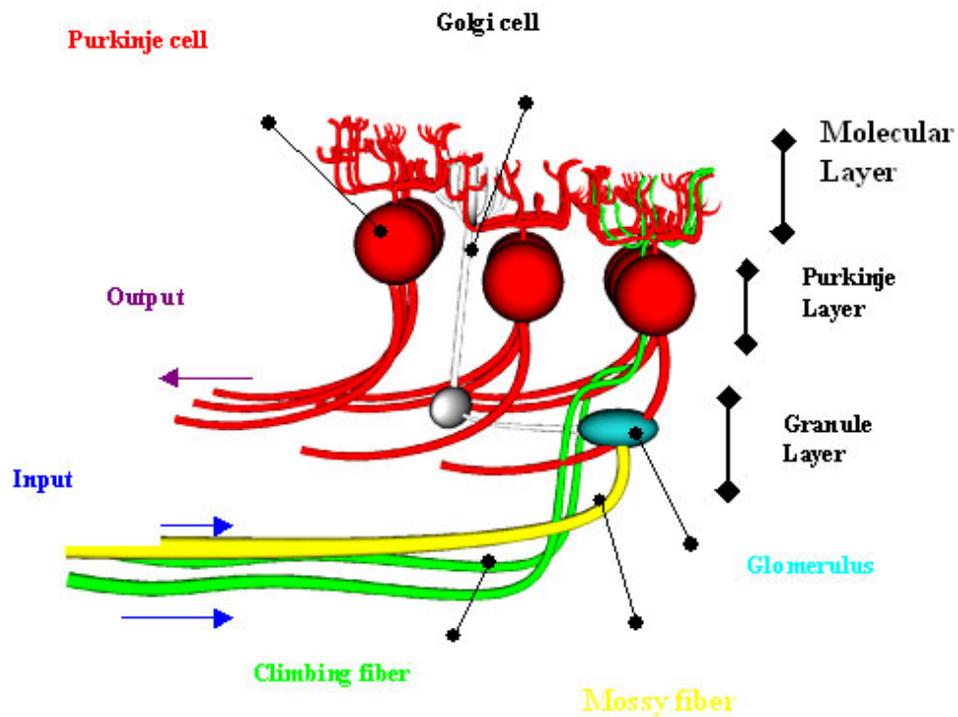


Fig. 2-7 Reconstruction of the histological morphology of the human cerebellar cortex.

Efferent system: Purkinje cells

Purkinje cells are some of the most fascinating and complex cells in the central nervous system (Figure 2-7). These cells are characterized by their considerable dendritic branching systems. Each Purkinje cell in the human cerebellum may form as many as 100,000 synapses with adjacent afferent neurons. The dendritic branches of the Purkinje cells are limited to the molecular layer of the cerebellum while the tear-shaped cell bodies reside in the Purkinje cell layer just below. These neurons also possess extremely elongated axon bodies which serve to carry all the processed efferent information out of the cerebellar cortex and into the dentate nucleus (Barr and Kiernan, 1988; Diamond et al., 1985; Llinas, 1975).

The orientation of these cells is of particular importance in terms of maximum space utilization. The dendritic tree of Purkinje cells is quite full in the sagittal plane spreading extensively both vertically and horizontally. In the coronal plane however, the extensive branching of the Purkinje dendrites is not visible at all. Only the flask-shaped cell body and a straight vertical line are visible. This two dimensional characteristic of the cerebellar Purkinje cells enables the cerebellum to have a maximum number of efferent cells in a restricted amount of space (between 14 and 26 million cells in humans (Blinkov and Glezer, 1968)). Each sagittal row of Purkinje cells is paralleled by similar closely packed sagittal rows running longitudinally across the cerebellum. This orientation is a very efficient way of increasing information processing power by fitting the highest number of processing units side by side (Leiner et al., 1986; Leiner and Leiner, 1997; Llinas, 1975).

Afferent system: Climbing fibers and Mossy fibers

Climbing fibers are the first afferent fibers to develop connections with Purkinje cells in the embryonic brain. These neurons get their name from the unique, one to one connections they have with Purkinje cells. During embryonic development an afferent climbing fiber, originating outside the cerebellum (in the inferior olive or reticular nuclei), pairs with a single Purkinje cell and essentially “climbs” the extensive dendritic tree. The exclusive bond between these two neurons produces a powerful “all or nothing” action potential in the Purkinje cell, strong enough to override any other input into the cell (Llinas, 1975). The second set of afferent fibers into the cerebellum has a much more diverse group of connection in the cerebellar cortex.

The fast conducting mossy fibers represent a large part of the afferent information transmitted to the cerebellar cortex. “Among all the neurons of the central nervous system, the mossy fiber stimulates one of the largest numbers of cells to be activated by a single efferent fiber (Llinas, 1975:61).” These fibers entering the cerebellar white matter represent the culmination of several major fiber pathways into the cerebellar cortex, such as the pontocerebellar, spinocerebellar, and vestibulocerebellar pathways. In the white matter proceeding to the cerebellar cortex, mossy fibers bifurcate and send terminal branches to the deep cerebellar nuclei as well as the granule cells in the cerebellar cortex. (Purves et al., 1999). Clearly though, the most important connections of the mossy fibers occur at the glomerular junction in the granule layer of cerebellar cortex. At this junction afferent information is transmitted to the interneurons of the cortex which carry action potentials to the Purkinje cells (Barr and Kiernan, 1988; Diamond et al., 1985; Llinas, 1975).

Interneurons: Granule, Basket, Stellate, Golgi II cells

Granule cells are neurons that have their cell bodies in the granule layer and send long vertical T shaped branches to the molecular layer. In the molecular layer the horizontal portions of the T (parallel fibers) runs perpendicular to the closely packed sagittal rows of Purkinje dendritic trees. This orientation allows an individual granule cell to synapse with as many as 450 different Purkinje cells (Barr and Kiernan, 1988). The densely packed parallel fibers of the granule cells also synapse with basket cells and stellate cells in the molecular layer of the cortex.

Basket cells and stellate cells are activated by granule cell parallel fibers and serve to inhibit groups of efferent Purkinje cells. Basket cells located in the molecular layer receive action potentials from the parallel fibers and synapse with several Purkinje cells on the lower dendritic branches and cell bodies. Stellate cells function much the same way, but they are confined to the upper parts of the Purkinje dendrites. The function of these cells is to prevent wide spread activation of the Purkinje cell network and confine cerebellar activation to particular regions depending on the type and location of the input. In other words, these inhibitory cells serve to “sharpen the boundary and increase the contrast between those cells that have been activated and those that have not” (Llinas, 1975:63).

Golgi II cells perform a particularly critical function in the granule cell layer by acting as a negative feedback to activated granule cells. These cells form part of the glomerulus and are activated by mossy fibers and granule cells. Activation of the Golgi II cells inhibit the continued activation of the parallel fibers and provide an important

shut off valve in the system (Llinas, 1975). More will be said about the powerful design and capabilities of this advanced neural circuitry later.

Cerebellar microcomplex

Experimental research has shown that these basic cellular units of the vertebrate cerebellum form functional and structural units called cerebellar corticonuclear microcomplexes (Ito, 1984;1997). These microcomplexes, like a computer chip, appear to perform the same types of actions in all parts of the cerebellum (i.e. medial and lateral), whether the input is sensory, motor, or even cognitive. Mossy fibers carry information from various reticular or neocortical centers and introduce data into the cerebellar microcomplex. Simultaneously, climbing fibers carry error signals to the Purkinje cells which are selectively activated or inhibited by the mossy fiber / climbing fiber input. This Purkinje cell activation is carried to the dentate nucleus and out of the cerebellum. It is believed that most cerebellar output is of an inhibitory nature (*ibid.*).

A simple example of this system is the vestibulo-ocular reflex. This reflex allows the eyes to maintain a constant position while the head or body is in motion. Mossy fibers carry the sensory and muscular information while the climbing fibers carry the error signals which cause the modification of muscular activation in the eyes that maintain a fixed gaze. Disturbances in groups of microcomplexes called modules can disrupt the proper functioning of the vestibulo-ocular reflex (Ito, 1984).

Neural circuitry

Cerebellar input

It has been understood for some time that there exists in the brain a closed neuronal circuit that connects many areas of the cerebral cortex to the cerebellum. Like any electrical circuit, the cerebrocerebellar loop contains both afferent (cerebellar input) and efferent (cerebellar output) sides which complete this circuit. A great deal of research over the past 20 years has attempted to locate the exact points of origin, transmitting fibers, and terminal sites in this complex neuronal loop (Schmahmann and Pandya, 1997).

In the major cerebrocerebellar input portion of the loop, signals are transmitted from the various motor and nonmotor neocortical centers to the pontine nuclei in the ventral pons (Brodal, 1979). From the pontine nuclei, mossy fiber bundles make their way to the dentate nucleus and to the appropriate lobules of the cerebellar cortex (Schmahmann and Pandya, 1997). Of great anthropological interest are the connections with nonmotor cortical association areas of the neocortex. Input from cerebral associations areas are responsible for crucial higher cognitive functions such as directed attention, complex visuospatial integration, language, memory, planning, foresight, judgement, musical ability, and working memory (Eccles et al., 1967; Falk, 2000; Leiner et al., 1986; 1991; 1995; Schmahmann and Pandya, 1997). Thus, the afferent (cerebellar input) portion of the cerebrocerebellar circuit suggests a clear relationship with higher cognitive processes (Figure 2-8).

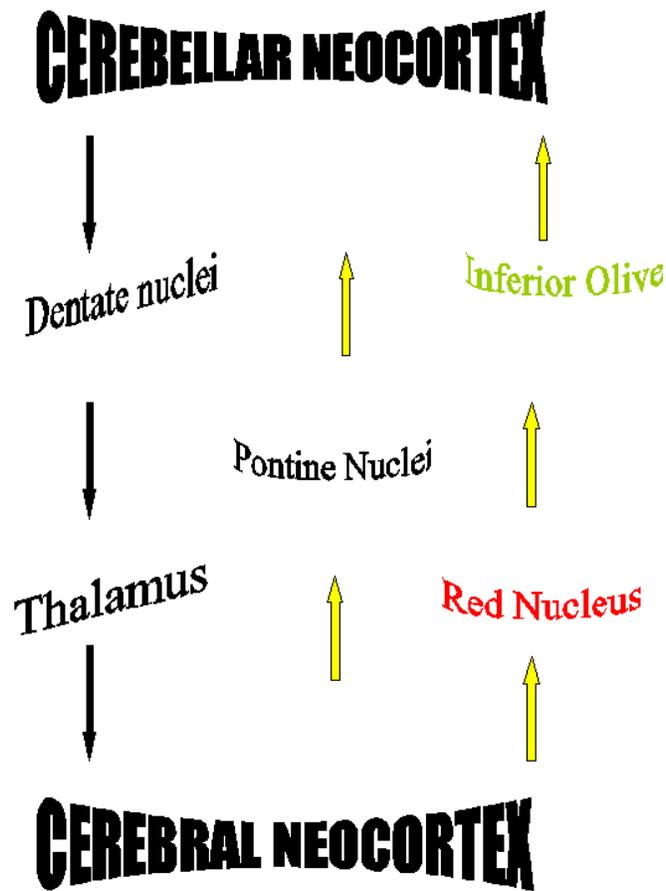


Fig 2-8 Diagram of cerebro-cerebellar input and output.

In addition, a second major cerebellar input path passes from the cerebral cortex to the red nucleus and the inferior olive before the climbing fibers enter the cerebellar cortex. The red nucleus in higher primates, like the dentate nucleus, also contains phylogenetically old and new portions. The older magnocellular part of the red nucleus in primates has been connected to motor functions while the new portion seems to perform some other function. The exact type of information that passes through this newer portion is still unknown, but may be involved in cognitive activities (Leiner et al.,1989). The following describes the major neocortical association areas that have been linked to relay nuclei located in the pons.

Parietal association cortex

Clinical research has shown that patients who have a lesion in the parietal association cortex often demonstrate an inability to attend to and recognize personal and extrapersonal space on the side of the body opposite the lesion. A patient with a right parietal lesion when presented their own left hand may actually deny that it belongs to them. Similarly, objects in the left visual field may not be attended to and ignored. Clinically, this is called contralateral neglect syndrome (Posner and Raichle, 1994; Purves et al., 1999).

Medical imagery (PET) has also shown that there is a clear lateralization of function in the superior parietal association cortex. When normal volunteers are instructed to attend to a visual cue in the left visual field, as expected, right superior parietal cortex is activated. But when attention is shifted to the right visual field both left and right superior parietal association areas activate. Therefore, while the left parietal association area is concerned uniquely with attention toward the right side of the body the right parietal region plays a role in attention toward both sides of the body as well as extrapersonal space (Posner and Raichle, 1994).

Research on laboratory animals has linked the parietal association cortex to the relay nuclei in the ventral pons. Specifically, studies using radiolabeled amino acids have shown that the homologous parietal region in rhesus monkeys projects fibers to a diverse number of pontine nuclei (Schmahmann, 1996).

Temporal association cortex

It is well established that the temporal lobe plays a part in such diverse functions as language, memory, and other complex behaviors (Schmahmann and Pandya, 1997). Damage to either the left or right temporal association areas can cause visual hallucinations as well as deficits in an individual's ability to recognize complex stimuli, such as faces, and to name familiar categories of objects (Damasio et al., 1996). These patients, unlike those who suffer from contralateral neglect syndrome, do not deny that an object on the contralateral side exists, but they are incapable of naming the object or stating its purpose (a key in the hand opposite the lesion for example) (Purves et al., 1999). Additionally, scientists have found specific neurons in the temporal lobes of rhesus macaques that activate almost exclusively when shown the face of another monkey. These cells are also orientation dependant, that is, one cell fires when the face is presented in profile view exclusively, while another might react only to face front view (Desimone, 1991).

Other research in laboratory monkeys has also clearly linked regions of the superior temporal lobe and parastriate occipitotemporal region to a number of sites in the ventral pons. The occipitotemporal regions process information from the peripheral field of vision and help in spatial orientation. Conversely, information from the central field of vision is not projected to the ventral pons (Schmahmann and Pandya, 1997).

Prefrontal association cortex

The frontal lobes of primates are well known for their great cytoarchitectonic diversity. This diversity coincides with the great variety of essential executive and integrative functions (planning, foresight, judgement, attention, language and working

memory) that are performed in the prefrontal association area. Neuroscientists have long considered the frontal lobe to be the seat of human intelligence and individualism (Purves et al., 1999).

One of the great dividing lines between *Homo sapiens* and our hominoid cousins has been the difference in the sizes of our frontal lobes. Although, it is true that the absolute volume of the frontal lobes of humans is quite large compared to other hominoids, recent research has shown that human frontal lobes are no larger than expected for a chimpanzee of equal brain size (Semendeferi et al., 1997). Although the uniqueness of the large human frontal lobes has been questioned, it is clear that there is something special about the development of the human prefrontal association cortex that sets *Homo sapiens* apart from the great apes and lower primates. Once again, radiolabeled amino acid analyses performed on macaque monkeys has shown clear connections between several behaviorally important regions of the prefrontal cortex and a diverse group of locations in the ventral pons. The specific areas include Brodmann's areas 46 (spatial and working memory), area 10 (planning, foresight and judgement), area 9, area 32 (motivational behavior and decision making) and area 45B (homologous to Broca's area in humans) (Schmahmann and Pandya, 1997).

Pontocerebellar connections

Much less is known about the relay of information to the cerebellar cortex once it has reached the pons. One set of classic experiments performed on macaque monkeys utilized a horseradish peroxidase (HRP) tracer injected into the cerebellar cortex (Brodal, 1979). Results from these experiments show that specific areas of the monkey

cerebellum receive input from several dispersed regions in the pons. This suggests that the cerebellar cortex integrates input from a diverse number of cerebral neocortical regions (Schmahmann and Pandya, 1997). This work shows that the lateral cerebellar hemispheres receive much more information from the pons (and neocortical association areas) than does the medial vermis. Additional research has also shown that many of these fibers pass through the dentate nucleus before reaching the cerebellar cortex (Schmahmann, 1996).

Cerebellar output

The second half of the cerebellar neural circuit is the transmission of postprocessed motor, vestibular, and cognitive information out of the cerebellar cortex. As detailed above, the Purkinje cells in the cerebellar cortex are the only cells charged with carrying processed information from the cerebellar cortex to the dentate nucleus and out of the cerebellum. There are three main targets for this cerebellar output depending on the type of information that is processed. One target of cerebellar output is the reticular system in the brain stem. This information is processed in the flocculonodular lobe and eventually reaches parts of the limbic system. A second target, the hypothalamus, is involved in homeostasis and autonomic activities (Haines et al., 1997). The third target is the thalamus. It is the cerebellar output to the thalamus that is most interesting in the present context because of its clear relationship to neocortical association areas (Leiner et al., 1991).

Thalamus

The thalamus is the major cortical relay station of sensory signals feeding into the cerebral cortex. It is a paired structure (left and right), consisting of groups of cortical nuclei that receive input from specific areas throughout the organism. Efferent fibers from the thalamus project to primary sensory areas as well as association areas in the frontal, temporal, occipital, and parietal lobes (Purves, et al. 1999; Schmammann and Pandya, 1997).

Of particular interest here is the ventrolateral portion of the thalamus, which receives motor and nonmotor cerebellar output fibers originating mainly in the dentate nucleus. The thalamus appears to have a specific anterior – posterior organization of fibers flowing from the dentate nucleus to rod-like columns in the thalamic lamellae. Different parts of the dentate nucleus send their output fibers to different, nonoverlapping rods in the ventrolateral thalamus (Thatch and Jones, 1979). Moreover, “[e]ach narrow parallel zone of the dentate nucleus sends its output fibers to one rod, which sends its output fibers as a unit to a column-like aggregate of cells in the cerebral cortex. Through such transmission lines, the anatomical modularity of the cerebellum is preserved, and the output of each module can reach a specific cerebral target (Leiner et al., 1991:121).”

Tracking dento-thalamocortical connections

Middleton and Strick (1994, 1997) developed a new fiber tracking technique (retrograde transneuronal transport of herpes simplex virus type 1) to directly identify the cerebral cortical areas that receive dento-thalamic input. To test the technique these researchers injected tracer virus into the well-known arm area of the primary motor

cortex of cebus monkeys. After three days, tracer virus was found where it was expected in the ventrolateral portion of the thalamus (specifically nucleus ventralis posterior lateralis pars oralis and ventralis lateralis pars oralis). After five days, tracer virus was found in the dorsomedial dentate and interpositus deep cerebellar nuclei exposing the well-known motor connection between the cerebellum and the neocortex (Dow and Moruzzi, 1958; Middleton and Strick, 1994).

Once satisfied with the reliability of this new technique, these researchers repeated the experiment in the ventral premotor association cortex and prefrontal association areas 46 and 9 of cebus monkeys. As predicted by Leiner et al. (1986) numerous fibers terminating in the premotor association areas originated in the dentate nucleus. This confirmed not only that cerebellar output contributes to premotor association areas but also that premotor output originates in an area on the dentate that is more ventral than the area for primary motor output. Furthermore, prefrontal association areas 46 and 9, which are involved in working memory and behavioral guidance, also receive fibers from the ventral part of the dentate nucleus.

To further test these anatomical data, Mushiake and Strick (1993) electrophysiologically recorded dentate activation in living monkeys performing motor and working memory tasks. The results of these experiments clearly confirmed earlier anatomical findings that the dorsal region of the dentate is activated during motor tasks while both ventral and dorsal regions are activated during working memory tasks. Further support came when the same group of workers, using functional magnetic resonance imaging (fMRI), demonstrated dentate activation in normal human subjects performing cognitive tasks (Kim et al., 1994).

Seven healthy volunteers were asked to perform two types of tasks while their brains were imaged by fMRI. The first task required the subjects to manipulate pegs in a pegboard in order to determine a baseline of cerebellar activity during visual and fine motor tasks. The second, cognitive, task required the subjects to solve a pegboard puzzle called the “Insanity test”. All subjects showed a pronounced bilateral activation of the dentate nucleus during the cognitive task. Furthermore, motor activity coincided with dorsal activation of the dentate nucleus while cognitive activity coincided with ventral bilateral activation of the dentate nucleus (Kim et al., 1994). These important results and the results from nonhuman primate studies, there support a clear relationship between the cerebellum and the prefrontal cortex in monkeys and humans alike.

Descriptive statistics of the human cerebellum

This section provides basic linear, weight, volumetric, and area data taken from the literature.

Linear dimensions

In a postmortem study of 195 normal adult men and 167 normal adult women Blinkov and Glezer (1968) [quoting Yurgutis (1955)] presented gross measurements of the human cerebellum (Table 2-4). In addition to the data provided by Blinkov and Glezer (1968), Table 2-4 includes linear data from Kochetkova (1978) and White (1995) taken on endocasts of normal adult *Homo sapiens*. A comparative sample of primates is provided in Chapter 3.

TABLE 2-4 Linear measurements of normal human cerebellums

Measure	Male ¹	Female ¹	Mean ¹	Mean ²	Mean ⁴
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(mm)					
Bicerebellar breadth	98.5	93.6	96.1	109.5	102
Cerebellar length Right	61.9	58.0	60.0	56.3 ³	55
Cerebellar length Left	60.9	58.0	59.5		60
Cerebellar Height	43.7	43.7	43.7	33.3	30

¹Data from Blinkov and Glezer (1968) citing Yurgutis (1957).

²Data from Kochetkova (1978) N=40 normal adults. Sex not identified.

³It is not clear whether the author averaged the left and right hemispheres or if only one measurement was taken.

⁴Data from my unpublished Masters thesis N=5 normal adult endocasts of unknown sex.

Weight

Ellis (1920) compiled data from earlier studies and provided brain and cerebellum weight means for 1,367 human adults grouped into age categories from 20 to 90 years of age. The means for all groups of males and females are combined in Table 2-5.

TABLE 2-5 Weight measurements of human adults from ages 20 to 90 from Ellis (1920)

Measure	Male (N=652)	Female (N=715)
Total brain weight (g)	1332.6	1203
Cerebellar weight (g)	143.7	131.8
% Cerebellum to total brain weight ¹	10.8	11.0

¹Luft et al. (1997) show the % cerebellum to total brain volume to be closer to 9.2 (sexes combined N=31).

Volume

Cerebellar volume measurements were obtained *in vivo* using positron emission tomography (PET) and magnetic resonance imaging (MRI) on normal human adults for the purpose of studying the effects of age and sex on cerebellar size (Table 2-6).

Cerebellar volume and area measurements were calculated by adding scanned cerebellar slices and correcting for slice thickness and interslice gap (Rhyu et al., 1999). The differences in each sample are probably due to normal human variation but one group of researches has suggested that some variation may be racial (Rhyu et al. 1999, Korean study). Unfortunately, body weight and total brain weight measurements were not collected for all these subjects to facilitate an analysis of relative cerebellar volume in males and females.

TABLE 2-6 Cerebellar volume in normal humans based on MRI volumetric studies

Measure	Male	Female	Sexes combined	N	Reference
Cerebellar volume (cm ³)	122±16	104±10	111.8±12.9	37	Escalona et al. 1991
	152.2±10.5	134.6±6.8	143.4±8.7	41	Filipek et al.1994
			134.3±14.9		Raz, 1997
	126±10.4	115.4±11.3	115.05	146	Raz et al., 1998
			120.7±10.9	67	Rhyu et al., 1999
	138.4	135.6	137	6	MacLeod, 2000
			155.1	10	Semendeferi and Damasio, 2000
152	137.4	144.7	46	Allen et al., 2002	
Mean	138	125.4	132.8		

Table 2-7 provides comparative primate volume data.

TABLE 2-7 Mean cerebellar volume of nonhuman primate species (Yerkes) represented in this study (MacLeod, 2000)

Species	Male	Female	Sexes combined	N
<i>Macaca mulatta</i>	7.2			6
<i>Hylobates</i>	9.7	13.6	11.6	4
<i>Pan troglodytes</i>	49.6	45.2	47.4	7
<i>Gorilla</i>	81.2	56.1	68.7	2
<i>Pongo</i>	52.2	42.7	49.8	4

Surface area

The highly convoluted external surface of the cerebellum is composed of transversely aligned parallel concentric folds called folia. The extensive gyrification of the human cerebellar cortex actually obscures between 80 - 85% of the total cerebellar surface area (Barr and Kiernan, 1988; Blinkov and Glezer, 1968). Total cerebellar surface area in humans averages ~85,000 mm² and varies between 50,000 and 120,000 mm² (*ibid.*). (To put this figure into palpable terms, the surface area of this page is 60,480 mm².) Amazingly, the total unfolded surface area of the cerebellum in *Homo sapiens*, as in the case of DNA density, is approximately half that of the cerebrum, a structure that is eight times larger (Blinkov and Glezer, 1968).

Sex and Age

The linear, weight, and volume data in Tables 2-4 – 2-8 show that males have absolutely larger cerebellums than females, although the ratio of total brain weight to cerebellum weight is quite close. Except for Ellis’s (1920) early postmortem study, all volume data were collected *in vivo* using either MRI or PET technology. These data

were collected in a clinical setting to measure cerebellar degeneration with age. Unfortunately, most of these studies did not include body size data to test the allometric effects of cerebellum size to body size. One group of researchers, however, (Raz, 1997; Raz et al., 1998), did use height to account for body size variation and found a less dramatic but obvious size difference between the sexes (males having larger cerebellums). Differences were also found at the subcerebellar level with males having greater anterior vermis area and lateral cerebellar hemisphere volume than females [also corrected for height] (Raz et al., 1998).

Ellis (1920) was one of the first to report negative age to cerebellum weight correlation, as well as a decrease in the number of Purkinje cells and molecular layer width over the age of 50 in a large postmortem sample. A consistent decline in cerebellar volume with age has also been reported by several groups of workers in living normal adult populations (Oguro et al., 1998; Raz, 1997; Raz et al., 1998; Rhyu et al., 1999). The only two studies to refute this decline (Escalona et al., 1991; Luft et al., 1997), were shown to be both statistically and allometrically flawed (Raz, 1997).

Lateralization

The degree of cerebellar lateralization has not been as extensively documented as has cerebral lateralization in humans. To my knowledge there has been only one large-scale attempt to measure the linear dimensions of the human cerebellum (but see Table 2-4). The report's data (written in Russian) were documented by Blinkov and Glezer who stated the following concerning cerebellar lateralization:

“In groups of both young and old women, the dimensions of the cerebellum were more symmetrical than in men. In 195 men the right hemisphere was longer than the left in 55.89% of cases, and the left longer than the right in 22.5%. In 167 women the right hemisphere was longer in 38.92% of cases and the left in 37.72% (Yurgutis, 1955) (Blinkov and Glezer, 1968:163).”

Although linear measurement techniques useful in studies focussing on endocasts, most medical and anthropological studies today obtain volume data using advanced medical neuroimaging techniques.

Raz et al., (1998) obtained volume data from 64 normal adult males and 82 normal adult females with magnetic resonance imaging. They showed that males had larger left cerebellar hemispheres by 6.5%, while females had larger right cerebellar hemispheres by 7.9%. Allen et al. (2002) imaged the brains of 23 normal adult males and 23 normal adult females and found no statistically significant lateralization in the cerebellum in either males or females.

In an another MRI based study of 15 normal adult males and 8 normal adult females, Snyder et al. (1995) found that the right anterior cerebellum was larger than the left anterior cerebellum and the left posterior cerebellum was larger than the right posterior cerebellum in the combined sex sample. They found that right-handed individuals demonstrated greater asymmetry than sinistrals and that the right anterior – left posterior asymmetry pattern resembles the common right frontal –left occipital neocortical petalia pattern found in humans.

Falk et al. (2005), also using MRI based techniques, demonstrated statistically significant shape differences in the left and right cerebral and cerebellar hemispheres of a large sample of men (n= 60 dextrals, 24 sinistrals) and women (n=56 dextrals, 26

sinistrals). They found very different patterns of cortical and cerebellar shape asymmetries in the four different groups. Of greatest interest to this study, is the finding that right-handed men have larger left antero-lateral and right medio-posterior portions of the cerebellum. Left-handed females have larger right antero-lateral portions of the cerebellum. These expanded zones appear to occur in what is considered the neocerebellum or posterior lobe of the cerebellum.

Interestingly, Andreasen et al. (1993) demonstrated, among other subcortical structures, the cerebellum is significantly correlated with verbal, performance and full scale IQ. These workers found that verbal IQ and full scale IQ are more highly correlated with the cerebellar volume of females than of males. These results may be of great importance if we consider that the right lateral cerebellar hemisphere has been implicated in language based processing and manipulation (discussed below), while the vermis and left lateral cerebellar hemisphere are linked to motor and visuospatial processing. If females are right cerebellum lateralized, this may mean that they have relatively more cerebellar processing power for language than males, whereas males may have more visuospatial and motor processing power than females (Andreasen et al., 1993; Falk et al., 1999).

Histological examination of the molecular layer of the cerebellum has shown that this layer in the right cerebellar hemisphere is thicker than in the left cerebellar hemisphere (Ellis, 1920). Furthermore, it has been suggested that the right cerebellar hemisphere may be the dominant hemisphere due to the fact that it processes a great deal of motor and nonmotor information from the dominant left cerebral hemisphere (Blinkov and Glezer, 1968). This right cerebellar dominance may also be linked to

higher cognitive processing functions in humans such as language and planning behavior (Leiner et al., 1986).

Another important lateralization concerns a greater loss of Purkinje cells in the right cerebellar hemisphere than in the vermis or left hemisphere during senescence (Ellis, 1920). This Purkinje cell loss has been invoked to explain loss of muscle coordination and tone in advancing age but may now also be related to the reduction in the ability to cognitively manipulate ideas and language (*ibid.*).

Experimental evidence

One of the greatest leaps in medical science at the end of the twentieth century was the invention of imaging technology that has allowed doctors and researchers to visualize the human brain at work. To measure brain activity, PET and fMRI take advantage of the principle that brain cells demand more oxygen (and therefore more blood) when they are active (Raichle, 1998). Changes in blood hemodynamics and oxygen metabolism are measured by firing charged particles through the brain in the PET scan and by measuring the magnetic polarity of brain tissue in the fMRI scan. Both techniques are relatively noninvasive and are becoming less expensive to employ. Many of the following scientific achievements presented here have been gained through use of this powerful technology.

Language

One of the first studies to utilize PET technology to map cognitive functions focused on the uniquely human ability to speak. Petersen et al. (1988) measured blood flow changes in the brains of 17 normal human volunteers performing verbal and

auditory cognitive tasks. The volunteers were asked in the control portion of the experiment to repeat out loud, nouns that were said to them and nouns they read. This established a baseline scan of motor activity that was subsequently subtracted from the cognitive experiment. In the cognitive part of the experiment, the volunteers were asked both to think (covertly) and to say (overtly) appropriate verbs for nouns presented orally and visually. Subtracting the controls from the experimental samples showed activation of parts of the left frontal region, (including Broca's area and the dorsolateral prefrontal area) as well as an unexpected activation of the right lateral cerebellar hemisphere (RLCH). Interestingly, simple motor activation was confined to the medial (vermal) cerebellum and did not involve the lateral cerebellar hemisphere.

Generating words

Since this first pioneering work, several other studies have shown that the RLCH is activated during verb generation tasks (Martin et al., 1995; Raichle et al., 1994). This work has confirmed that activation of the RLCH corresponds directly to activation of the cortical association regions in the left (contralateral) cerebral hemisphere. Activation of the RLCH has also been reported when verbs were generated after lexical (reading nouns), visual (object), and auditory (nouns read out loud) cues. It is, thus, more and more evident that the RLCH plays an integral part of a neural circuitry which allows the brain to search and retrieve appropriate verbal information in a timely fashion. In one of these studies, Martin et al. (1995) demonstrated that the neural circuitry for verbal retrieval is task dependent. This team showed that the RLCH is activated when subjects are asked to generate verbs and name

appropriate colors in response to pictures of objects, although these two word generation tasks activate two different neocortical regions in the cerebral cortex. The verb generation task involves parts of the left middle temporal cortex (known for the perception of movement) and the color naming task involves a different region in the left inferior temporal cortex (associated with color perception) (see also Damasio et al., 1996).

Other studies have shown that the RLCH is involved when subjects are asked to make words from three letter cues (Buckner et al., 1995), one letter cues (Schlosser et al., 1998), as well as cues possessing many and few completion choices (Desmond et al., 1998). Tasks such as generating synonyms, rhymes, and translations based on cue words (Klein et al., 1995) and tests of verbal fluency (Akshoomoff and Courchesne, 1992; Schlosser et al., 1998) also cause RLCH activation. Verbal fluency tasks require a subject to think of groups of words that begin with a letter that is presented visually or auditorily and can be expressed overtly or covertly (Fiez and Raichle, 1997). It appears that both verbalized and un verbalized completions of these tasks activate the RLCH. Silent thinking, however, appears to produce fMRI signals in the RLCH that are as strong or stronger than verbalized thoughts (Fiez et al., 1996; Ryding et al., 1993; Yetkin et al., 1994).

Verbal working memory

Working memory is the ability to keep information online in order to use this information after a period of delay. A great deal of research on humans has shown that both verbal and nonverbal working memory tasks elicit cerebellar, fronto-opercular

(areas 44/45), and supplementary motor activation (Fiez and Raichle, 1997 and Table 2-8). Unlike word searching and generating tasks, working memory tasks activate diverse areas in the left medial and intermediate cerebellum. It has been suggested that the activation of these regions of the cerebellum is related to silent or verbalized mouthing of words called covert articulatory rehearsal (i.e. repeating a phone number several times in your head to commit it to memory) (*ibid.*).

TABLE 2-8 Cerebellar activation in normal adults during verbal working memory tasks

Technique	Reference	Year
PET	Grasby et al.	1993
PET and fMRI	Paulesu et al.	1993, 1995
PET	Petrides et al.	1993
PET	Frackowiak	1994
PET	Démonet et al.	1994
PET	Awh et al.	1996
PET	Fiez et al.	1996
fMRI	Paradiso et al.	1997

A typical working memory experiment requires the subject (human or experimental animal) to retain some kind of visual, lexical, or auditory information for a specified delay period. After the delay period, the subject is asked to recall what they have stored and the accuracy of recall is examined in terms of the type and the amount of information stored. In one study, Awh et al. (1996) showed human subjects a target group containing four letters for 200 milliseconds. Three seconds later the subjects were shown a test letter and were asked to acknowledge, by clicking a mouse button, whether the test letter had appeared in the first group of four. After this, the subjects were shown a single letter every three seconds and asked to acknowledge whether the letter was the same as the letter presented two times before (*i.e.* 1st trial = F, 2nd trial = T, 3rd trial=F, affirmative response). In general, longer delays and more complicated tasks (*i.e.* larger groups) required longer and more intense processing time.

As mentioned above, some workers believe that words presented visually or auditorily in verbal working memory tasks are recoded into phonological representations by silently articulating the words to commit them to memory (Fiez and Raichle, 1997). Other imaging studies have shown similar cerebellar activation when volunteers were asked to silently imagine themselves performing body movements

(such as playing tennis) (Decety et al., 1990; Fiez and Raichle, 1997). Thus the question arises: How do we know that the lateral cerebellum activation is not due simply to some hidden motor input? One hypothesis suggests that RLCH activation is strongest during discriminating and comparing tasks (Middleton and Strick, 1994; Parsons and Fox, 1997; Schmahmann and Pandya, 1997). The cerebellum may act as an inhibitor to incorrect choices before any decision is made. A similar inhibitory process may also be occurring in the part of left lateral cerebellar hemisphere that is associated with verbal working memory.

Sensory discrimination

Several stepwise experiments have been designed to distinguish perceptual / cognitive function from somatomotor function in the cerebellum (Gao et al., 1996; Parsons and Fox, 1997; Sergent et al. 1992). In these studies, cerebellar or dentate activation was measured using PET/fMRI technology and cerebellar activation was compared to activation of known motor or cognitive areas in the cerebral neocortex. In one of the first studies, Parsons et al. (1995) showed subjects two sets of paired three-dimensional objects and asked them to covertly (silently) discriminate between them. The control set showed two pairs of 3d objects. One pair had exactly identical shapes in the same orientation and the other set were exact mirror images of each other. This portion of the experiment activated encoding, comparison, and shape judgement areas of the brain. The experimental portion of the experiment again showed two pairs of 3d objects with an identical pair and a mirror image pair. But, in the experimental portion of the experiment, the objects in each pair were rotated in opposite direction to confuse

the subject. Once again encoding, comparison, and shape judgement areas of the brain were activated, but to these areas were added mental rotation areas. By subtracting the the control activation areas from experimental activation areas, a clear picture of the mental rotation regions could be viewed. The cerebellum showed bilateral (but stronger right) activation of the superior vermis, deep nuclei, and inferior and superior lateral hemispheres. Parsons et al. (1995) also noted that the brain does not utilize areas that are known to be involved in imagined or planned body movements to perform mental rotations. Thus, to answer the question in the previous section, it appears that the cerebellum participates in perceptual/cognitive tasks without imagined or planned motor involvement (Parsons and Fox, 1997).

In a subsequent study, the same group from the University of Texas Health Science Center were able to measure dentate activation during tactile sensory, motor, and sensory discrimination tasks (Gao et al., 1996). In the control portion of the experiment subjects received light tactile stimulation on the pads of their fingers and a small bilateral activation of the dentate nuclei was detected. The next part of the experiment required the subjects to covertly discriminate between two grades (coarse-fine) of sandpaper rubbed across their finger pads. Activation from this experiment was bilaterally three to four times more intense and the right side showed stronger activation than the left. The third part of the experiment asked the subjects to first grasp and drop variously shaped objects in each hand and then grasp and covertly discriminate between the objects in each hand. As expected the discrimination portion of the experiment caused a strong bilateral (right biased) activation over the simple motor task (*ibid.*).

In the last part of the experiment the researcher tested whether fine finger and hand manipulation caused a large dentate activation. In this experiment, the control portion of the experiment asked subjects to perform a fine finger coordination task. The experimental portion added a discrimination task on top of the coordination task. Results showed that fine finger coordination tasks do not require extensive dentate output while sensory discrimination tasks do (Gao et al., 1996; Parsons and Fox, 1997). Thus, the much-touted hypothesis that human neocerebellar evolution is directly linked to fine manipulatory coordination is not supported by these latest experiments (Matano et al., 1985a,b; Tilney, 1928;).

Music

Activation of the lateral cerebellar hemispheres has also been detected during the production of music (see also Falk, 2000 for review). Parsons and Fox (1997) using PET found differential bilateral activation of the temporal cortices and the cerebellum when professional musicians performed two different musical tasks. The first task required that the subjects play musical scales and the second task required them to play a piece of music (third movement of Bach's Italian concerto). Each task was performed with two hands. The first task (scales) substantially activated the left auditory temporal cortex (area 22) and the right intermediate lateral cerebellum, which corresponds well with previous work (Sergent et al., 1992). The second task activated both the left and right auditory temporal cortices as well as both left and right intermediate lateral cerebellar hemispheres. In fact, the act of listening to music also activated temporal area 22 and the lateral cerebellar hemispheres (Sergent et al., 1992). This suggests that

the lateral cerebellum is called upon by the contralateral temporal cortex to process (discriminate?) nonmotor cognitive aspects of listening to and playing music.

Attention

In addition to problem solving (Kim et al., 1994), verbal processing (Petersen et al., 1988), verbal working memory (Table 2-8), sensory discrimination (Gao et al., 1996), and musical processing (Sergent et al., 1992), the lateral cerebellar hemisphere has been implicated in the evolutionarily important function of attention orientation, shifting, and direction (Akshoomoff et al., 1997). Interest in cerebellar involvement in attention shifting grew out of studies of patients suffering from autism, which is a behaviorally defined syndrome whose symptoms include “atypical social interaction, disordered language and cognitive skills, impaired imaginary play, poor eye contact, and an obsessive insistence on sameness (Bauman et al., 1997:367).” Postmortem examination of the brains of autistic patients has shown distinct wasting in the vermal area (Larsell’s lobules VI-VII) and Purkinje cells of the cerebellum (Bauman et al., 1997). This condition reveals itself very early in postnatal development and may extend into the lateral cerebellar hemispheres with age (Akshoomoff et al., 1997).

From these anatomical data, Courchesne et al. (1994) tested the hypothesis that cerebellar degeneration impairs the ability of autistic patients to rapidly and fluidly shift attention in social, visual and auditory modalities. They found that when autistic patients are compared to a normal control group, the autistic group has a substantially diminished capacity to shift attention between visual and auditory modalities. This is also true for patients suffering from focal cerebellar lesions.

Allen et al. (1997) using fMRI technology localized the sites of activation in normal cerebellums during a focused attention task. These workers showed that the left superior posterior lateral cerebellar hemisphere is strongly activated when a subject passively attends to a stationary visual stimulus. The motor task causes antero-medial cerebellar activation. Additionally, Le and Hu (1996) and Le et al. (1998) have also shown that when subjects are asked to actively shift attention between different visual stimuli as opposed to maintaining a steady focused attention, the right lateral cerebellar hemisphere was strongly activated instead of the left. This suggests again that the RLCH is involved in important nonmotor complex processing.

Clinical evidence

The development of theories of brain function owes a great deal to clinical research involving patients suffering from brain disease and trauma. Much of our understanding of motor and processing aspects of the cerebellum were gained through clinical and anatomical analyses. Until recently however, very little clinical evidence pointed to any nonmotor, particularly cognitive, function of the cerebellum. There are several reasons that explain this absence.

One reason discussed earlier in this dissertation has to do with the strong historical bias toward relegating the cerebellum to proprioceptive and motor coordination tasks. In the twentieth century, no mention of cerebellar involvement in cognitive deficiencies can be found before Dow (1942). It took approximately another forty years before the technology existed to further test Dow's hypotheses. A second reason stems from this historical bias. Physicians have long understood that cerebellar

damage may degrade motor skills for a period of time after a trauma, but it never abolishes them completely. There is generally a period of recovery and compensation where skills are diminished and then seem to return with various levels of permanent impairment (Clarke and O'Malley, 1968). These motor deficiencies are well documented, but few physicians in this century have noticed or tested for the subtle verbal or other cognitive deficiencies of cerebellar patients (Schmahmann and Sherman, 1997).

A third reason is the nature of clinical evidence. Cerebellar damage may come in many different forms, resulting from autism to gunshot wounds to vascular occlusions. Rarely is this type of damage confined to one particular functional region of the cerebellum. Cerebellar damage may also co-occur with damage to other (neocortical) areas, which can confound the subtle cognitive deficits hypothesized for cerebellar damage. Furthermore, even with modern clinical technology the various methods of testing patients, choosing study subjects, and analyzing results can confound scientific agreement about what is really happening in the cerebellum (Daum and Ackerman, 1997). Nonetheless, the study of cerebellar disorders has provided insightful clues as to about the various cognitive functions the cerebellum may be called upon to coordinate. (Table 2-9 provides a list of task-based cognitive deficits observed in a variety of patients with cerebellar dysfunction.) The following example demonstrates the kind of information clinical observations have provided linking the cerebellum to higher cognitive abilities.

TABLE 2-9 Cerebellar studies of clinical patients

Task due to cerebellar damage	Reference	Year
Conditional associative learning deficits	Bracke-Tolkmitt et al.	1989
	Canavan et al.	1994
Memory deficits	Appollonio et al.	1993
Agrammatism	Silveri et al.	1994
	Nespoulous et al.	1988
Dysgraphia	Molinari et al.	1997
Deficits in judging time and velocity of moving stimuli	Ivry and Baldo	1992
Nonmotor learning and error detection deficits	Fiez et al.	1992
Cognitive planning deficit	Grafman et al.	1992
Visuo-spatial deficits	Botez	1992
Attention shifting deficit	Courchesne et al.	1994
Behavioral degeneration	Pollack et al.	1995

One of the most interesting cases demonstrating cerebellar interaction with higher cognitive cortical centers involved agrammatical speech in a man who suffered a right focal cerebellar lesion (Silveri et al., 1994). The patient did not suffer from any other cognitive disorders and the cerebellar lesion coincided with uncoordinated movements of the right side of the body (dysmetria, adiadokokinesia). His speech deficit was specifically limited to an inability to choose the appropriate conjugation of a verb during speech production. Although, the correct verb for the thought being expressed was chosen. There were signs of neither comprehension nor articulation difficulties. As expected, both motor and cognitive deficits improved with time and only occasional instances of incorrect conjugation were noticed. This clinical case supports the link between the cognitive grammatical functions of the left temporal/prefrontal cortexes and the right lateral cerebellar hemisphere.

A theory of cerebellar function

As demonstrated above, an enormous amount of clinical and experimental research has shown a link between the lateral cerebellar hemispheres and cognitive association areas in humans and nonhuman primates. The diversity and strength of this connection appears to coincide anatomically with the increase in size of cerebral and cerebellar structures as well as the improvement of processing capabilities. This benefit of improved processing power helps to obviate the evolutionary risks of crowding two enlarged metabolically expensive structures, namely the cerebellum and the cerebrum, in an already overcrowded human cranium. The cerebellum has increased in size throughout mammalian evolution but has remained uniform in basic cytoarchitecture.

This uniformity requires the basic units of cerebellar processing (i.e. microcomplexes and modules) to adapt to various types of cerebral, vestibular, and somatomotor input. Theoretically, there is reason to believe that the information emitted by the rabbit cerebellum to modulate motor skills carries the same type of signal as information emitted by the human cerebellum to modulate verb selection. This conservative yet versatile system has been compared to the powerful versatility of a computer chip (Leiner et al., 1986, 1989, 1991, 1993; Leiner and Leiner, 1997). Moreover, information systems theory states that the processing power of a computer is improved by aligning greater numbers of these basic units (chips or modules) in parallel. This type of parallel alignment can be seen in the Purkinje cells of the cerebellar cortex. Thus, more cerebellar volume means more basic units of processing and great processing power.

Leiner and Leiner (1997) have proposed an eloquent model of cerebellar function that simply explains how cerebellar output can influence various types of cognitive, sensory, and vestibular tasks. The authors hypothesize that, like a computer chip, the modules in the cerebellar cortex must recognize three types of incoming messages: “which” messages, “where” messages, and “when” messages. “The “which” message can tell the recipient module which kind of transformation it should perform on the inflowing stream of information; the “where” messages can tell it where in the system to send the transformed stream; and the “when” messages can tell it at what times and under what conditions it should transmit this output (Leiner and Leiner, 1997:543).”

If the output of several modules or groups of modules are bundled together an enormous amount of information about word discrimination, error detection, planning, timing etc. can be transmitted to the appropriate cortical and subcortical structures. In fact, anatomical evidence suggests that cerebellar output leaves the dentate nucleus in bundles of fibers that transmit information from groups of cerebellar cells to specific rod to column projections in the thalamus. The thalamic cells in turn project to specific groups of cells in the neocortex.

Leiner and Leiner (1997) provide a convincing example of how this bundling process could work. They suggest that each fiber in a bundle transmit only one type of message; either the fiber is active (on) or inactive (off). If each fiber in a bundle of three fibers works independently the greatest number of signals that the three fibers can transmit is three. But, if each of the three fibers (emitting only on and off signals) is bundled together into a unit, combinatorial mathematics shows that they could produce

2^3 or 8 different signals. As the number of fibers in each bundle grows, the combination of different signals grows exponentially (i.e. 10 bundled fibers could produce 2^{10} or 1024 different combinations).

Leiner and Leiner liken these different combinations of signals to the letters, words, sentences, paragraphs, and volumes of an internal cerebellar language. By combining different bundles of fibers from different groups of cerebellar modules linking to various sites in the cerebral cortex, the cerebellum could communicate in literally millions of different ways. The simplicity of the system would allow many different cortical or subcortical region to call upon the rapid, universal processing power of the cerebellum in order to function with greater speed and accuracy (Leiner and Leiner, 1997).

This theory successfully explains the conservative nature and universality of the vertebrate cerebellum while also considering the great specificity of cerebellar output shown in medical imagery and clinical studies of cognition. The cerebellum appears to have adapted wonderfully to the specific exigencies of each vertebrate phylogeny while maintaining its relatively simple and elegant design.

Paleoneurological contributions

As discussed in Chapter 1, paleoneurology has only recently begun to make a contribution to the study of human cerebellar evolution (Weaver, 2005). However, paleoneurological evidence is the only direct link modern science has with the fossilized traces of the brains of extinct organisms that contributed to human phylogeny. By studying the changes in morphology, size, and shape of the cranial remains and

endocranial casts (natural, artificial, and virtual) of our fossil hominin ancestors, we may be able to understand the timing of cerebellar growth and its behavioral correlates.

Figure 2-9 depicts the endocast of *Pongo* in four views.

Many of the authors cited in this work have referred to the enlarged size of the lateral cerebellar hemispheres in modern *Homo sapiens* and their importance in human evolution. These authors note that Passingham (1975) reported that the human cerebellum is three times larger, in absolute measures, than the cerebellum of a chimpanzee. (This is, however, expected since total brain size in humans is three times larger than chimpanzees.) Unfortunately, most of these authors fail to understand that this fact derives from the study of only *one* modern human cerebellum and *one* chimpanzee (Stephan et al., 1970; MacLeod, 2000).

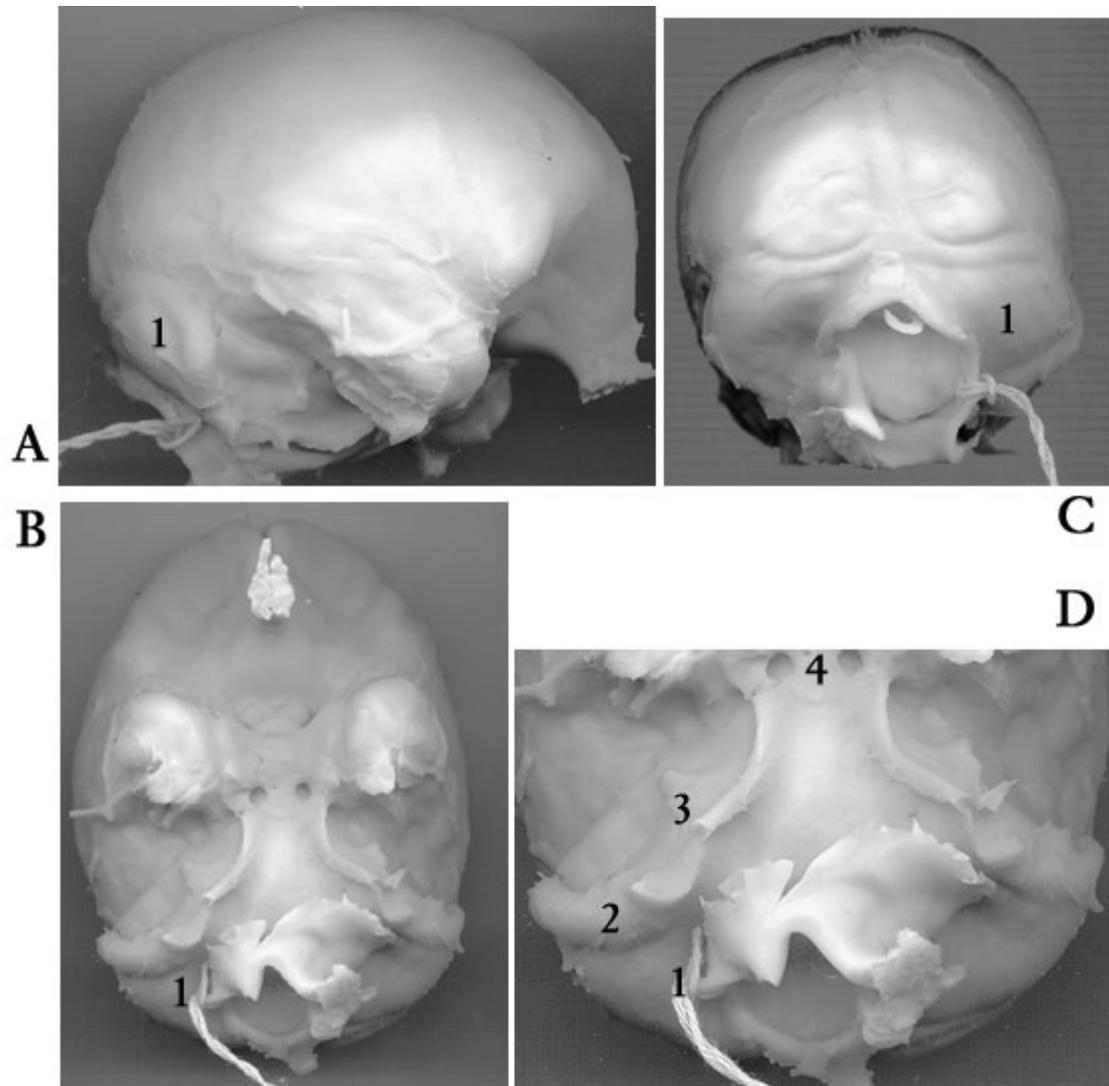


Fig. 2-9 Four views of a *Pongo* endocranium. A) *norma lateralis*, B) *norma basilaris*, C) *norma occipitalis*, D) Close up of cerebellum region in *norma basilaris*. 1) Right lateral cerebellar hemisphere, 2) venous sinus, 3) impression of the internal auditory meatus, 4) dorsum sella.

One of the benefits of paleoneurology is that we can compare evidence from both extant primate species (human and nonhuman) and extinct hominin species to provide a clearer picture of phylogenetic development.

Within the cerebellum of each specimen it would be possible to estimate the ratio of lateral cerebellar hemisphere to vermis. Matano et al. (1985a,b) have demonstrated that organisms with large hemispheres relative to the vermis are generally more progressive and skillful than organisms with relatively large vermal areas. These findings can now be applied to a comparative study of endocasts from fossil hominins, extant hominoids, and nonhuman primates. Endocasts can provide information, not only about phylogenetic development, but also about ontogenetic development in extant and extinct species. Of particular interest is the relative position of the cerebellum inside the cranium and the adjustments the cranial base must make in order to accommodate both a large cerebrum and cerebellum. The position and angle of the petrous bones and clivus are evident on the basilar surface of endocasts and can easily be quantified to provide data for prediction models.

PART 1 SUMMARY

Clearly the study of human cerebellar function and evolution has come a long way since Aristotle first declared it a unique organ. The promising use of neuromedical imagery has created a knowledge boom, but this type of research cannot answer all of our questions about the cerebellum. Part 2 of this work contains three empirical sections that use our current understanding of the robust cerebro-cerebellar connections in the primate cerebellum to better understand how the size and shape of the cerebellum have evolved in catarrhines.

PART 2: RESULTS

Chapter 1 of this dissertation traced the historical development of the classical definition of cerebellar function. Chapter 2 introduced cerebellar anatomy, cytoarchitecture, and recent scientific experiments that have challenged the classical motor-only definition of cerebellar function. Strong empirical evidence from varied neuroscientific communities has led to a more profound appreciation of cerebro-cerebellar interconnections. The cerebellum plays an important role in both motor and nonmotor (i.e. cognitive) functions.

This appreciation has opened a new avenue for paleoneurological research (Dean, 1986, 1988; MacLeod, 2000, 2001, 2003; Weaver 2001, 2005; White, 1996, 1998, 2000; White and Falk, 2002). As demonstrated in Chapter 1- until quite recently, paleoneurological investigation of hominin brain evolution focused almost exclusively on cerebral size and form. The seminal work of Leiner et al. (1986) among others, prompted paleoneurologists to thoroughly examine evidence of the cerebellum impressed within the cranial bases of extinct fossil hominins in order to expand our knowledge of the evolution and cognitive attributes of extinct hominin species.

The evolution of the hominoid (living and extinct) cerebellum has been most recently addressed by MacLeod (2000, 2001, 2003) and Weaver (2001, 2005). Where it concerns this work, MacLeod's (2000) major finding is that the lateral cerebellar hemispheres in the hominoid lineage have increased in volume relative to vermis volume. MacLeod's extensive work suggests larger-brained primates with more cognitive versatility also possess larger cerebellar hemispheres in order to process

information derived from the concomitantly enlarged structures in the cerebral neocortex. Her study benefits from large sample sizes of primates and a combination of serial section and neuroimaging volume data.

Weaver (2001) provides important empirical results that bolster the heuristic value of endocasts for understanding cerebellum evolution. Weaver's significant contribution establishes a clear empirical relationship between the size of the posterior cranial fossa and the cerebellum in hominoids. Weaver (2001) demonstrates convincingly that cerebellum volume in hominoids is highly predictable. Based on this observation, cerebellum volume in fossil hominin specimens can be calculated and analyzed in an evolutionary framework. Her major conclusion is that there is a demonstrable reciprocal evolution of the cerebellum and cerebrum (Weaver, 2005).

In the following three chapters, I present novel research on the size and shape of the catarrhine primate cerebellum. Two methods of data analysis are employed. In Chapter 3, I use traditional linear morphometric techniques to compare the cerebellar portion of endocasts. In Chapters 4 and 5, I use geometric morphometric techniques to study the cerebellum and endo-basiscranial shape of my sample of *Macaca*, *Hylobates*, *Pongo*, *Gorilla*, *Pan*, Plio-Pleistocene hominins, and *Homo sapiens* endocasts. Chapter 4 focuses on the size and shape of the posterior cranial fossa. Chapter 5 focuses on the entire endo-basiscranium size and shape.

Three general hypotheses of significant paleoneurological interest are tested in each chapter; 1) evidence for grade shifts in cerebellum size and shape, 2) asymmetry in cerebellum size and shape, and 3) sexual dimorphism in cerebellum size and shape.

CHAPTER 3: CEREBELLUM SIZE IN EXTANT CATARRHINES AND PLIO- PLEISTOCENE FOSSIL HOMININ ENDOCASTS: A TRADITIONAL LINEAR MORPHOMETRIC ANALYSIS.

In this chapter, five linear measurements are used to investigate size, lateral asymmetry, and sexual dimorphism of the cerebellum on endocasts of *Macaca*, *Hylobates*, *Pongo*, *Gorilla*, *Pan*, Plio-Pleistocene hominins, and modern *Homo sapiens*. Primates and fossil hominins are also compared using a bicerebellar index and bicerebellar quotient.

The representation of the cerebellum on an endocast is derived from the posterior cranial fossa. The cerebellum is not the only structure housed in the posterior cranial fossa but it is by far the largest structure (Matano et al, 1985a,b). Weaver (2005) demonstrates that the volume of the posterior cranial fossa is strongly correlated ($r^2=.89$) with the volume of the human and ape cerebellum. Thus, measuring the posterior cranial fossa represented on the endocasts of both extant and fossil primate taxa provides a reasonable approximation of cerebellum size.

Rilling (1998) points out that “relative to brain size, apes clearly have larger cerebella than either monkeys or humans (p. 312).” Pongids and hylobatids have cerebellums that are approximately 1.45 times larger than expected for a monkey of equal brain size (Rilling, 1998). This deviation from allometry in apes has been explained by reference to the extraordinary locomotor, acrobatic, and manipulative skills of these species (MacLeod, 2001, Matano et al., 1985b).

As discussed in the preceding chapter, developments in medical neuroimaging technology have demonstrated that the human cerebellum plays a role in processing both motor and vital cognitive functions such as the generation of verbs, synonyms, rhymes (Martin et al., 1995; Petersen et al., 1988; Raichle et al., 1994), translation (Klein et al., 1995), working memory (Fiez et al., 1996; Fiez & Raichle, 1997), musical ability (Falk, 2000; Hutchinson et al. 2003), planning behavior, attention shifting, procedural learning, and abstract reasoning (Leiner et al., 1986; 1989; 1991; 1995). Ancestral hominins evolved in a complex ecological and social environment that demanded rapid decision making, planning, procedural learning, and group communication. Individuals who were better able to quickly utilize information gathered by their senses were more likely to pass on their genes to the next generation. Thus, one would also expect the human cerebellum to show a deviation from allometry similar to the apes.

In fact, most recent studies using volume data obtained from *in vivo* MRI scans of apes and humans conclude that the human cerebellum is smaller than would be expected for a primate or ape of similar brain size (MacLeod et al. 2001; Rilling and Insel, 1998; Semendeferi and Damasio, 2000; Semendeferi, 2001). Thus, the absolute size of the human cerebellum is on average larger than any other primate species but cerebellum size relative to brain size is smaller than in apes. This suggests that the neocortex has reorganized and expanded at a faster pace than the cerebellum during hominin evolution.

Weaver (2005) reports that throughout most of hominin evolution, the cerebral hemispheres were large in relation to the cerebellum but in modern *Homo sapiens* the

cerebellum is larger than expected for an anthropoid of similar brain size. The differences in the results may be due to the size and composition of the data sets and the regression models chosen for each analysis (Holloway and Post, 1982). Traditional linear morphometric data presented below support the conclusion that modern human cerebellums are smaller than expected for an ape of equal brain size.

In addition to the allometric issue referred to above, the biologically important and interesting issues of lateralization and sexual dimorphism in primate cerebellum evolution are addressed. Brain imaging studies have shown activation of the right lateral hemisphere during tasks that challenge verbal fluency, word selection, and language processing in humans (Desmond et al, 1998; Riva and Giorgi, 2000; Schlosser et al, 1998). It is of great paleoneurological interest to know if the cerebellum became lateralized in size and perhaps function during hominin evolution. Of equal interest is the question of male/female differences in cerebellum size (Falk et al., 1999). The literature contains conflicting reports about sexual dimorphism of the human cerebellum and almost nothing about cerebellum dimorphism in apes (Andreasen et al., 1993; Blinkov and Glezer, 1968).

Materials and Methods

The extant primate data set is obtained from endocast from *Macaca mulatta* (30 male, 30 female), *Hylobates syndactylus* (6 male, 7 female), *Pongo pygmaeus* (5 male, 3 female), *Gorilla gorilla* (5 male, 5 female), *Pan troglodytes* (3 male, 5 female), and *Homo sapiens* (5, sex unknown). All materials, except for the *Hylobates* casts, are housed in Dean Falk's laboratory. Siamang endocasts were kindly provided by John

Redmond (Redmond, 2000). The fossil hominin specimens measured for this dissertation include Sts 5, Sts 19, OH 5, KNM-ER 1813, KNM-ER 1805, KNM-ER 3883, and La Chapelle-aux-Saints.

The measurement of endocasts with calipers has a long tradition (Connolly, 1950; Falk et al., 1999; Holloway et al., 2004). It is a simple method that requires simple tools and is highly repeatable. Chord measurements provide relatively accurate estimations of the major dimensions of endocasts when comparing extant primates and fossil hominins. Inter- and intra-observer error always exists in metric studies but it can be reduced by adhering to strict measurement criteria such as properly aligning endocasts before taking measurements.

A series of five linear measurements were taken to estimate the maximum breadth, length and height of the cerebellum from the endocasts. The measurements are; 1) bicerebellar breadth, 2) cerebellar lobe (medio-lateral length), 3) cerebellar lobe (antero-posterior length, 4) cerebellar lobe height, and 5) cerebral length. Tables 3-1 and 3-2 provide a list of measurement landmarks and Figures 3-1 and 3-2 demonstrate their locations.

TABLE 3-1 Endocast anatomical landmarks

Abbreviation	Measurement	Description
F	Frontal pole	Most anterior point of the endocast representing the cerebral hemisphere in basicranial view. Measured bilaterally.
Ci	Inferior cerebellar point	Point representing the most inferior point of the posterior cranial fossa impression. (Endocast aligned in the F-O plane.)
Cl	Lateral cerebellar point	Most lateral point on the cerebellar hemisphere impression on the endocast.
Cc	Medial cerebellar point	Most medial aspect of the cerebellar hemisphere.
Co	Occipital cerebellum	Point representing the most caudal point on the impression of the cerebellar hemispheres.
Cv	Superior cerebellum	Most superior point on the impression of the cerebellar hemispheres (taken inferior to the transverse venous sinus).
IAM	Internal Auditory meatus	The impression of the internal auditory meatus on the endocast
O	Occipital pole	Most posterior point on each cerebral hemisphere in basicranial view.

Table 3-2 Linear Measurements

Measurement	Description	Number
Bicerebellar breadth	Cl-cl	1
Cerebellar lobe medio-lateral length	cl-cc	2
Cerebellar lobe antero-posterior length	co-IAM	3
Cerebellar lobe height	cv-ci	4
Cerebral length	F-O	5

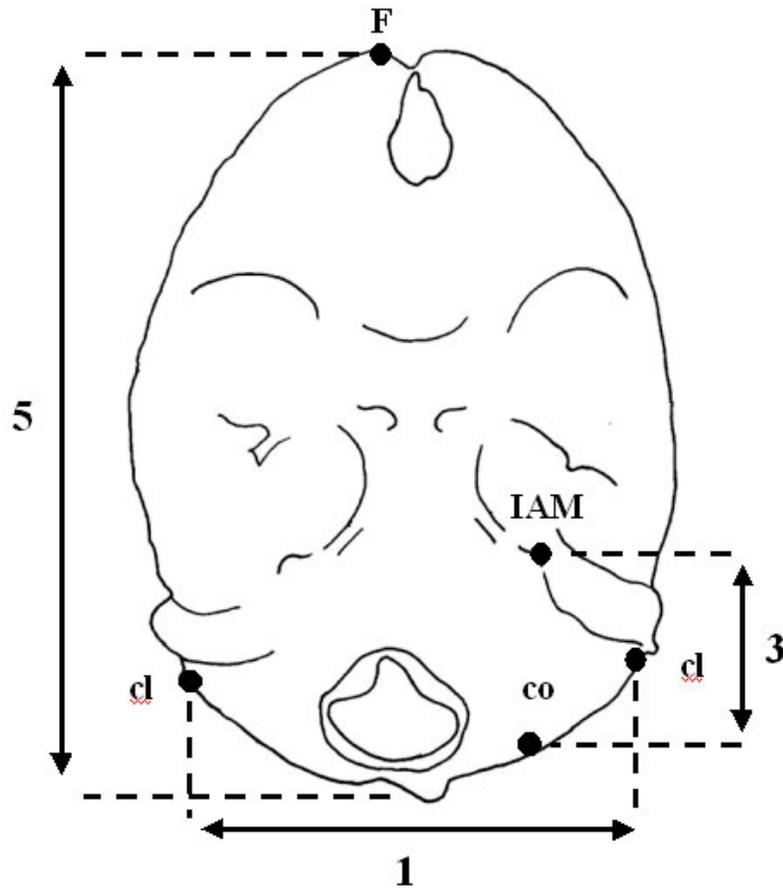


Fig. 3-1 Basal view of *Pongo* endocranium demonstrating linear measurements and projections. Measurement **1** – bicerebellar breadth, measurement **3** – cerebellar lobe antero-posterior length, measurement **5** – cerebral length. **F**- frontal pole, **cl**- lateral cerebellar point, **co** – occipital cerebellum, **IAM** – internal auditory meatus.

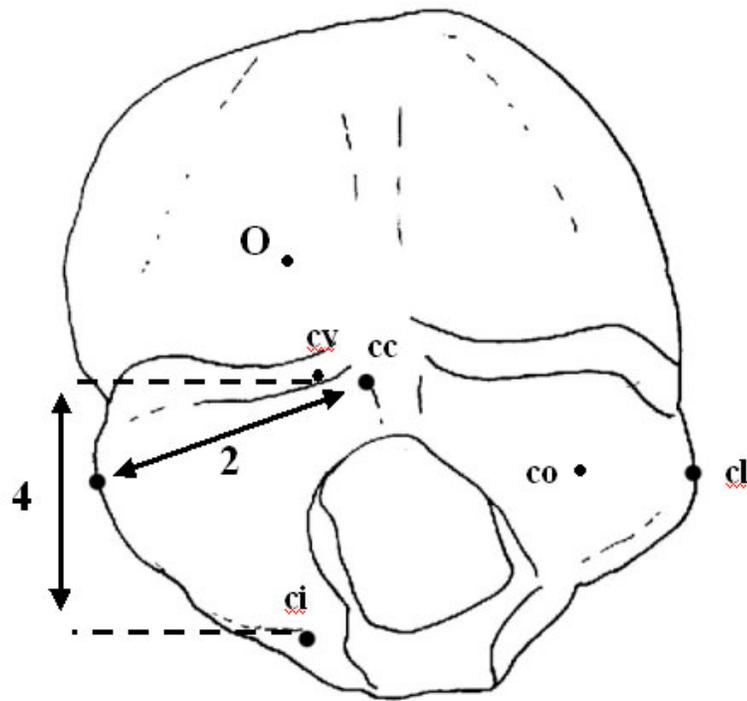


Fig. 3-2 Posterior view of *Pongo* endocranium demonstrating linear measurements and projections. Measurement **2** – cerebellar lobe medio-lateral length, measurement **4** – cerebellar lobe height. **O** – occipital pole, **cc** – medial cerebellar point, **cv** – superior cerebellum, **ci** – inferior cerebellar point, **co** – occipital cerebellum.

In order to test remeasurement error, I measured five macaque endocasts on two different occasions separated by several days. I employ the technique found in Falk et al. (2000) for determining remeasurement error. Remeasurement error is “calculated as the mean of the absolute differences (determined for each specimen) between the first and second sets of measurements (Falk et al., 2000:697).” Remeasurement errors are “then expressed as a percentage of the average length for each measurement (Falk et al., 2000:697).” Table 3-3 contains the results of these calculations for each of the five measurements utilized in this chapter.

TABLE 3-3 Remeasurement error for linear measurements

	Mean diff.	<u>1</u> Percent diff.	Mean diff.	<u>2</u> Percent diff.	Mean diff.	<u>3</u> Percent diff.	Mean diff.	<u>4</u> Percent diff.	Mean diff.	<u>5</u> Percent diff.
<i>M.mulatta</i> (n=10)	.16	<1%	.08	<1%	.02	<1%	.07	<1%	.03	<1%

Table 3-4 shows the mean, standard deviation, range, and coefficient of variation for each primate species and fossil specimen measured for this study. Table 3-5 provides the same information for the indices calculated. Table 3-6 provides the means for each index.

TABLE 3-4 Endocast linear measurements

Specimen	Cranial Capacity (cc)	1		2		3		4		5	
		Left	Right								
<i>Macaca</i>											
Female											
Mean	94	39	18	18	18	18	10	11	70	70	
SD	9	2	1	1	2	2	2	2	3	3	
Min	70	30	16	16	16	14	5	8	60	62	
Max	114	42	20	21	22	21	16	15	75	74	
CV	10	6	6	7	8	9	24	17	4	4	
N	30	30	30	30	30	30	30	30	30	30	
Male											
Mean	104	40	19	19	19	19	10	11	73	73	
SD	9	1	1	2	2	2	2	2	3	3	
Min	91	37	15	16	17	16	3	8	66	68	
Max	130	43	21	21	22	21	13	15	79	80	
CV	8	4	8	9	8	8	22	17	5	4	
N	30	30	30	30	30	30	30	30	30	30	
<i>Hylobates</i>											
Female											
Mean	121	55	25	26	26	25	14	15	77	77	
Stdev	11	3	2	2	3	2	2	1	2	3	
Min	104	50	23	22	24	24	12	13	74	73	
Max	133	58	27	28	30	29	16	17	80	80	
CV	9	6	7	9	10	8	11	10	3	4	
N	5	5	5	5	5	5	5	5	5	5	
Male											
Mean	125	53	24	25	26	27	17	17	77	78	
Stdev	9	3	2	1	1	2	2	2	1	1	
Min	116	49	22	24	24	25	16	14	75	76	
Max	138	57	27	26	28	29	20	20	79	79	
CV	7	6	8	3	6	7	11	13	2	1	
N	5	5	5	5	5	5	5	5	5	5	
<i>Pan</i>											
Female											
Mean	392	76	42	41	41	41	19	18	107	107	
StDev	34	1	3	3	3	4	2	3	3	4	
Min	360	74	38	38	37	38	17	15	105	103	
Max	445	78	45	45	45	45	21	22	111	113	
CV	9	2	6	6	8	9	9	15	3	4	
N	5	5	5	5	5	5	5	5	5	5	

TABLE 3-4 Endocast linear measurements continued

Specimen	Cranial Capacity (cc)	1		2		3		4		5	
		Left	Right								
Male											
Mean	393	76	43	44	44	43	18	18	109	109	
StDev	11	2	1	2	3	3	5	4	3	4	
Min	378	73	41	42	40	40	14	15	106	104	
Max	402	78	44	46	47	46	25	24	112	114	
CV	3	3	3	4	7	6	27	24	2	4	
N	4	4	4	4	4	4	4	4	4	4	
Pongo											
Female											
Mean	385	77	41	40	40	37	23	19	103	103	
Stdev	90	10	4	3	4	5	1	3	8	8	
Min	317	66	37	38	37	32	22	17	96	96	
Max	487	86	45	43	44	42	24	22	112	112	
CV	23	13	10	7	9	14	5	14	8	8	
N	3	3	3	3	3	3	3	3	3	3	
Male											
Mean	392	74	39	39	42	43	19	18	105	105	
Stdev	55	7	5	5	3	3	5	2	3	3	
Min	325	64	33	33	39	38	14	16	101	101	
Max	434	81	44	44	45	46	26	21	109	108	
CV	14	10	11	12	7	7	24	13	3	3	
N	5	5	5	5	5	5	5	5	5	5	
Gorilla											
Female											
Mean	414	77	43	43	46	46	21	20	114	113	
Stdev	34	3	1	3	4	4	2	2	1	1	
Min	375	73	41	40	42	43	18	17	114	112	
Max	455	80	44	47	51	52	24	23	115	115	
CV	8	4	3	6	9	8	11	11	0	1	
N	5	5	5	5	5	5	5	5	5	5	
Male											
Mean	545	83	47	47	49	50	23	22	126	126	
Stdev	31	4	2	5	3	4	5	4	3	3	
Min	508	80	45	42	45	46	16	16	122	122	
Max	575	89	50	52	52	56	28	26	130	129	
CV	6	4	5	10	6	9	20	19	2	2	
N	4	5	5	5	5	5	5	5	5	5	

TABLE 3-4 Endocast linear measurements continued

Specimen	Cranial Capacity (cc)	1		2		3		4		5	
		Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Human											
Mean	1349	93	57	55	59	58	25	25	155	158	
Stdev	101	8	6	5	7	5	8	7	7	5	
Min	1231	86	51	49	53	53	16	16	144	150	
Max	1489	105	67	61	70	67	36	34	161	164	
CV	7	9	11	10	11	9	30	29	4	3	
N	5	5	5	5	5	5	5	5	5	5	
Fossil											
Hominins											
Sts5	48577 (73)		38	37	38	39	22	22	118 (124)	119 (122)	
Sts19	436		38		39	39	22				
OH5	500*	86 (84)	48	51	49	50	19	19	127 (128)	126 (131)	
KNM-ER 1813	509	79 (79)	40	44	40	44	31	29	125 (125)	126 (126)	
KNM-ER 1805	582	80 (82)	45	45	51	48	26	28	134 (134)	134 (133)	
KNM-ER 3883	804	102 (102)	54	55	59	57	25	24	152 (152)	151 (151)	
LaChapelle	1625	118 (115)	61	55			35	36	180 (184)	181 (185)	

1) Bicerebellar breadth, 2) Cerebellar lobe breadth (medio-lateral), 3) Cerebellar lobe length (antero-posterior), 4) Cerebellar height, 5) Cerebral length. Italicizes numbers are estimates from the endocasts. Fossil hominin cranial capacities were obtained from Holloway et al. (2004) except OH5 which, was obtained from Falk et al. (2000). Figures in parentheses are measurements made by Holloway et al. (2004).

TABLE 3-5 Descriptive statistics of endocast measurement indices.

Specimen		1/5	2/5	3/5	4/5
<i>Macaca</i>					
Female	Mean	0.57	0.26	0.25	0.15
	SD	0.02	0.01	0.02	0.03
	Min	0.53	0.23	0.22	0.09
	Max	0.63	0.28	0.28	0.21
	CV	4.16	4.67	6.69	20.10
	N	30.00	30.00	30.00	30.00
<i>Macaca</i>					
Male	Mean	0.55	0.26	0.26	0.15
	SD	0.02	0.01	0.01	0.03
	Min	0.50	0.23	0.23	0.08
	Max	0.60	0.29	0.29	0.20
	CV	4.15	5.51	5.61	20.15
	N	30.00	30.00	30.00	30.00
<i>Hylobates</i>					
Female	Mean	0.71	0.33	0.33	0.19
	SD	0.04	0.02	0.02	0.02
	Min	0.68	0.30	0.32	0.16
	Max	0.77	0.35	0.37	0.21
	CV	5.99	6.36	5.86	9.24
	N	5.00	5.00	5.00	5.00
<i>Hylobates</i>					
Male	Mean	0.69	0.32	0.34	0.22
	SD	0.04	0.02	0.03	0.02
	Min	0.63	0.30	0.31	0.20
	Max	0.73	0.34	0.38	0.26
	CV	6.18	5.59	7.31	10.45
	N	5.00	5.00	5.00	5.00
<i>Gorilla</i>					
Female	Mean	0.67	0.38	0.41	0.18
	SD	0.02	0.01	0.03	0.02
	Min	0.64	0.37	0.37	0.15
	Max	0.70	0.40	0.45	0.20
	CV	3.38	2.82	8.20	10.41
	N	5.00	5.00	5.00	5.00

TABLE 3-5 Descriptive statistics of endocast measurement indices continued

Specimen		1/5	2/5	3/5	4/5
<i>Gorilla</i>					
Male	Mean	0.66	0.37	0.39	0.18
	SD	0.02	0.03	0.02	0.04
	Min	0.64	0.34	0.37	0.13
	Max	0.69	0.40	0.43	0.21
	CV	3.23	6.82	5.66	19.54
	N	5.00	5.00	5.00	5.00
<i>Pongo</i>					
Female	Mean	0.74	0.39	0.38	0.21
	SD	0.08	0.00	0.05	0.03
	Min	0.65	0.39	0.32	0.18
	Max	0.81	0.39	0.42	0.24
	CV	11.27	0.45	14.40	14.26
	N	3.00	3.00	3.00	3.00
<i>Pongo</i>					
Male	Mean	0.71	0.37	0.41	0.18
	SD	0.05	0.03	0.03	0.03
	Min	0.63	0.33	0.38	0.15
	Max	0.75	0.42	0.45	0.22
	CV	6.86	9.14	6.71	16.09
	N	5.00	5.00	5.00	5.00
<i>Pan</i>					
Female	Mean	0.71	0.39	0.38	0.17
	SD	0.02	0.02	0.02	0.02
	Min	0.70	0.36	0.36	0.15
	Max	0.73	0.41	0.42	0.20
	CV	2.25	5.52	6.48	12.78
	N	5.00	5.00	5.00	5.00
<i>Pan</i>					
Male	Mean	0.70	0.40	0.40	0.17
	SD	0.02	0.01	0.03	0.05
	Min	0.68	0.38	0.37	0.13
	Max	0.72	0.41	0.43	0.23
	CV	2.22	2.55	6.36	27.89
	N	4.00	4.00	4.00	4.00

TABLE 3-5 Descriptive statistics of endocast measurement indices continued.

Specimen	1/5	2/5	3/5	4/5
<i>Human</i>				
Mean	0.60	0.36	0.37	0.16
SD	0.04	0.03	0.03	0.05
Min	0.55	0.32	0.34	0.10
Max	0.65	0.40	0.42	0.22
CV	6.33	8.28	8.77	28.21
N	5.00	5.00	5.00	5.00

TABLE 3-6 Endocast index means

Specimen	Sex	1/5	2/5	3/5	4/5
<i>Macaca</i>	Female	0.56	0.26	0.25	0.15
<i>Macaca</i>	Male	0.55	0.26	0.26	0.15
<i>Hylobates</i>	Female	0.71	0.33	0.34	0.19
<i>Hylobates</i>	Male	0.69	0.32	0.34	0.22
<i>Pongo</i>	Female	0.74	0.39	0.37	0.21
<i>Pongo</i>	Male	0.71	0.37	0.41	0.18
<i>Gorilla</i>	Female	0.67	0.38	0.41	0.18
<i>Gorilla</i>	Male	0.66	0.37	0.39	0.18
<i>Pan</i>	Female	0.71	0.39	0.38	0.17
<i>Pan</i>	Male	0.70	0.40	0.40	0.17
Sts5		0.65	0.32	0.32	0.19
OH5		0.68	0.39	0.39	0.15
KNM-ER 1813		0.63	0.33	0.33	0.24
KNM-ER 1805		0.60	0.34	0.37	0.20
KNM-ER 3883		0.67	0.36	0.38	0.16
LaChapelle		0.65	0.32	0.00	0.20
<i>Homo sapiens</i>		0.60	0.36	0.37	0.16

Cerebellum size. In order to compare large and small primates the five linear measurements are scaled to brain size by dividing each by cerebral length. Cerebral length is highly correlated with total endocast volume and is therefore a good linear proxy for total brain size ($r^2=.94$ in this sample of living and extinct primates). The cubed root of cranial capacity would also be an appropriate scalar for total brain size but cerebral length provides more easily interpretable graphs and results. Multiple ANOVAs corrected with the Bonferroni method are calculated to compare each of the

four indices listed in Table 3-5 between monkeys and apes and apes and modern *Homo sapiens*.

Lateral asymmetry. Cerebellar length (measurement 3), cerebellar breadth (measurement 2), cerebellar height (measurement 4), and cerebral length (measurement 5) of the entire extant primate, sample sexes-combined (including humans) and sexes-separate (excluding humans), are tested for side asymmetries using multiple ANOVA and the P values were corrected using the Bonferroni method.

Sexual dimorphism. Bilateral measurements are averaged and used to test for statistically significant sexual dimorphism in the nonhuman primate sample. Humans are excluded because sex of the individuals is unknown. All five linear measurements are tested using multiple ANOVA and corrected using the Bonferroni method.

Results: Cerebellum size

Multiple ANOVAs corrected with the Bonferroni method reveal statistically significant differences between all four indices in Table 3-5 when the monkey and ape grades are compared ($P < .001$, Bonferroni-corrected). Only index 1/5 (Bicerebellar breadth/ Cerebral length) is significant when apes and modern *Homo sapiens* are compared. When the *Hylobates* specimens are dropped from the comparison, pongids and modern *Homo sapiens* also differ significantly for index 1/5 ($P < .001$, Bonferroni-corrected). This is because cerebral length in modern humans is relatively long compared to bicerebellar breadth.

MacLeod (2000) found a clear positive grade shift when comparing lateral cerebellar hemisphere volume to vermis volume between monkeys and hominoids

(including gibbons and humans). My data set comparing apes and *Homo sapiens* is small so I am cautious about making broad statements about grade shifts in this group. Among the measurements provided here, bicerebellar breadth seems to have the most explanatory value when comparing apes and *Homo sapiens*. Fortunately, this is one of the few measurements of the cerebellum that is routinely collected when endocasts are described.

Holloway et al. (2004) provide cerebral length and bicerebellar breadth (measurement M) for 36 fossil hominins that range in date from 3 million to 50,000 years ago. (Where ranges of lengths are reported by Holloway et al. (2004), I selected only the smallest measurement for this analysis.) To this sample, I have added the monkey, ape and human sample from this dissertation in order to regress bicerebellar breadth on cerebral length. Bicerebellar breadth in apes is highly correlated ($r=.93$) with the cubed root of cerebellar volume as calculated by Weaver (2001). Similar to Weaver's (2005) regression residual comparison technique, I develop a bicerebellar quotient ($\text{BiCbQ} = \text{Actual bicerebellar} / \text{Predicted bicerebellar}$) with which to compare apes, fossil hominins and modern *Homo sapiens*. Reduced major axis regressions are calculated using cerebral length and bicerebellar breadth and graphed in Figure 3-3 (Bohonak and van der Linde, 2004).

Weaver (2005) uses cerebellum volume as the independent variable and net brain (brain minus cerebellum) as the dependent variable. I have chosen to use the more traditional whole brain parameter (cerebral length) as the independent variable and the brain substructure parameter (bicerebellar breadth) as the dependent variable. This is a more conservative way of approaching cerebellum size evolution because it

assumes that selective pressures influence neocortical evolution, which in turn influence cerebellum evolution.

The equation for the line is (A) $Y = .62(X) + 7.765$ when only apes are utilized and (B) $Y = .55(X) + 13.6$ when all specimens are utilized and (C) $Y = .47(X) + 6.48$ when macaques are utilized. The slopes of these lines should not be confused with the slopes obtained from encephalization quotients. Although the technique is similar the results are not necessarily equivalent. The bicerebellar quotient is a product of how brain substructures scale to brain size while EQ is a product of how brain size scales to body size. The bicerebellar quotients (BiCbQ) and Bicerebellar breadth/ Cerebral Length (1/5) ratios for each species are depicted in Figure 3-4.

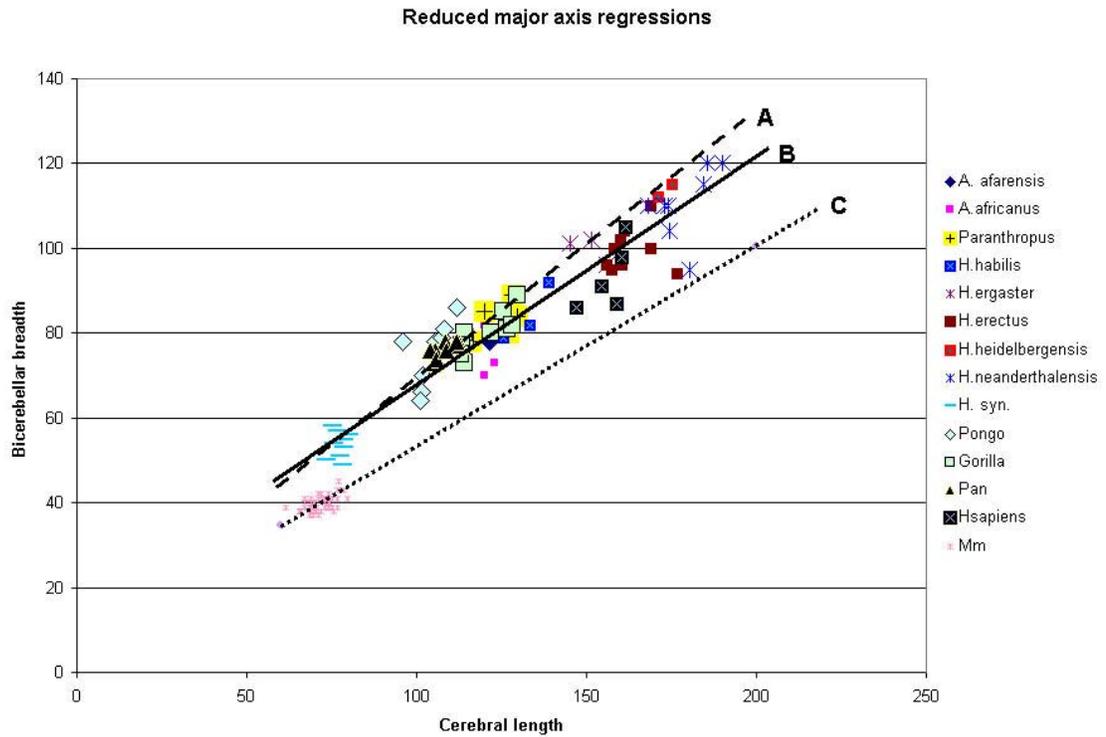


Fig. 3-3 Reduced major axis regressions of bicerebellar breadth on cerebral length. A) RMA regression of apes, B) RMA regression of all data points (including fossil hominins), C) RMA regression of *Macaca* only. Data from Holloway et al. (2004) and present study. Fossil specimens from Holloway et al. (2004): *A. afarensis* (AL 333-45, AL 444-2), *A. africanus* (Taung, Sts 5, Sts 60, Sts 71), *Paranthropus* (KNM-WT 17000, Omo L338y-6, OH 5, KNM-ER 23000, Konso (KGA-10-525)), *H. habilis* (KNM-ER 1813, KNM-ER 1805, KNM-ER 1470), *H. ergaster* (KNM-ER 3733, KNM-ER 3883, KNM-WT 15000), *H. erectus* (Sangiran 10, OH9, Sangiran 17, Trinil 2, Sangiran 12, Zhoukoudian I,L (Z10), Zhoukoudian III, E, (Z 2), Zhoukoudian III, L (Z 12)), *H. heidelbergensis* (Sale, Reilingen, Kabwe) *H. neanderthalensis* (Krapina 6 (Cranium E), Krapina B, Jebel Irhoud 1, La Ferrassie, La Quina 5, Monte Circeo (Guat 1), Gibraltar (Devil's), La Chapelle-aux-Saints, Amud).

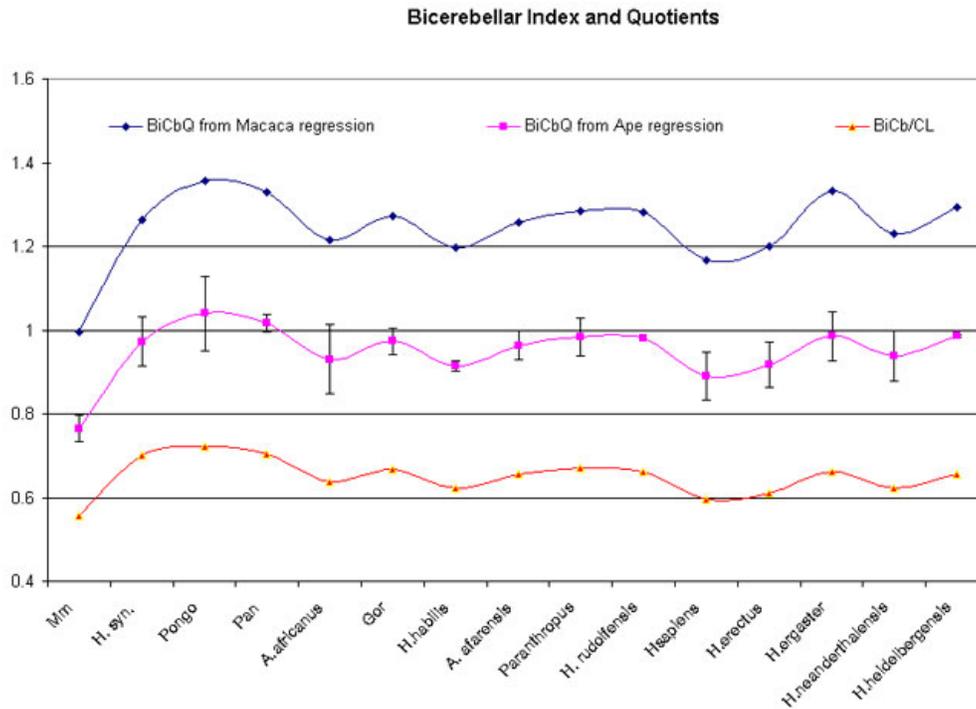


Fig. 3-4. Index 1/5 (Bicerebellar breadth/Cerebral length) and bicerebellar quotient from a reduced major axis regression derived from apes only (middle line) and from a reduced major axis regression derived from *Macaca* only (top line). The larger the ratio for index 1/5 the broader the cerebellum per unit cerebral length. Bicerebellar quotient is the ratio between the actual and expected bicerebellar breadth based on RMA regression (apes or macaques). Species means are ordered along the x-axis in increasing Bicerebellar breadth.

In Figure 3-4, species are ordered left to right from smallest to largest absolute bicerebellar breadth. Siamangs have the smallest bicerebellar breadth and *H.heidelbergensis* and *H.neanderthalensis* have the largest bicerebellar breadths. Values for index 1/5 rise as bicerebellar breadth broadens in relation to cerebral length. Humans and *Pongo* fall on opposite ends of this spectrum in my sample. Humans have relatively narrow bicerebellar breadths relative to cerebral lengths and orangutans have relatively broad bicerebellar breadths in relation to cerebral length, which gives an overall impression of the endocast shape. Bicerebellar quotients (BiCbQ) that are smaller than expected fall below 1.0 and quotients that are larger than expected rise above 1.0. All but 2 species (*Pan*, and *Pongo*) fall below the line of unity. These species have larger bicerebellar breadths than apes of equal cerebral length. It is important to note however, that the standard deviations of both of these species cross the line of unity.

Non-parametric Kruskal-Wallis rank tests for multiple groups of unequal sample size indicate that there are no statistically significant differences when living apes and modern *Homo sapiens* are compared (alpha=.05 level). The null hypothesis that all of the groups are sampled from the same population cannot be rejected. Within the genus *Homo* when Early (*H.habilis*, *H.ergaster*), Middle (*H.erectus*, *H.heidelbergensis*), Late (*H.neanderthalensis*), and Modern (*H. sapiens*) *Homo* are compared, there are no statistically significant differences in BiCbQ. When our next closest ape relative, *Pan* is added into the analysis, a statistically significant difference is observed (P<.001). *Pan* is thus significantly different from members of the genus *Homo* as measured by

BiCbQ. If *Australopithecus* and *Paranthropus* are added instead of *Pan*, no statistical difference is revealed.

The same non-parametric tests are used to test absolute bicerebellar breadth and statistically significant differences are detected when apes ($P < .001$) and fossil members of the genus *Homo* ($P < .01$) are compared to humans.

BiCbQ and Index 1/5. Weaver (2005) observes the following in her analysis of net brain volume regressed on cerebellum volume: “In the australopithecines and early members of the genus *Homo*, the cerebral hemispheres were large in proportion to the cerebellum, compared with other hominoids. This trend continued in Middle and Late Pleistocene humans, including Neandertals, and Cro Magnon 1, who have the largest cerebral hemispheres relative to cerebellum volume of any primates, including earlier and Holocene humans. In recent humans, however, the pattern is reversed; the cerebellum is larger with respect to the rest of the brain (and conversely, the cerebral hemispheres are smaller with respect to the cerebellum) (p. 3576).”

In accord with Weaver (2005), my analysis indicates that australopithecines and early members of the genus *Homo* had smaller cerebellums than would be expected of an ape of equal cerebral length. In fact, all of the fossil hominins have smaller bicerebellar breadths than expected for an ape of equal cerebral length. The only species that have larger bicerebellar breadths than expected are *Pan* and *Pongo*. (BiCbQs lower than 1.0 for all of the hominins is possible because the RMA regression was derived from *Hylobates*, *Pongo*, *Gorilla*, and *Pan* only.)

My analysis disagrees with that of Weaver (2005) in relation to modern humans however. Humans have the lowest ratio of bicerebellar breadth to cerebral length as

well as the lowest BiCbQ in my sample. In this, my analysis is in accord with other volumetric studies (Rilling and Insel, 1998). I point out, however, that my sample of modern human endocasts is much smaller (n=5) than Weaver's (2005) sample of 51 data points compiled from the literature. Undoubtedly, my sample does not fully represent the variation of human bicerebellar breadth and cerebral length. A larger sample of human endocasts is necessary to settle this discrepancy.

What is most striking is the general lack of pattern associated with BiCbQ. Figure 3-4 is ordered left to right by species bicerebellar breadth size. Ordered in this way, apes and small-brained fossil hominins group together on the left and the larger-brained fossil hominins and humans group together on the right. As bicerebellar breadth increases in absolute size so roughly does the expected (or real -in the case of humans) cognitive versatility and general intelligence. On the other hand, if we order the graph by BiCbQ and index 1/5, no discernible pattern corresponding to known or surmised cognitive abilities is evident. These results recall the work of Gibson et al. (2001) who found that absolute measures of brain size and brain size components (i.e. cerebellum) correlate highly with measures of intelligence while encephalization quotients do not. Saltations in cognitive abilities from australopithecines to early *Homo* to modern humans are essential components in every model of human evolution. Absolute brain size data seem to depict these leaps better than quotients or ratios.

Results: Lateral asymmetry of the cerebellum

The null hypothesis that the cerebellar lobes are equivalent in size is not rejected. All P-values for the pairwise tests (with Bonferroni corrections) are >1.0.

Based on these linear dimensions, there is no cerebellum hemisphere lateralization in this sample of catarrhine primates in either the sex-combined or sex-separate sample. A perusal of the fossil hominin data in Table 3-4 indicates that the fossil hominins do not exceed the comparative sample in lateralization.

Linear measurements of endocasts are at best proxies for the size of the cerebellum from the posterior cranial fossa. Clearly, it is possible that no lateral asymmetry exists between the cerebellar hemisphere of humans, macaques, and apes but other confounding error factors may also play a role. Weaver (2001) observes that the human cerebellum rises in the superior region of the midline, an area that is completely obscured in endocasts. This could be a large source of error in a linear analysis. Further analysis of cerebellum volume, cerebellum component volume (Makris et al., 2005), increased sample sizes, and a focus on endocast shape may reveal more information about the lateral asymmetries in the primate cerebellum (Falk et al, 2005). Chapters 4 and 5 address primate cerebellum shape in more detail.

Results: Sexual dimorphism in the cerebellum

The null hypothesis that the cerebellar lobes of males and females are the same absolute size based on linear methods cannot be rejected. As in the case above, all P-values for the pairwise tests with Bonferroni corrections were >1.0 . Thus, when these catarrhine primates are analyzed together, no statistically significant sexual dimorphism is detected. When species are analyzed individually by ANOVA and corrected for multiple tests, cerebral length (measurement 5) is statistically larger in male macaques (Bonferroni corrected P-value = 9.12×10^{-5}) and gorillas (Bonferroni corrected P-value

= 5.5×10^{-5}). Cerebellum hemisphere breadth and length (measurements 2 and 3) are also statistically larger in male macaques than in female macaques (Bonferroni corrected P-value = 9.7×10^{-4} and 7.94×10^{-5} respectively). All other linear measurements by species are statistically equivalent. Interestingly, cerebral length does not differ statistically in all species but males tend to outsize females in every case while in some cerebellar measurements females outsize males (Tables 3-4, 3-5 and 3-6).

Although male and female apes are statistically equivalent in all but the cerebral length measurement, it is interesting to note some tendencies in the data. Female *Pongo* and *Hylobates* tend to have larger cerebellar breadths (measurement 2) for both left and right sides than males. Female *Pongo* specimens also have larger cerebellar heights (measurement 4) bilaterally while female *Pan troglodytes* has a larger cerebellar height on the left side only. Thus, the size relationship between overall brain size and cerebellum size may not be equivalent in male and female apes and macaques.

These findings suggest that female cerebellum size may be relatively larger than male cerebellum size in the ape and monkey species studied. This relative size advantage is most evident in index 1/5 from Table 3-6. The ratio of Bicerebellar breadth/Cerebral length shows that female apes and macaques are relatively larger than male apes and macaques. Although these results do not reach the level of statistical significance in all cases, I believe that these trends in sexual dimorphism deserve further scrutiny. Why would females benefit from having relatively larger cerebellar hemispheres than males? Is this just an artifact of allometric scaling or was there a real underlying functional or behavioral pressure in primate brain evolution to increase female cerebellum size relative to the rest of the brain. Perhaps male cerebral

hemispheres have enlarged without concomitant cerebellar enlargement. There is no clear answer at this time.

I suggest that *Homo sapiens* males and females recruit the cerebellum in a greater array of cognitive tasks than is observed in nonhuman primates. Differences in the organization of male and female neocortices may also influence the structure and size of neural tissue in the cerebellum (Kimura, 1992). Determining when in human phylogeny cerebellum dimorphism begins is thus a worthy endeavor. Sexing fossil hominin specimens may be the most challenging aspect of this type of research.

Endocasts are the only direct evidence we have of the brains of our fossil hominin ancestors. I, therefore, submit that it is essential to continue to create links between advanced medical neuroimaging techniques and plaster endocasts. The next logical step in this research is to obtain larger samples of human endocasts (virtual or real) of known sex (and handedness) to measure the cerebellum with this linear technique. I expect to find the same results observed in the MRI-based volume studies. In the future, I plan to obtain a large sample of macaque and ape cerebellums for volumetric analysis. Either *in vivo* MRI or cadaveric specimens could be utilized. Lastly, I suggest a formal analysis of the shape of the posterior cranial fossa in monkeys, apes, and fossil hominins by geometric morphometric analysis. This is a powerful tool which allows biological shape to be quantified objectively (Zelditch et al., 2004). Shape and size of extant primate and fossil hominin endocasts can be analyzed separately by multivariate techniques. Chapters 4 and 5 include geometric morphometric analyses that address this last suggestion.

Summary of Chapter 3 Results

Analysis of the linear dimensions of fossil and extant catarrhine endocasts indicates 1) no statistically significant lateralization in cerebellum size; 2) no statistically significant sexual dimorphism in catarrhine cerebellum size (although there is a tendency for males to have larger cerebral lengths); and 3) a clear positive grade shift between monkeys and apes and a tendency for apes to differ from *Homo sapiens*. Lateralization of cognitive functions and concomitant size differences by side are not evident in this data set. The tendency for males to have larger cerebral lengths than females but statistically equivalent bicerebellar breadths raises a question about sexual dimorphism in brain component size that cannot be fully addressed here but is an intriguing question that deserves further work. A larger sample of modern human endocasts and a larger sample of comparative primate casts are needed to explore these questions further.

CHAPTER 4: CEREBELLUM SHAPE IN EXTANT CATARRHINES AND PLIO-PLEISTOCENE FOSSIL HOMININ ENDOCASTS: A GEOMETRIC MORPHOMETRIC ANALYSIS.

In this chapter, I use geometric morphometric techniques to analyze how cerebellum *shape* evolved in catarrhine evolution. Previous work, including Chapter 3 of this dissertation, has focused on the relative and absolute volume and linear dimensions of the cerebellum. The development of powerful geometric morphometric techniques has allowed shape to be quantified and analyzed using multiple landmarks and multivariate statistical methods. The geometric morphometric techniques utilized in this work are derived from Zelditch et al. (2004).

This chapter tests four main hypotheses concerning the evolution of the catarrhine cerebellum.

Hypothesis 1 Null: The catarrhine cerebellum shows no distinct lateralization (asymmetry) in shape and centroid size.

The definition of shape used in this chapter and Chapter 5 comes from Kendall (1977) and is as follows: “Shape is all the geometric information that remains when location, scale and rotational effects are filtered out from an object (quoted in Zelditch et al. 2004:73).” Centroid size is “a measure of geometric scale, calculated as the square root of the summed distances of each landmark from the centroid of the landmark configuration (Zelditch et al., 2004:412).” Centroid size is not correlated with shape in the absence of allometry and is therefore the universal measure of size in geometric morphometric analyses.

Alternate hypothesis: Distinct lateralization in the cerebellum suggests a functional disparity between the two sides. If cerebellum shape lateralization exists it is expected in species that also demonstrate marked cerebral lateralization due to the demands of expanded cortico-cerebellar connections.

Hypothesis 2 Null: The catarrhine cerebellum shows no distinct sexual dimorphism in shape and centroid size.

Alternate Hypothesis: A distinct sexual dimorphism in cerebellum shape and centroid size exists between male and female members of species that show distinct brain and body sexual dimorphism.

Hypothesis 3 Null: The shape of the catarrhine cerebellum does not change in relation to increasing cerebellum centroid size (shape is independent of size).

Alternate hypothesis: The shape of the catarrhine cerebellum changes in relation to increasing cerebellum centroid size (shape is partially dependent on size).

Hypothesis 4 Null: There are no statistically significant shape differences between the monkeys, apes, and hominins.

Alternate hypothesis: Shape differences are evident between the different grades of primates observed in this study. Rejecting the null hypothesis lends support to the claim that the cerebellum shows clear grade differences in primates (MacLeod et al, 2001).

Fossil hominin cerebellum shape is also quantified and analyzed in relation to the larger catarrhine sample. African fossil hominins from *Australopithecus*, *Paranthropus*, and early *Homo* are included in the sample.

Materials and Methods

The primate and modern *Homo sapiens* data set is the same as in Chapter 3. The fossil hominin data set includes endocasts of KNM-WT 17000, OH 5, Sts 5, Sts 19, KNM-ER 1805, KNM-ER 1813, KNM-ER 3883, and La Chapelle-aux-Saints.

Landmarks. Ten landmarks were chosen on endocasts in *norma basilaris*. Table 4-1 lists the landmarks with their abbreviations and definitions. Figures 4-1 and 4-2 depict the positions of the landmarks on the endocast of a macaque in *norma basilaris*. All landmark information was collected with a Microscribe digitizing arm and Rhinoceros 1.0 modeling software. Three coordinates (x, y, z) were recorded for each landmark. Raw landmark coordinates were processed with Integrated Morphometric Programs (IMP) software developed by Sheets (2001). (Information about this software can be found in Zelditch et al. (2004)). Simple3d (IMP) was used to superimpose the raw data by the Procrustes generalized least squares method. The superimposed, oriented, translated, and scaled data were then reduced to two coordinates (x, y) as in Rosas and Bastir (2002). The set of landmarks for each specimen is considered as a single multivariate shape variable.

TABLE 4-1 Landmarks for geometric morphometric analysis

Number	Abbreviation	Measurement	Description
1	O	Occipital pole	Most posterior point on each cerebral hemisphere in basicranial view.
2	Ds (side)	Dorsum sella (medial)	Impression of the dorsum sella on the basicranial aspect of the endocast. Serves as a central point for size and shape measurements.
3	Ds'		
4	IAM	Internal auditory meatus	Impression made by the IAM.
5	Pt	Petrous temporal point	Most lateral point of the impression of the petrous temporal bones on the endocast.
6	Ba	Endobasion	Most anterior point on the impression of the foramen magnum on the endocast.
7	Cl	Lateral cerebellar point	Most lateral point on the cerebellar hemisphere impression on the endocast.
8	Ci	Inferior cerebellar point	Point representing the most inferior point of the posterior cranial fossa impression. (Endocast aligned in the F-O plane.)
9	Co	Occipital cerebellum	Point representing the most caudal point on the impression of the cerebellar hemispheres.
10	Cv	Superior cerebellum	Most superior point on the impression of the cerebellar hemispheres (taken inferior to the transverse venous sinus).

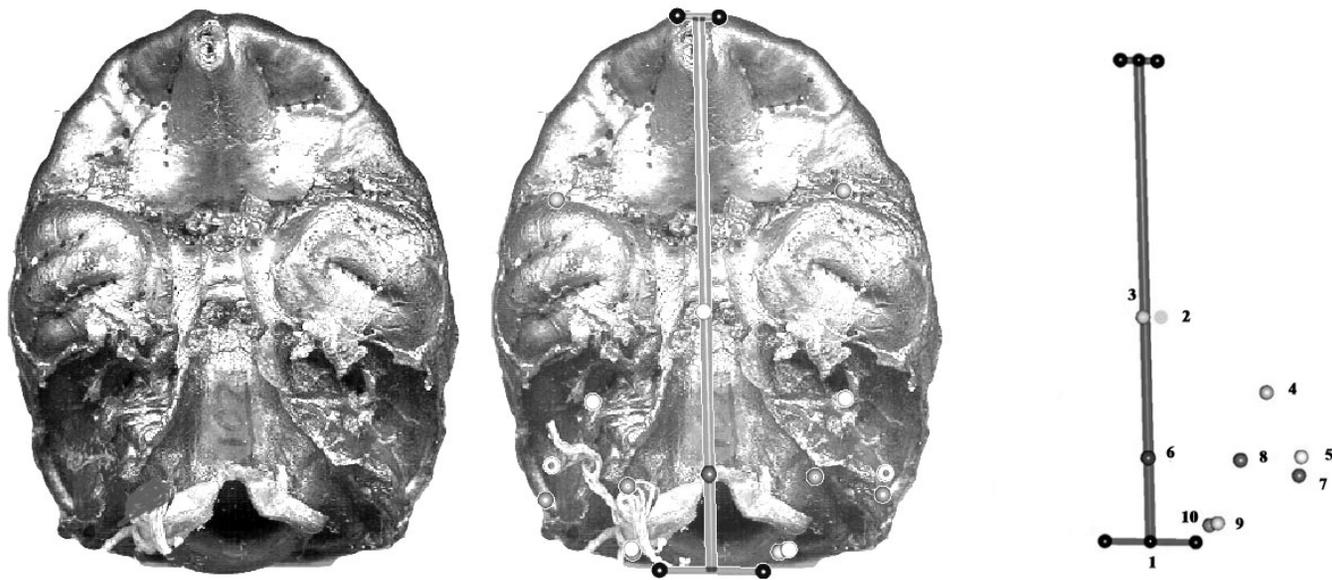


Fig. 4-1. Left: Macaque endocast in *norma basilaris*. Center: Macaque endocast with landmark positions superimposed. Right: Landmarks used in this study. 1- Midline Occipital pole, 2- dorsum sella (lateral), 3- dorsum sella (medial), 4- Internal auditory meatus, 5- Petrous temporal, 6- endobasion, 7- lateral cerebellum, 8- inferior cerebellum, 9- occipital cerebellum, 10 – superior cerebellum.

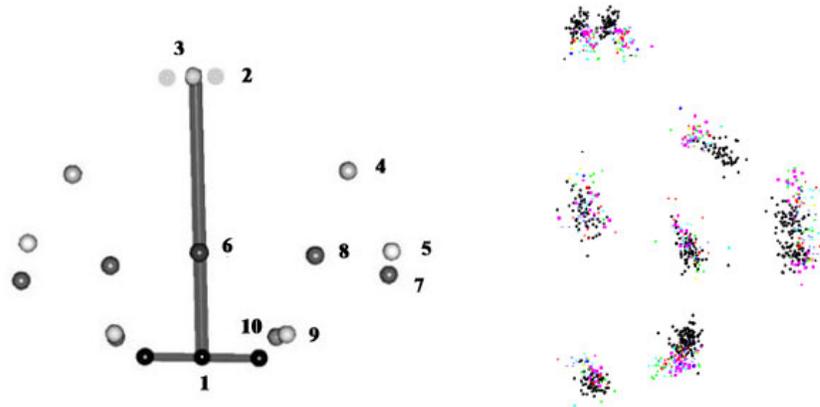


Fig. 4-2 Cerebellum landmarks. Landmark diagram and scatterplot of all specimens in Procrustes superimposition. Numbers are the same as in 4-1. Numbers are depicted on the left hemisphere of endocasts in *norma basilaris*. Scatterplot shows both left and right sides. Right side is reflected over left.

Selecting landmarks on the rounded structure of the primate endocast is challenging. “Ideally, landmarks are (1) homologous anatomical loci that (2) do not alter their topological positions relative to other landmarks, (3) provide adequate coverage of the morphology, (4) can be found repeatedly and reliably, and (5) lie within the same plan (Zelditch et al., 2004:24).”

Fortunately, the posterior cranial fossae of catarrhine primates are relatively similar in shape and location. Determining homologous anatomical loci and loci that are relatively consistent in their position is relatively easy. More challenging and potentially problematic is the need to balance the number of landmarks to adequately represent posterior cranial fossa morphology with the relatively small sample of endocasts available for this study. Adding too many landmarks risks producing spurious statistical results while not choosing enough landmarks risks poorly

representing the true shape of the posterior cranial fossa. A balance is struck with the number and position of landmarks presented here.

Repeatability of landmarks is assessed by examining the scatter of points at each landmark in 30 female macaques (left and right sides combine and reflected over the midline). Figure 4-3 depicts the scatterplots. Circular scatterplots indicate random error that can be considered digitizing noise (Zelditch et al., 2004). All of the landmarks retained for this chapter have roughly circular scatterplots except points 8 and 4 representing the inferior point on the cerebellar lobe and the internal auditory meatus impression, respectively.

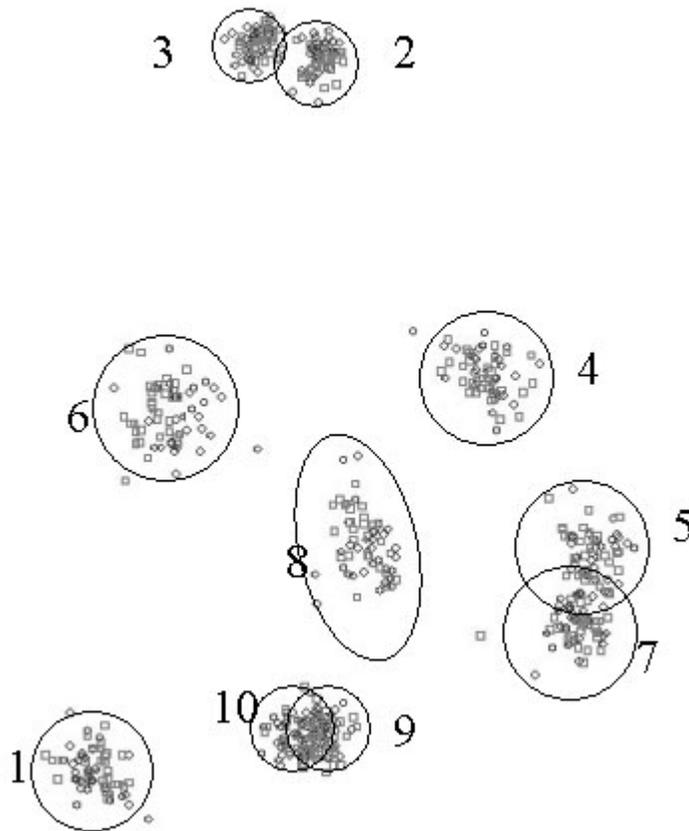


Fig. 4-3 Repeatability scatterplots. Left and right sides of 30 female macaques. Right side is reflected over the midline onto the left side.

Point 4 deviates only moderately from circularity and this variability is considered when interpreting my shape results. Point 8 defines the most inferior point of the cerebellum on the endocast and is therefore an important component in the analysis of cerebellum shape. The oval around point 8 is mediolaterally compressed and anteroposteriorly elongated. This implies a systematic error in the y coordinate but

it does not mean that the point cannot be utilized in a shape analysis (Zelditch et al., 2004). Results will be interpreted with this error in mind.

Lastly, problems with coplanarity arise when the shapes of three-dimensional objects are analyzed in two dimensions (such as in photographic images). This problem is reduced in this dissertation because shape data were first collected in three dimensions and subsequently reduced. Deformations that exist in the photographic method of collecting data are therefore eliminated.

Statistical analysis. Multivariate tests of significance are performed with TwoGroup6h (IMP) to test lateral asymmetry (Hypothesis 1) and sexual dimorphism (Hypothesis 2) and grade differences (Hypothesis 4) in cerebellum shape. Multivariate analyses of covariance are calculated by Regress6K (IMP) to determine if cerebellum shape change is size dependant (Hypothesis 3). The covariate in these analyses is centroid size, which is statistically independent of shape in the absence of allometry (Zelditch et al. 2004). One factor analysis of variance is used to compare centroid size for each hypothesis. Principal components analysis is performed with PCAGen6n (IMP) in order to reduce the multivariate data set into a smaller group of interpretable variables. Graphing the principal components demonstrates the relationship between the fossil hominins and the extant primate sample.

Results: Lateral shape asymmetry in the cerebellum (Hypothesis 1)

The groups tested for asymmetry are; all-catarrhines (including *Homo sapiens* and fossil hominins), all-catarrhines – sexes-combined and sexes-separate (excluding *Homo sapiens* and fossil hominins), apes – sexes-combined and sexes-separate, and *Macaca*-only – sexes-combined and sexes-separate. (The term “ape” is used here to designate both lesser and great apes.) There is no statistically significant difference between the left and right side cerebellum shapes in the all-catarrhine sample.

Statistically significant lateralization is found in the combined sex ape-only test and in the *Macaca* sex-combined and sex-separate tests (Table 4-2). These results demonstrate that it is reasonable to average the left and right sides when examining my entire catarrhine sample but that at lower taxonomic groupings it is more prudent to separate the sides for individual analysis.

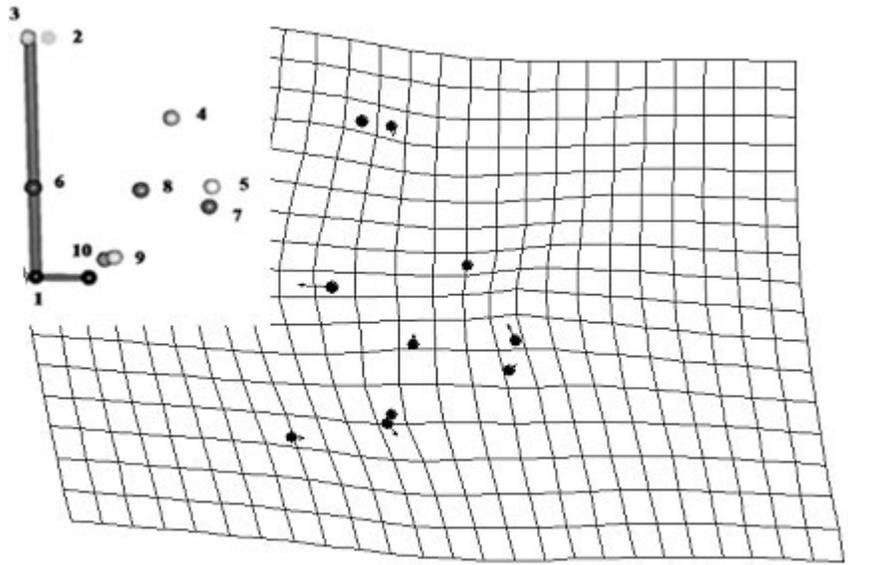
TABLE 4-2 MANOVA tests for lateral asymmetry

Groups – Left side vs Right side	Sex	F score	Df	p
Catarrhines (including <i>Homo sapiens</i> and fossil hominins)	MF	1.66	16, 3136	.048
Catarrhines (excluding <i>Homo sapiens</i> , fossil hominins)	M	.83	16, 1536	.653
Catarrhines (excluding <i>Homo sapiens</i> , fossil hominins)	F	1.04	16, 1568	.412
Apes	MF	2.32 *	16, 1216	.002
Apes	M	1.31	16, 592	.181
Apes	F	1.99	16, 608	.118
<i>Macaca</i>	MF	3.64 *	16, 1888	<.0001
<i>Macaca</i>	M	2.69 *	16, 928	.0003
<i>Macaca</i>	F	1.76 *	16, 928	.032

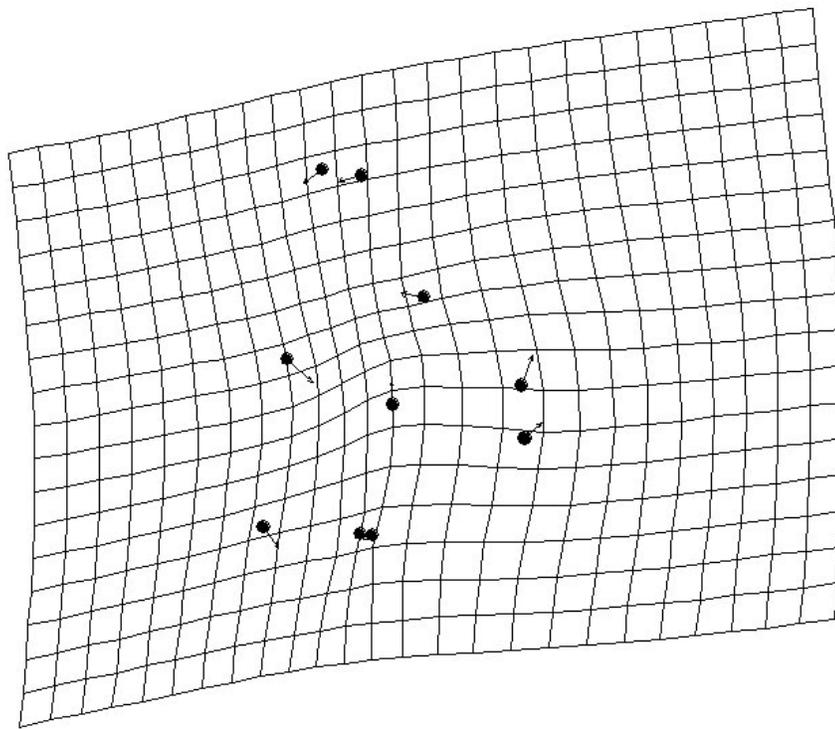
Significant at alpha=.05 M=males, F=females

Lateral shape asymmetry in the sexes-combined macaque samples and sexes-combined ape sample are depicted in the thin-plate spline deformations in Fig. 4-4.

Black dots depict left side landmark means and arrow tips depict right side landmark means.



A



B

Fig. 4-4 A) *Macaca* combined sex left side vs right side. Insert shows landmark numbers. B) Ape combined sex left side versus right side.

The left and right side shapes of the macaque sample appear to differ most at points 5 (petrous temporal), 6 (basion), 8 (inferior cerebellar), 10 (superior cerebellum). The deformation shows that basion (point 6) is shifted toward the right side and points 5 and 8 are anteriorly oriented relative to each other. As mentioned earlier, point 8 (inferior cerebellar point) contains a larger antero-posterior error (y coordinate) than the other points. Point 10 (superior cerebellum) expands posteriorly. In the ape sample the right side landmarks seem to be twisted in a counterclockwise direction.

Human cerebellum lateral shape is depicted in the thin plate spline deformation grid in Figure 4-5. The sample size is too small to conduct a MANOVA so I restrict my comments to descriptive remarks. The left and right shape configurations appear to differ in the location of basion and the most lateral cerebellar point. These shape configurations do not allow me to support or reject the presence of the right anterior-left posterior size pattern reported by Snyder et al. (1995) (Chapter 2).

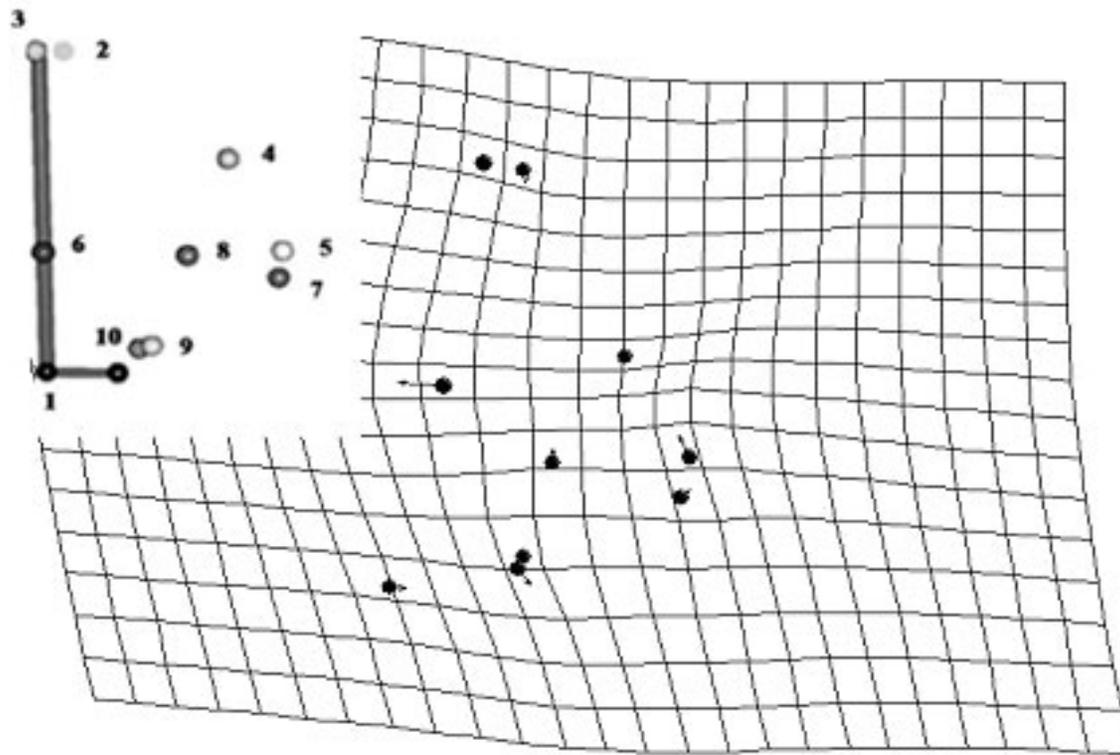


Fig. 4-5 Thin plate spline diagram depicting the side difference in the 6 *Homo sapiens* endocasts. Left =black dots, Right= arrow tips.

Functional lateralization of the cerebellum in nonhuman primates is much less well documented than in humans. Thus, it is difficult to link the statistically significant lateral shape differences in macaques and apes to any specific functional attribute in these animals. Macaque and chimpanzees have been shown to possess hand preferences and other cortical lateralizations that may contribute to this pattern (Falk, 1987). It should also be noted that the basicranium is a dynamic structure that links the postcranium, face, and brain. Any one or combination of these structures can influence the shape of the posterior cranial fossa (Dean and Wood, 1981; McCarthy, 2001).

Lateral shape asymmetry and centroid size. One factor analysis of variance of centroid size between the groups listed above revealed no statistically significant results between sides. Left and right side shapes are equivalent in size.

Results: Sexual dimorphism and cerebellum shape (Hypothesis 2)

Multiple analysis of variance with left and right sides combined reveals a statistically significant difference between males and females in the all-catarrhine sample (partial Procrustes distance .0382, $df= 16, 3136$, $p<.0001$) but not in the ape-only sample. A statistically significant difference is also observed between male and female macaques with sides averaged (partial Procrustes distance .0467, $df= 16, 1888$, $p<.0001$) and sides separate (Left: partial Procrustes distance .0412, $df= 16, 928$, $p<.0007$; Right: partial Procrustes distance .0555, $df= 16, 928$, $p<.0001$.) The significant sexual dimorphism in the total sample appears to be driven by the important shape differences in male and female macaques particularly from the right side (Figs. 4-6 and 4-7).

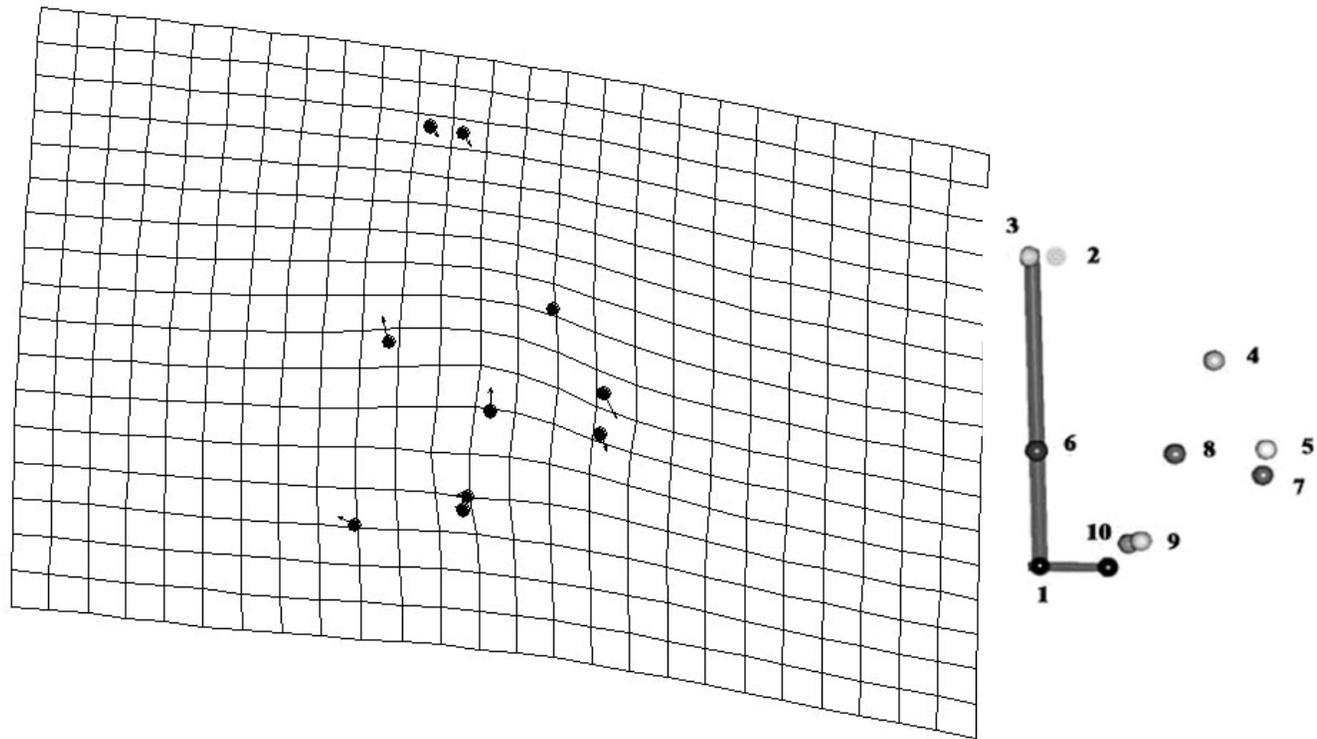


Fig. 4-6 Macaca sexual dimorphism. A) Black dots represent the male shape. Arrow tips represent female shape. Insert shows landmark numbers.

Note: The same pattern of dimorphism is seen in the left, right, and left-right combined samples.

Figure 4-6 depicts the thin plate spline deformation between males and female macaques. These shapes appear to differ mainly in the antero-posterior and medio-lateral axes. Female macaque cerebellum shape is reduced antero-posteriorly but expanded medio-laterally when compared to males (Fig 4-6). Nevertheless, male and female macaques have similarly sized cerebellums but differently sized crania. It appears that female macaques may accommodate a relatively larger cerebellum by expanding laterally.

Statistically significant sexual dimorphism in our catarrhine sample appears to be highly influenced by *Macaca*. Rhesus macaques are known to be moderately dimorphic in brain size with male brains outweighing female brains by 10%. Falk et al. (1999) demonstrated that this brain size dimorphism goes beyond what would be expected by simple brain to body size allometry. They hypothesize that these sex differences relate to the selection for increased visuospatial processing power in male monkeys that live in a competitive polygynous society and occupy a highly complex terrestrial environment.

My sample lacks volumetric evidence of male and female macaque cerebellum size but linear measurements of cerebellum hemisphere length and breadth indicate a statistically significant size dimorphism between male and female macaques (Chapter 3).

Sexual Dimorphism and centroid size. One factor analysis of variance of left-right averaged centroid size in males and females revealed no statistically significant differences in the combined catarrhine sample, the ape sample or the macaque sample. Only *Macaca* showed statistically significant sexual dimorphism in centroid size when

male left/female left ($P = 3.01 \times 10^{-5}$) and male right/female right sides left ($P = 8.87 \times 10^{-5}$) were tested with single factor ANOVA. Thus, shape differs but size does not.

Results: Cerebellum shape and size (Hypothesis 3)

Multivariate regression is used to test the null hypothesis that shape and centroid sizes co-vary isometrically. Multivariate linearity is tested by regressing PD against the natural logarithm of centroid size. (PD is defined as the Procrustes distance of each specimen from the shape with the smallest size.) For the all-catarrhine sample, the relationship proves to be only weakly linear ($r^2 = .33$). All subsets of the full sample prove to be non-linear and not determinative. It is therefore imprudent to analyze these data using a multivariate linear model (Zelditch et al. 2004).

Results: Cerebellum shape differences by grade (Hypothesis 4)

Female side-average data are utilized to test for statistically significant shape differences by grade. All three pairwise tests reveal statistically significant differences in cerebellum shape at $\alpha = .05$ (Table 4-3).

TABLE 4-3 MANOVA of shape difference by grade

	F score	Df	<i>p</i>
<i>Macaca</i> vs Apes	44.43*	16, 1538	$p=0$
<i>Macaca</i> vs <i>Homo sapiens</i>	41.23*	16, 1120	$p=0$
Apes vs <i>Homo sapiens</i>	10.81*	16, 800	$p=0$

- Significant at $\alpha = .05$

Results: PCA of cerebellum shape

Before performing the principal components analysis (PCA), all bilateral landmarks are reflected across the midline and averaged to reduce the number of landmarks analyzed (Zelditch et al., 2004). This reduction is warranted by the multivariate analyses of variance for lateral asymmetries reported above (i.e. no statistically significant lateralization in the data set as a whole).

The PCA includes all of the catarrhine specimens, modern *Homo sapiens* and the fossil hominins. Together the first two principal components explain 57% of the total variance (PC1= 42%, PC2=15%) and Anderson's χ^2 (PCAGen6n-IMP) indicates that there is one distinct eigenvalue. Figure 4-8 shows PC1 graphed on PC2. Figures 4-9 and 4-10 depict the deformation of shape along PC1 at the *Macaca* and *Homo sapiens* means.

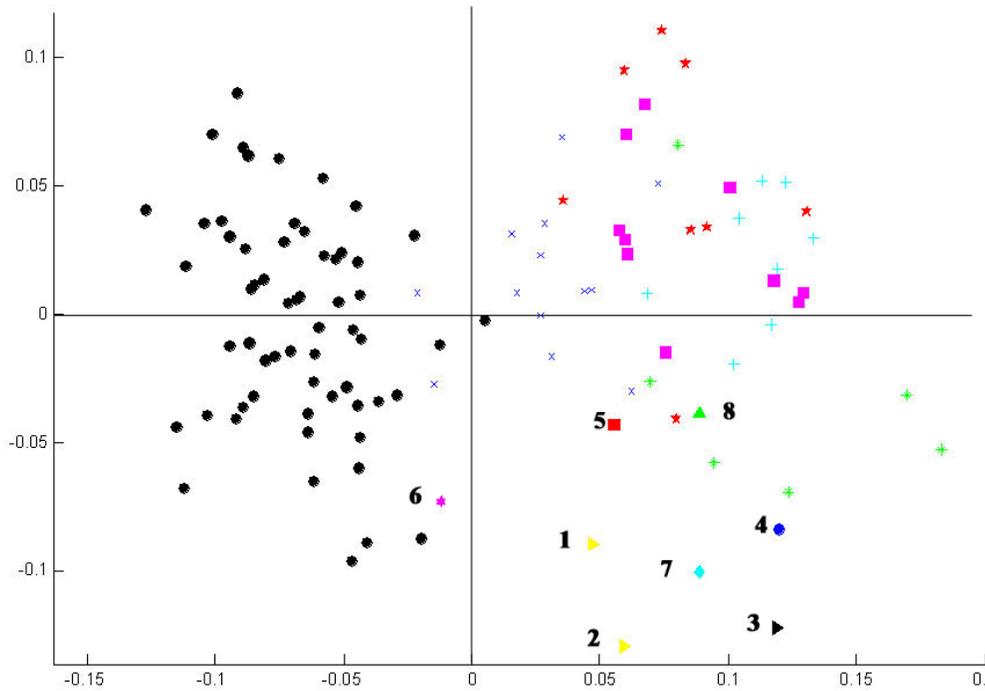


Fig. 4-8 Principal components analysis of all specimens. PC1 graphed on PC2. Fossil hominins are numbered 1-8. 1) Sts5, 2) Sts19, 3) KNM-ER 1813, 4) KNM-ER 1805, 5) OH5, 6) KNM-WT 17000, 7) LaChapelle-aux-Saints, 8) KNM-ER 3883. Dots=*Macaca*, X=*Hylobates*, Red Stars=*Pongo*, Squares=*Gorilla*, Cross=*Pan*, Green Stars=modern *Homo sapiens*.

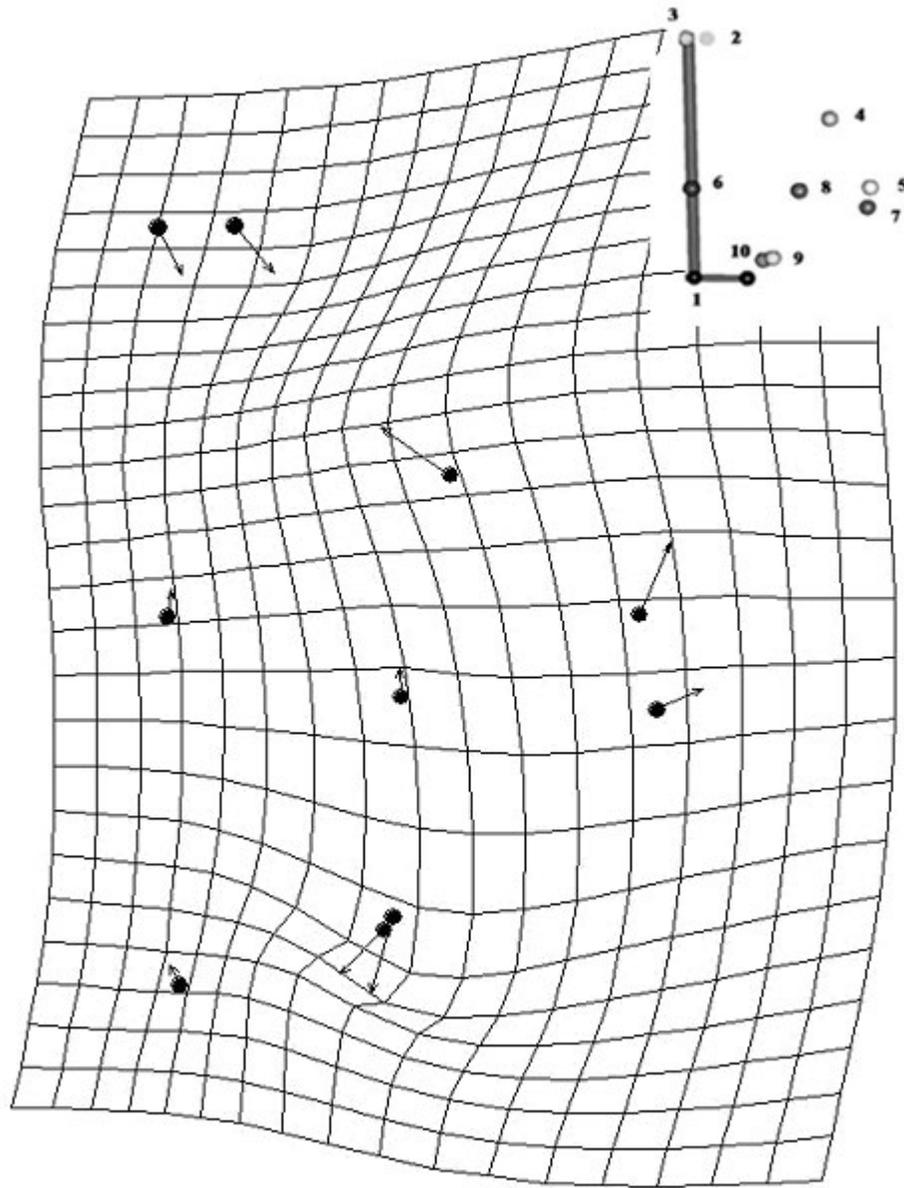


Fig. 4-9 Deformation grid, landmarks and vectors depicting the deformation from the *Macaca* mean on PC1 to *Homo sapiens* mean on PC1. Black dots depict *Macaca* shape and the arrow tips (connected by lines) depict *Homo sapiens* shape. The two shapes are in Procrustes superimposition (centroid size=1.0).

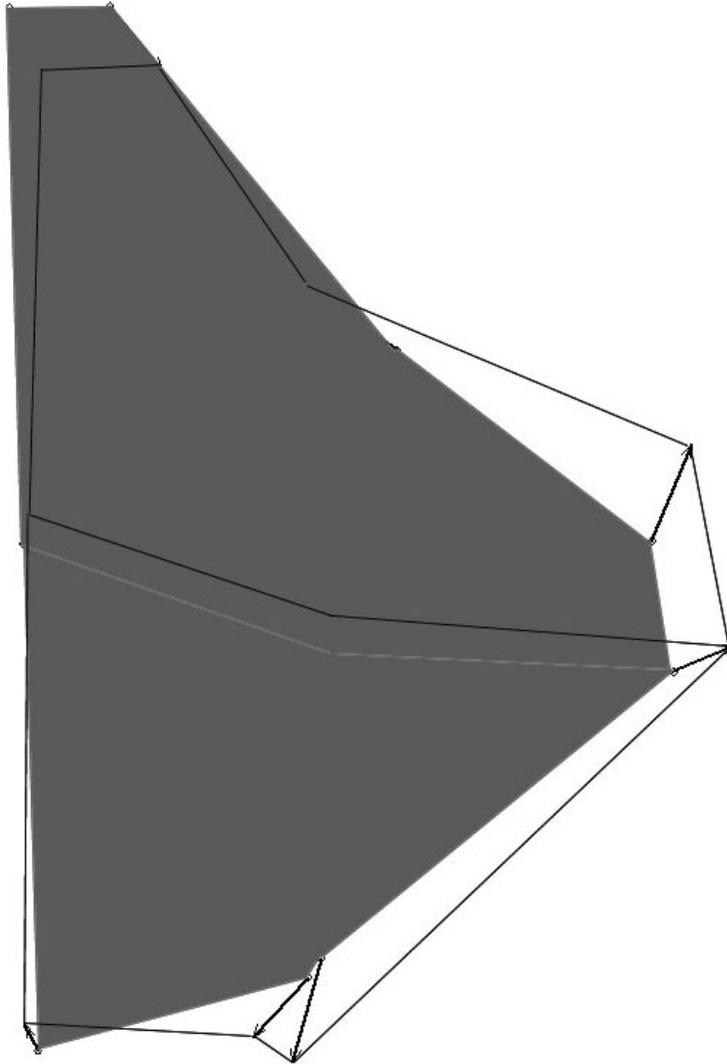


Fig. 4-10 Shape configuration of *Macaca* and *Homo sapiens* along PC1. Colored shape represents *Macaca* and black lines represent *Homo sapiens*.

The principal components analysis indicates a separation between primate grades (Fig 4-8). The mean for monkeys falls in the lower left quadrant, the mean for the great apes and the mean for the lesser apes fall in the upper right quadrant. The mean for *Homo sapiens* and the fossil hominins fall in the lower right quadrant. Interestingly, the organisms that fall into the lower right quadrant are all known to possess relatively large brains, to have highly versatile hands, and to be habitual bipeds. Furthermore, some of these extinct hominins may also have used vocal and other communication techniques in subsistence and social interaction. It is likely that these attributes are what separate the hominin quadrant from the ape quadrant above it. The only exceptional fossil hominin specimen is KNM-WT 17000, which falls in the same quadrant as the *Macaca* mean. Holloway (1988) points to a number of primitive characteristics in the endocast of this specimen, which includes the lateral flare of the cerebellar hemispheres that will be discussed below and in Chapter 5.

The shape difference along PC1 at the mean of *Macaca* and *Homo sapiens* is depicted in Figs. 4-9 and 4-10. The main shape difference along PC1 appears to be an antero-posterior foreshortening and a medio-lateral expansion in humans (similar to what is observed between male and female macaques). Studies of basicranial anatomy show that the human basioccipital is relatively shorter than that of apes and the petrous temporal bones are oriented coronally. Dean (1988) has proposed that an expanding cerebellum in a relatively foreshortened and highly flexed cranial base creates an infratentorial spatial packing problem (see also Jeffrey, 2002). Pressure exerted from an infero-posteriorly rotated tentorium cerebelli, enlarged neocortex, and cerebellum

expands the posterior cranial fossa laterally and anteriorly. This pressure forces the petrous bones coronally. The shapes seen here appear to fit this model.

The shape analysis also indicates that the occipital lobe overhangs the cerebellum in the macaque while in the human, point 9 representing the most posterior projection of the cerebellar hemispheres extends beyond the occipital pole in this orientation. (The endocast orientation in this chapter makes dorsum sella and midline occipital pole horizontal. It is not in normal anatomical position.) We also point out that point 9 is more anterior to point 10 in macaques and the opposite is true in *Homo sapiens*. This shows that lower portion of the cerebellar hemispheres in humans bulges posteriorly.

The shape difference between the lower and upper quadrants along PC2 appears to be most highly influenced by basion and the most inferior point in the posterior cranial fossa on the hemisphere (point 8). As PC2 increases basion shifts posteriorly and point 8 (ci) shifts anteriorly. As noted above, the inferior cerebellum point is prone to error along the y coordinate but is much less variable along the x coordinate.

These results are in accord with our understanding of the form of the ape cranial base, which is in general, long and narrow. Dean and Wood (1981) illustrate the relative position of basion to the bi-temporal line in Figure 3 of their report. Basion falls anterior to the bi-temporal line in *Paranthropus* and *Australopithecus*, on the bi-temporal line in *Homo sapiens*, and posterior to the bi-temporal line in great apes. This is the general pattern we see in PC2 of our analysis. However, we are cautious about these results because PC2 only explains 15% of the variance in this PCA.

Cerebellum shape and Plio-Pleistocene hominins. Total brain size, absolute cerebellum volume, and cerebellum hemisphere to vermis size all show clear grade shifts in the primate lineage. The results presented here indicate that cerebellum shape may also be added to this list. As brains and brain sub-structures become absolutely and relatively larger concomitant morphological shape changes take place. The shape changes that separate humans from monkeys and most apes are influenced by a number of factors including the postero-inferior rotation of the tentorium, the expansion of the neocortex, the anterior displacement of the foramen magnum, and the coronal orientation of the petrous temporal bones.

However, the PCA does not provide an uncomplicated view of grade shifts within the hominin lineage. The shape that most diverges from the human mean along PC1 is that of KNM-WT 17000 (Fig. 4-8). The other *Paranthropus* and *Australopithecus* specimens are next on the continuum, followed by *Homo erectus*, *Homo neanderthalensis*, and the two enigmatic specimens KNM-ER 1813 and KNM-ER 1805. It is also important to consider the relative location of the ape means along PC1. The lesser apes are furthest from the *Homo sapiens* mean, followed by *Pongo*, *Gorilla*, and *Pan*, which is closest.

KNM-WT 17000. Holloway et al. (2004) describing the endocast of KNM-WT 17000 state that “the lateral cerebellar lobes show a lateral flare and posterior protrusion, suggesting a more primitive condition (p. 103).” I agree that the shape of KNM-WT 17000 is more primitive as evidenced in the PCA above. I also agree that when the entire endocast of KNM-WT 17000 is viewed in *norma basilaris* the cerebellar lobes appear to flare laterally and posteriorly. This configuration is tested

empirically in Chapter 5. However, these landmark data, considering only cerebellum (posterior cranial fossa) shape, do not reveal a tendency toward lateral flaring or posterior protrusion. In fact, they demonstrate the opposite effect in Fig. 4-8. The antero-posterior axis is elongated and the medio-lateral axis is reduced in comparison to humans and other hominins.

The difference in cerebellum shape between KNM-WT 17000 and OH 5 raises the possibility of cerebellum reorganization within the robust australopithecine lineage. Some researchers have suggested an evolutionary link between *Australopithecus afarensis* (*Preanthropus*) and later robust australopithecines (Falk and Conroy, 1983). It would therefore be interesting to include *A. afarensis* and a larger sample of robust australopithecines within this data set. If *A. afarensis* is closely related to *P. aethiopicus*, one might expect *A. afarensis* to have a cerebellum shape similar to KNM-WT 17000.

Paranthropus and Australopithecus africanus. Tobias (1967) first described the cerebellar hemispheres of OH 5 in detail. He considered the cerebellum to be better developed in OH 5 than in other australopithecine endocasts available at the time. He based his conclusions on the size, qualitative shape information, and morphometric indices. This geometric morphometric shape analysis indicates that along PC1, the cerebellum of OH 5, Sts 5, and Sts 19 are very similar while Sts 5 and Sts 19 group together more closely on both axes. PC2 indicates a displacement of the foramen magnum and inferior cerebellum that differs moderately in *Paranthropus* and *Australopithecus africanus*. These data do not indicate that either *Paranthropus* or

Australopithecus africanus more closely resemble modern human morphology than ape morphology. Their morphology might be better described as unique.

Some researchers have hypothesized that the cerebellum and neocortex have had independent selective pressures that have influenced their evolution in the hominin lineage (Rilling and Insel, 1998). Based on this study and the the work of Falk et al. (2000), I would agree with this hypothesis. Falk et al. (2000) show that *Paranthropus* and *Australopithecus africanus* share similar cranial capacities but clearly divergent frontal, orbital, and temporal morphologies. The PCA in this study indicates that OH 5, Sts 5, and Sts 19 are configured similarly in the antero-posterior and medio-lateral aspects of their shape but differ in the position of basion. Thus, it appears that the shape of the anterior and middle cranial fossa in *Paranthropus* and *Australopithecus africanus* are more divergent than the shape of the posterior cranial fossa suggesting at least some independent selective pressure.

KNM-ER 1805 and KNM-ER 1813. The PCA demonstrates that both of these specimens cluster more closely with *Homo erectus*, *Homo neanderthalensis*, and modern *Homo sapiens*. The taxonomic affiliation of KNM-ER 1805 and KNM-ER 1813 is still under considerable debate but this analysis indicates that the shape of the cerebellum in these specimens more closely resembles the genus *Homo* than *Australopithecus* (Wood and Collard, 1999).

Summary of Chapter 4 Results

The major conclusions of this chapter are: 1) cerebellum shape appears to differ between grades of primates; 2) *Macaca* cerebellum shape is lateralized and sexually

dimorphic; 3) ape cerebellum shape is also lateralized but functional implications are unclear; 4) principal components analysis reveals an antero-posterior foreshortening and a medio-lateral expansion in shape from *Macaca* to *Homo sapiens*. Hominins are most clearly distinguished from apes by their position along PC2, which represents the position of the foramen magnum. Apes have posteriorly oriented foramina magna and hominins have anteriorly oriented foramina magna.

This analysis also reveals that the pattern of shape change through time in the posterior cranial fossa within the hominin lineage may differ from that seen in the anterior and middle cranial fossae. Inclusion of more fossil hominin specimens in future work will enable me to examine trends within the robust lineage and test links between *Paranthropus* and *Australopithecus africanus* and earlier African fossil hominins (*Australopithecus afarensis* for example).

**CHAPTER 5: ENDO-BASICRANIAL SHAPE IN EXTANT CATARRHINES
AND PLIO-PLEISTOCENE FOSSIL HOMININ ENDOCASTS: A GEOMETRIC
MORPHOMETRIC ANALYSIS**

The cranial base of anatomically modern *Homo sapiens* has been shown to possess a distinctly derived morphology (Dean and Wood, 1981, 1982). A flexed, foreshortened basicranium, and a deep posterior cranial fossa characterize the human cranial base. The foramen magnum is directed antero-inferiorly and the petrous temporal bones are oriented coronally. This configuration differs significantly from the condition seen in great apes where the basicranium is relatively long and unflexed at sella, the posterior cranial fossa is shallow, the foramen magnum is directed posteriorly, and the petrous temporal bones are sagittally oriented (Aiello and Dean, 1990). The overall configuration of the gracile australopithecines tends to be apelike with the exception of an anteriorly positioned foramen magnum. Robust australopithecines share anteriorly projected foramina magna but have humanlike broad cranial bases associated with longer basioccipitals (Aiello and Dean, 1990; Dean and Wood, 1981; 1982).

The majority of scientific work devoted to the evolution of the hominin cranial base is derived from either sagittal radiographic evidence or measurements of the external basicranial anatomy of comparative primate samples (Dean and Wood, 1981, 1982; Ross and Ravosa, 1993). In this chapter, I employ the same comparative sample of living catarrhine and fossil hominin endocasts from Chapter 4 and geometric

morphometric techniques (Zelditch et al., 2004) to explore the size and shape of the hominin internal cranial base in *norma basilaris*.

Four hypotheses are tested:

Hypothesis 1 Null: The catarrhine endo-basiscranium (henceforth called basicranium) shows no distinct lateralization (asymmetry) in centroid size and shape (defined in Chapter 4). Lateralization in brain structures are either not sufficiently large to reveal statistically significant variation or are simply not translated to cranial base morphology.

Alternate hypothesis: Dean (1988) remarked that “the endocranial aspects of the cranial base are profoundly influenced by the growth and development of the brain; indeed, the cranial fossae are a near perfect mold of the undersurface of the brain (pg. 107).” Evidence of brain lateralization in humans and apes is well documented (Falk, 1987) and should thus influence the position of internal cranial base structures (Dean, 1988).

Hypothesis 2 Null: The catarrhine basicranium shows no distinct sexual dimorphism in shape and centroid size.

Alternate Hypothesis: A distinct sexual dimorphism in basicranium shape exists in species that show distinct brain sexual dimorphism. The early work of Dean and Wood (1981, 1982) on the external surface of the hominoid skull in *norma basilaris* did not focus on sex differences. We expect species that demonstrate large body size dimorphism, to reveal sexually dimorphic basicranial morphology.

Hypothesis 3 Null: The shape of the catarrhine basicranium does not change in relation to increasing centroid size (shape is independent of size).

Alternate hypothesis: The shape of the catarrhine basicranium changes in relation to increasing centroid size (shape is partially dependent on size).

Literature exists to support the hypothesis that basicranial flexion is influenced by relative brain size in primates (Ross and Ravosa, 1993). Basicranial flexion is measured by cranial base angle, which is defined as the angle formed by a chord between basion and sella and sella and foramen caecum (Spoor, 1997). Adding these same chords provides a measure of basicranial length, which is used to determine relative brain size (index of relative encephalization: cubed root of cranial capacity divided by basicranial length) (Ross et al., 2004). It has also been proposed that flexion of the human cranial base is an adaptive response to maintain a spherically shaped brain (Lieberman et al, 2000), although more recent testing fails to support this hypothesis (Ross et al., 2004).

It is therefore hypothesized that basicranial shape is in part influenced by increased centroid size. It is important to note that centroid size is not a measure of brain size but a product of the landmarks chosen for this study.

Hypothesis 4 Null: There are no statistically significant shape differences between monkeys, apes, and hominins.

Alternate hypothesis: Scaled to centroid size of 1.0, shape differences are evident between different grades of primates. Based on previous research, I expect robust australopithecines to share some basicranial characteristics with late and modern *Homo* and gracile australopithecines to share characteristics with great apes (Dean and Wood, 1982). Monkeys are expected to be different from all living and extinct hominoids.

Materials and Methods

The comparative sample of primate and fossil endocasts used in this chapter is the same as in Chapter 4.

Fourteen landmarks on the basilar surface of the primate endocast are utilized. Table 5-1 lists the landmarks with their abbreviations and definitions. Figures 5-1 depicts the positions of the landmarks on the endocast of a macaque in *norma basilaris*. All landmark data were collected as in Chapter 4. Integrated Morphometric Programs (IMP) software developed by Sheets (2001) is utilized to perform the geometric morphometric analysis.

TABLE 5-1 Landmarks for geometric morphometric analysis

Number	Abbreviation	Measurement	Description
1	F'	Frontal pole midline	Mid-point between the most anterior projections of the left and right cerebral hemispheres. This point was found using Rhinoceros 1.0 modeling software.
2	O'	Occipital pole midline	Mid-point between the most posterior projections of the left and right occipital lobes. This point was derived using Rhinoceros 1.0 modeling software.
3	F	Frontal pole (side)	Most anterior point of the endocast representing the cerebral hemisphere in basicranial view. Measured bilaterally.
4	mat	Anterior temporal point	Most anterior point of the temporal lobe in basicranial view.
5	ds	Dorsum sella (side)	Most lateral point of the impression of the dorsum sella on the basicranial aspect of the endocast.
6	ds'	Dorsum sella (center)	Point at the center of the impression of the dorsum sella on the basicranial surface of the endocast.
7	IAM	Internal auditory meatus	Impression of the internal auditory meatus on the basicranial surface of the endocast
8	pt	Petrous temporal point	Most lateral point of the impression of the petrous temporal bone on the endocast.
9	ba	Endobasion	Most anterior point on the impression of the foramen magnum on the endocast.
10	cl	Lateral cerebellar point	Most lateral point on the cerebellar hemisphere impression on the endocast.
11	ci	Inferior cerebellar point	Point representing the most inferior point of the posterior cranial fossa impression. (Endocast aligned in the F-O plane.)
12	co	Occipital cerebellum	Point representing the most caudal point on the impression of the cerebellar hemispheres.
13	cv	Superior cerebellum	Most superior point on the impression of the cerebellar hemispheres (taken inferior to the transverse venous sinus).
14	O	Occipital pole (side)	Most posterior point on each cerebral hemisphere in basicranial view.

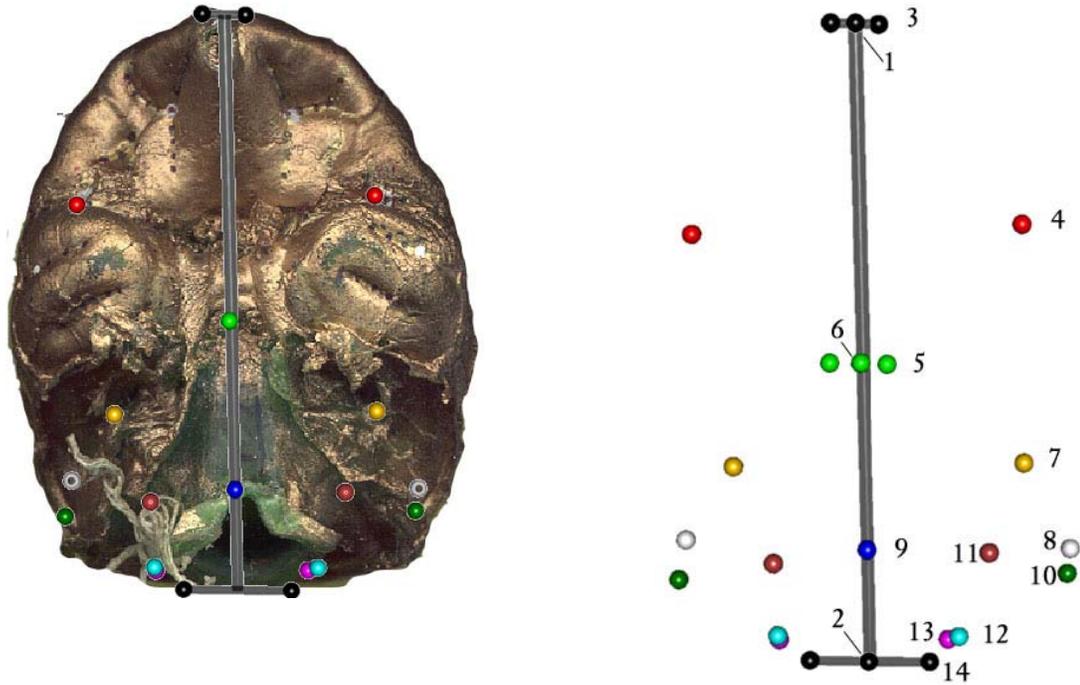


Fig 5-1. Left: Macaque endocast in *norma basilaris* with landmark positions superimposed. Right: Landmarks used in this study.

Repeatability of landmarks is assessed, as in Chapter 4, by examining the scatter of points at each landmark in 30 female macaques (left and right sides combine and reflected over the midline). Figure 5-2 depicts the scatterplots. Circular scatterplots indicate random error that can be considered digitizing noise (Zelditch et al., 2004). All of the landmarks retained for this chapter have roughly circular scatterplots except points 11 and 7 representing the inferior point on the cerebellar lobe and the internal auditory meatus impression, respectively. These are the same two landmarks that were variable in the previous chapter. Results are interpreted with these errors in mind.

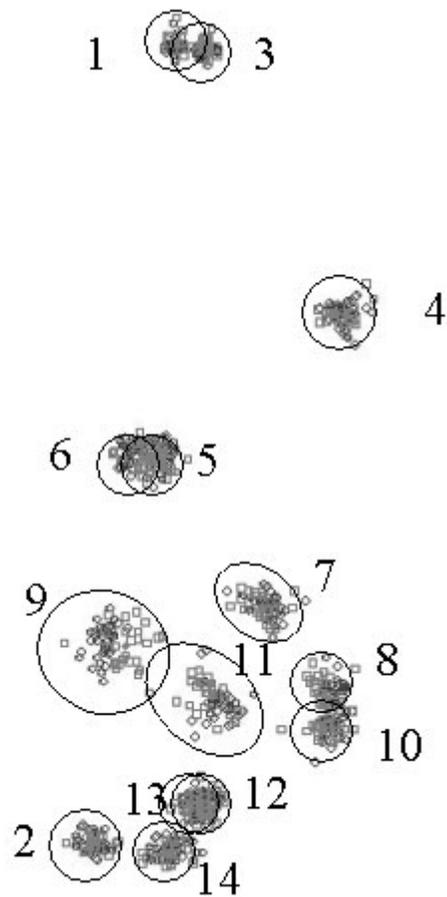


Fig. 5-2 Repeatability of 14 landmarks utilized in this chapter. Data from the endocasts of 30 female macaques, right side reflected over left side at the midline.

Statistical tests. Multivariate tests of significance are performed with TwoGroup6h (IMP) to test lateral asymmetry (Hypothesis 1), sexual dimorphism (Hypothesis 2) and grade differences (Hypothesis 4) in basicranium shape. Multivariate analyses of covariance are calculated by Regress6K (IMP) to determine if basicranium shape is size dependant (Hypothesis 3). The covariate in these analyses is centroid size, which is statistically independent of shape in the absence of allometry (Bookstein,

1991; Zelditch et al. 2004). One factor ANOVA is used to test for statistical difference in centroid size between groups. Principal components analysis is performed with PCAGEN (IMP) in order to reduce the multivariate data set into a smaller group of interpretable variables.

Results: Lateral shape asymmetry in the basicranium (Hypothesis 1)

The groups tested for asymmetry are all-catarrhines (including *Homo sapiens* and fossil hominins), all-catarrhines – sexes-combined and sexes-separate (excluding *Homo sapiens* and fossil hominins), apes (excluding *Homo sapiens* and fossil hominins) – sexes-combined and sexes-separate, and *Macaca*-only – sexes-combined and sexes-separate. There is no statistically significant difference between the left and right side shapes in the all-catarrhine sample. Statistically significant lateralization is found in the combined sex ape-only test and in the *Macaca* sex-combined and sex-separate tests (Table 5-2). These results demonstrate that it is reasonable to average left and right sides when examining the entire catarrhine sample but that at lower taxonomic levels it is more prudent to separate the sides for individual analysis.

TABLE 5-2 MANOVA tests for lateral asymmetry

Groups – Left side vs Right side	Sex	F score	Degrees of freedom	<i>P</i>
Catarrhines (including <i>Homo sapiens</i> and fossil hominins)	MF	1.0	24, 5352	.46
Catarrhines (excluding <i>Homo sapiens</i> , fossil hominins)	M	.68	24, 2304	.88
Catarrhines (excluding <i>Homo sapiens</i> , fossil hominins)	F	.72	24, 2352	.83
Apes	MF	1.91 *	24, 1344	.01
Apes	M	1.33	24, 864	.14
Apes	F	2.2*	24, 912	.0008
<i>Macaca</i>	MF	5.39 *	24, 2832	<.0001
<i>Macaca</i>	M	3.83 *	24, 1392	<.0001
<i>Macaca</i>	F	2.46 *	24, 1392	.0001

* Significant at alpha=.05 M=males, F=females

Lateral shape asymmetry in the sexes-combined macaque samples and sexes-combined apes are depicted in the thin-plate spline deformations in Figs. 5-3 and 5-4. We observe opposite shape patterns in these two groups. Most of the difference between the sides differs in the position of landmarks 9 (basion), 10 (lateral cerebellar point) and 5 (lateral dorsum sella point). In macaques the right side (depicted as arrow tips) is narrower medio-laterally while in apes it is wider. It is unclear at this stage whether these differences are related to functional differences in the brain or mechanical constraints on the basicranium.

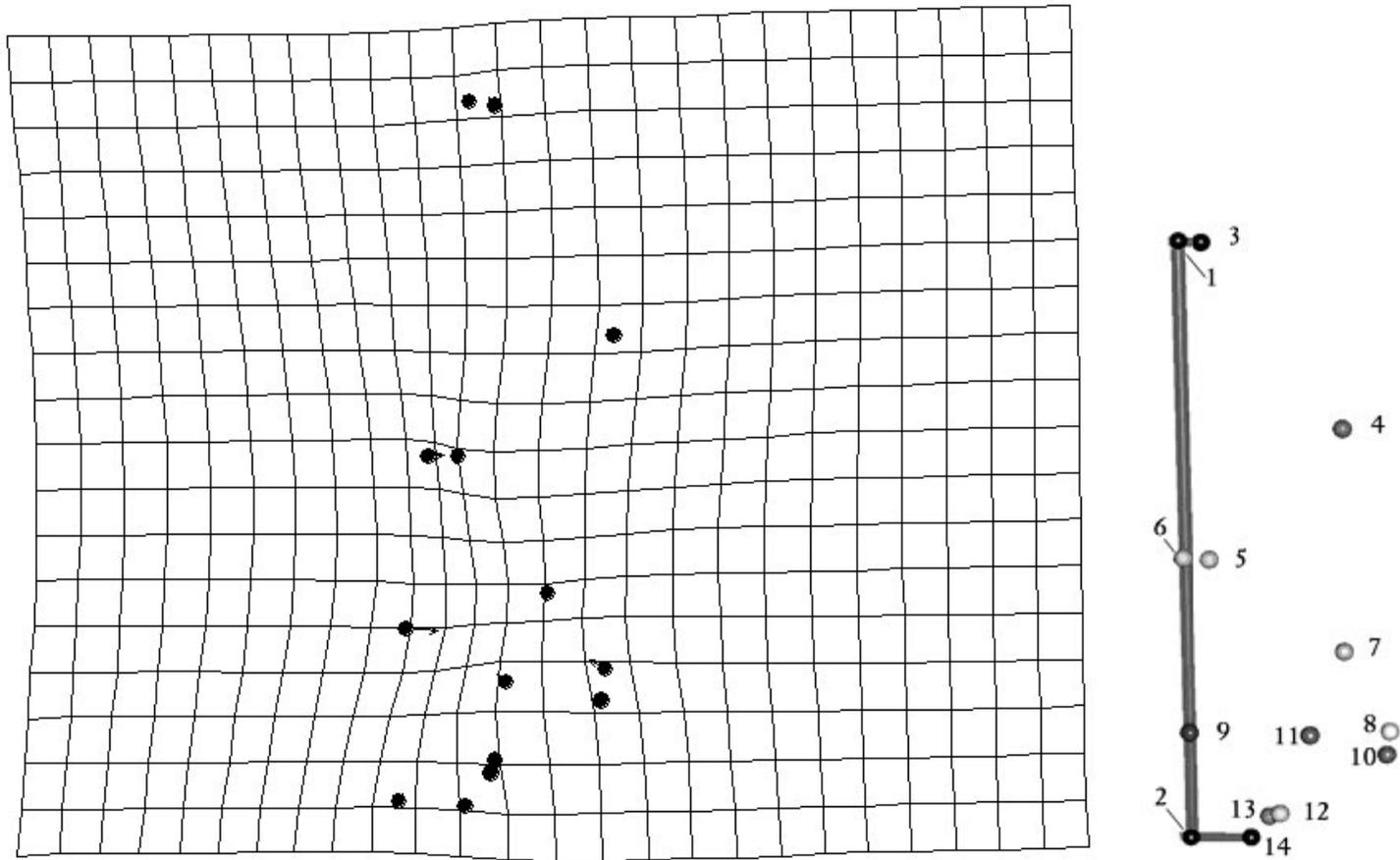


Fig. 5-3 *Macaca* combined sex left side vs right side.

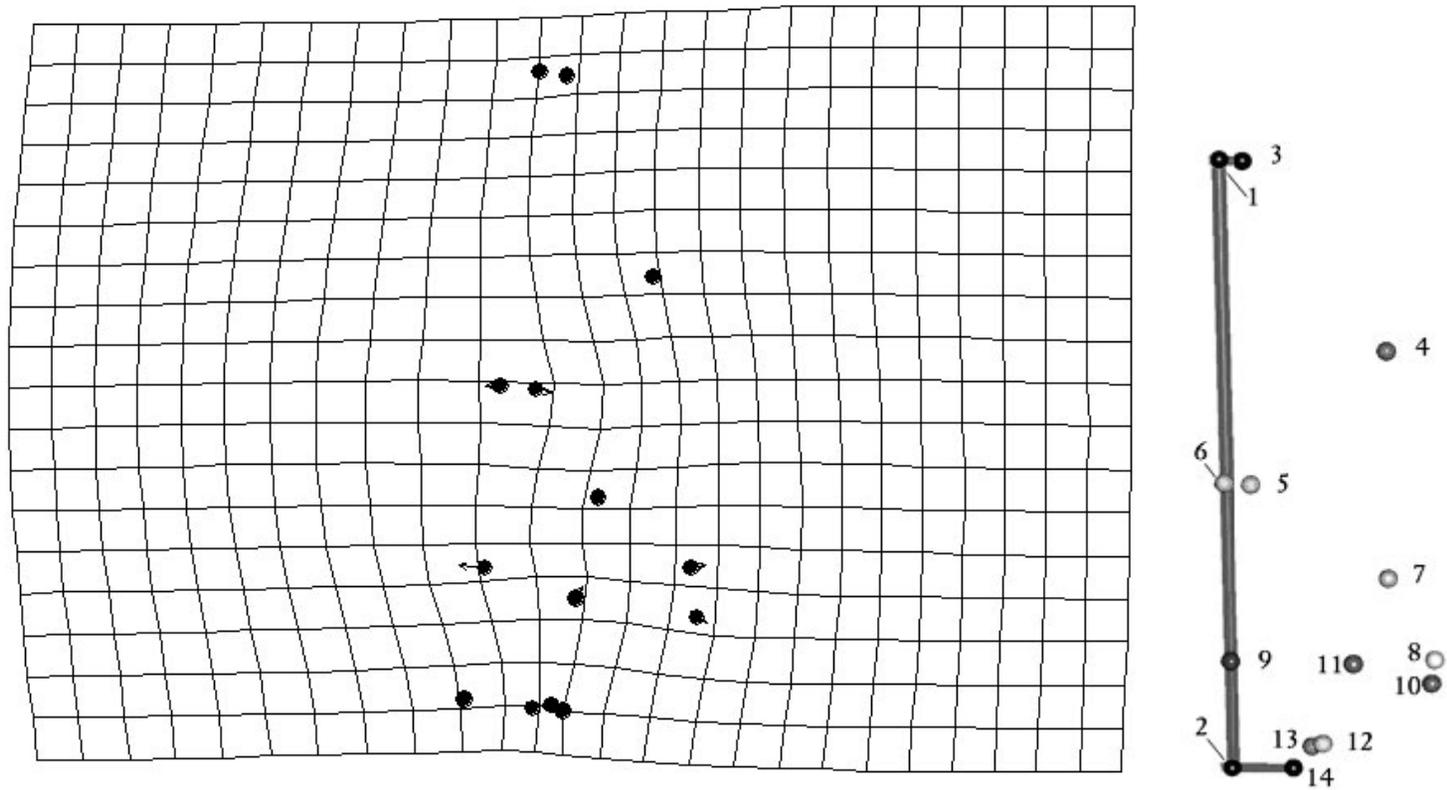


Fig. 5-4 Apes combined sex left side versus right side. Black dots represent left side morphology and arrow tips represent right side morphology.

Lateral shape asymmetry and centroid size. Centroid sizes from the original 3d Procrustes superimposition are tested with ANOVA to determine if left and right side basicranial shapes differed statistically. No statistically significant differences are detected in any of the samples listed in Table 5-2. Effectively, left and right sides are equivalent in size in this sample.

These results show that in the all-catarrhine sample no statistically significant differences are detected between the left and right sides of the basicranium. Side asymmetry is detected in the sub-sample of apes and macaques but the pattern (Figs. 5-3 and 5-4) is not consistent between the groups. The midline landmark 9 (basion) shifts laterally in opposite directions in apes and macaques. Macaques appear to have slightly more compressed shapes in the right hemisphere than in the left while apes have slightly more expanded shapes in the right. It is unclear at this stage whether there is any evolutionary significance to this finding.

Results: Sexual dimorphism and basicranium (Hypothesis 2)

Multiple analysis of variance with left and right sides averaged reveal a statistically significant differences between males and females in the all-catarrhine sample (partial Procrustes distance .019, Goodall's $F= 2.76$, $df= 24, 4704$, $p<.0001$). At lower taxonomic levels only macaques show statistically significant differences between male left vs. female left (partial Procrustes distance .02, Goodall's $F= 1.94$, $df= 24, 1392$, $p<.004$) and male right vs. female right (partial Procrustes distance .027, Goodall's $F= 2.82$, $df= 24, 1392$, $p<.0001$) (Figs. 5-5 and 5-6).

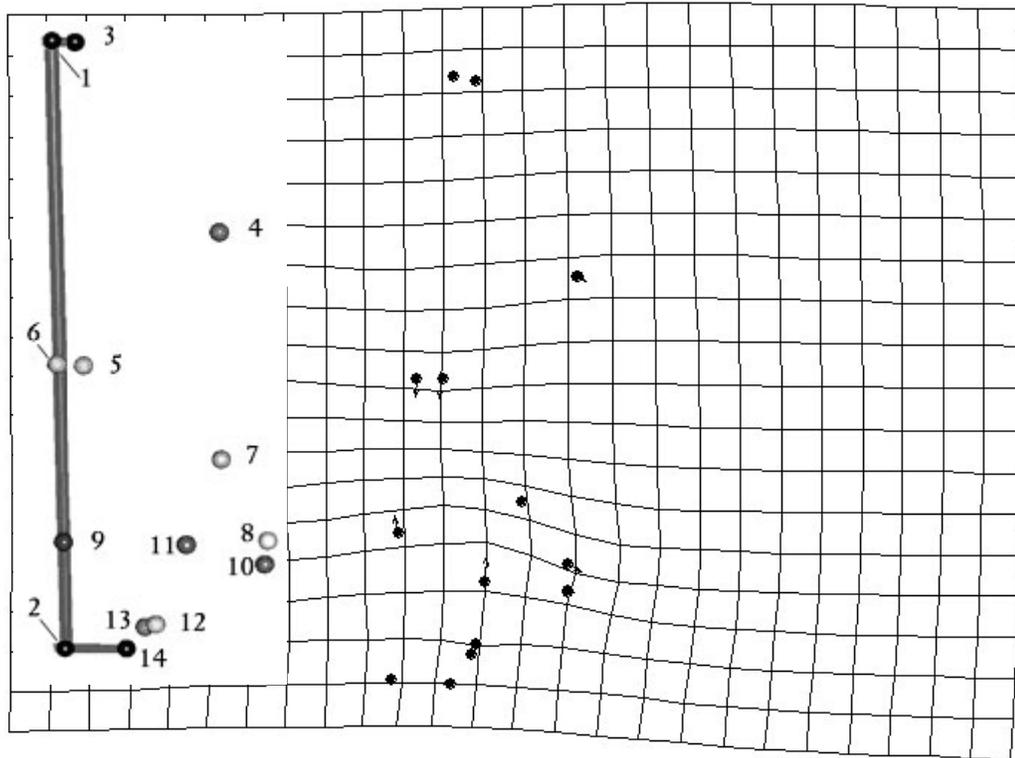


Fig. 5-5 *Macaca* sexual dimorphism. Black dots represent the male shape. Arrow tips represent female shape. Diagrams reflect male left vs. female left basicranial shape.

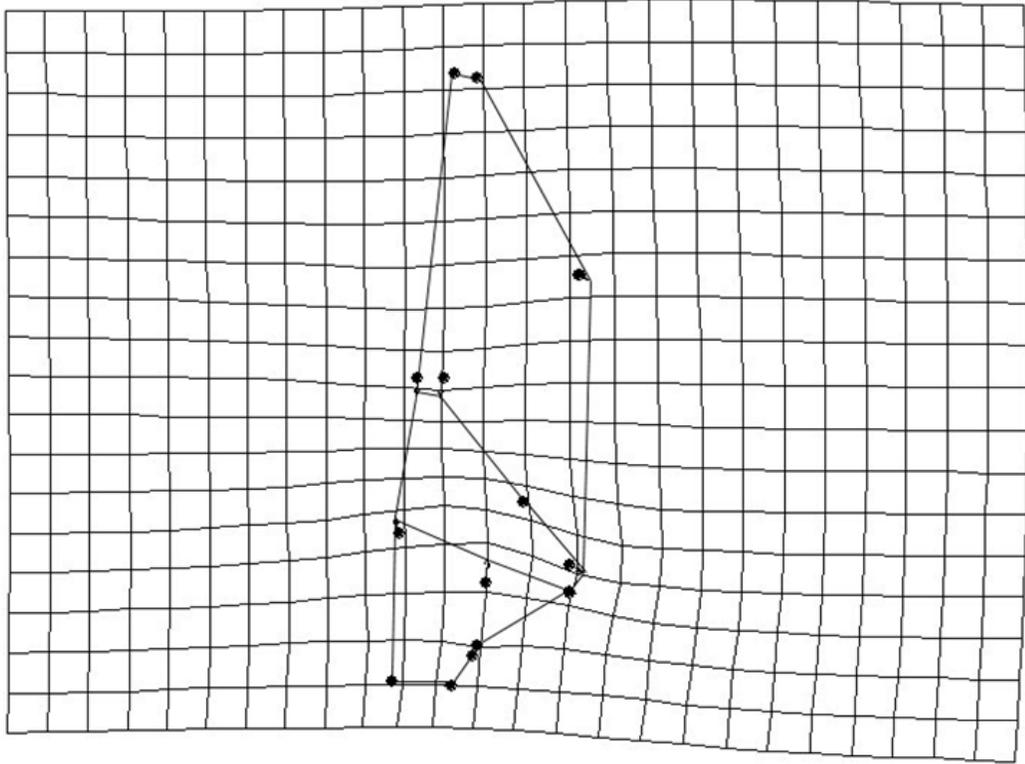


Fig. 5-6 *Macaca* sexual dimorphism. Black dots represent the male shape. Arrow tips represent female shape. Lines connect arrowheads to depict female shape.

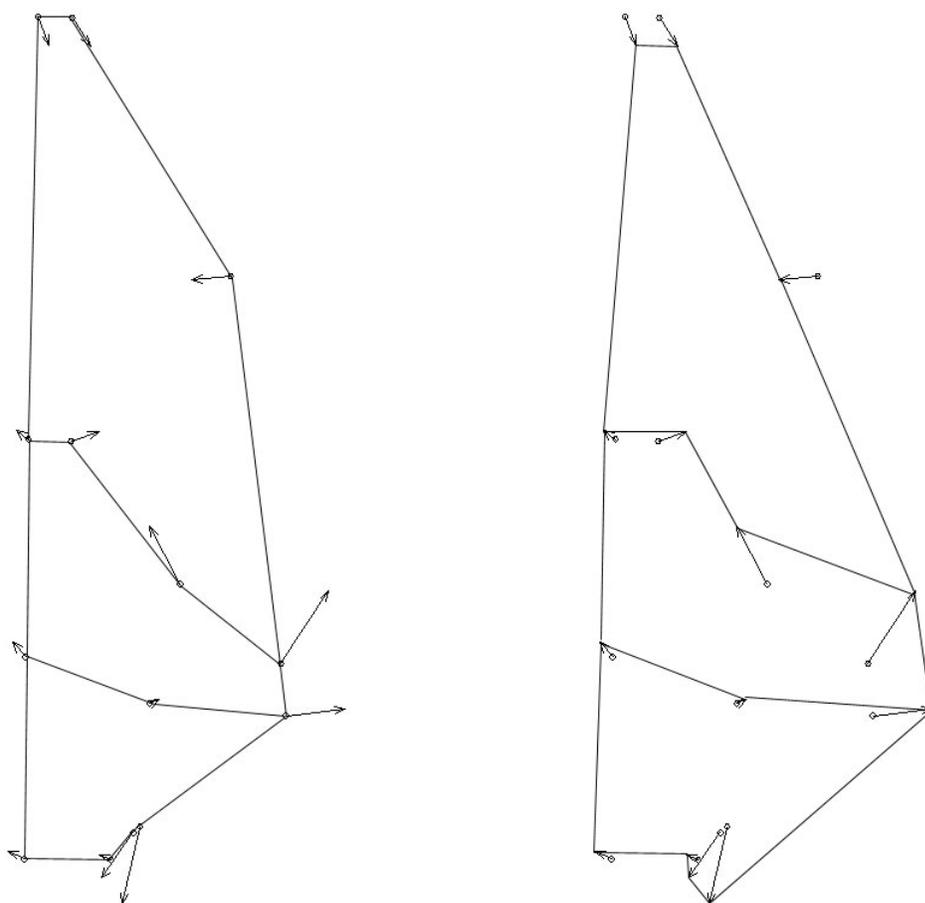
Sexual Dimorphism and centroid size. Centroid sizes from the original 3d Procrustes superimposition are tested with ANOVA to determine if males and females differed statistically. *Macaca* is the only group to show statistically significant sexual dimorphism in centroid size. In both the sides-averaged and sides-separate tests, centroid size is found to be significantly larger in males (Sides averaged - $F= 20.4$, $p=.00003$, $df=1,58$; Left - $F= 17.5$, $p=.00009$, $df=1,58$; Right - $F= 22.6$, $p=.00001$, $df=1,58$).

Sexual dimorphism in shape and centroid size appears to be driven by my macaque sample. The quantity of male and female specimens in my ape sample is too small to test for statistically significant sexual dimorphism in basicranial shape. Macaque females have more anteriorly located basion landmarks and are slightly expanded medio-laterally. Female shapes compared to male shapes move in the direction of the larger-brained ape and human shapes even though they have smaller centroid sizes than males. Previous research has established that *Macaca mulatta* and *Homo sapiens* share similar patterns of body and brain size dimorphism (Falk et al, 1999). Although, it is unlikely that macaque basicranial morphology is as affected by brain growth as in *Homo*, these parallels in shape are intriguing. Further work is necessary to uncover the root mechanisms in *Macaca* basicranial dimorphism.

Results: Basicranial shape and size (Hypothesis 3)

Multivariate regression is used to test the null hypothesis that shape and centroid sizes co-vary. Multivariate linearity is tested by regressing PD against the natural logarithm of centroid size (Zelditch et al., 2004). (PD is defined as the Procrustes

distance of each specimen from the mean shape.) For the all-catarrhine sample, the relationship proves to be linear ($r^2 = .71$). The regression of the partial warp scores on ln centroid size (from raw 3d landmarks) using Regress6k software (IMP) yields a Wilks lambda score of .1232 ($F=25.8$, $df=24$, 87 $p=0$). Regress 6k also provides the variance explained by the regression, in this case, 88%. These results indicate that size (centroid size) influences shape. We reject the null hypothesis that size and shape are independent of each other. Examination of the deformation of shape with increasing centroid size shows that as size increases the shape of the basicranium becomes antero-posteriorly compressed and medio-laterally expanded (Figure 5-7).



A.

B.

Fig. 5-7 Centroid size and shape. Open circles in A connected by lines depict shape of smallest centroid size. Arrow tips in B connected by lines depict shape of largest centroid size. Shape B is antero-posteriorly compressed and medio-laterally expanded.

Thus, this multivariate analysis of the influence of centroid size on basicranial shape reveals that size and shape covary significantly. As centroid size increases the overall shape of the catarrhine internal cranial base becomes antero-posteriorly compressed and medio-laterally expanded. Dean (1988) suggests that an infratentorial spatial-packing problem is produced when a relatively enlarged cerebellum grows on a short posterior cranial fossa. The human cerebellum exerts force on the petrous temporal bones and basicranium to push them into their derived configuration. This idea is supported by measurements of absolute cerebellum volume that show vast increases in size from prosimians to hominins (Stephan et al., 1981) and strong reciprocal relationships between the cerebellum and the expanding neocortex (Schmahmann, 1997; Weaver, 2005).

Interestingly, cerebellum size relative to brain size does not appear to be larger in humans than expected for apes of equal brain size (Rilling and Insel, 1998; Semendeferi and Damasio, 2000; Semendeferi, 2001; see Weaver, 2005 for dissenting view). These data seem to confound the idea that the cerebellum is driving the morphological changes evident in the cranial base. Ontogenetic evidence from human fetuses (Jeffery, 2002) and phylogenetic evidence from a large sample of primates and fossil hominins (Weaver, 2005) demonstrate a profound expansion of the supratentorial space in modern humans. This neocortical expansion in conjunction with a more moderate cerebellar expansion compresses the space available for structures in the posterior cranial fossa. The two compartments of the brain act synergistically to reshape the human basicranium.

Results: PCA of basicranial shape (Hypothesis 4)

As in the previous chapter, all bilateral landmarks are reflected across the midline and averaged to reduce the number of landmarks analyzed (Zelditch et al., 2004). The PCA includes all of the catarrhine specimens, modern *Homo sapiens* and the fossil hominins. Together the first two principal components explain 56% of the total variance (PC1= 42%, PC2=14%) and Anderson's χ^2 (PCAGen6n-IMP) indicates that there is one distinct eigenvalue. Figure 5-8 shows PC1 graphed on PC2. Figures 5-9 and 5-10 depict the deformation of shape along PC1 at the *Macaca* and *Homo sapiens* means.

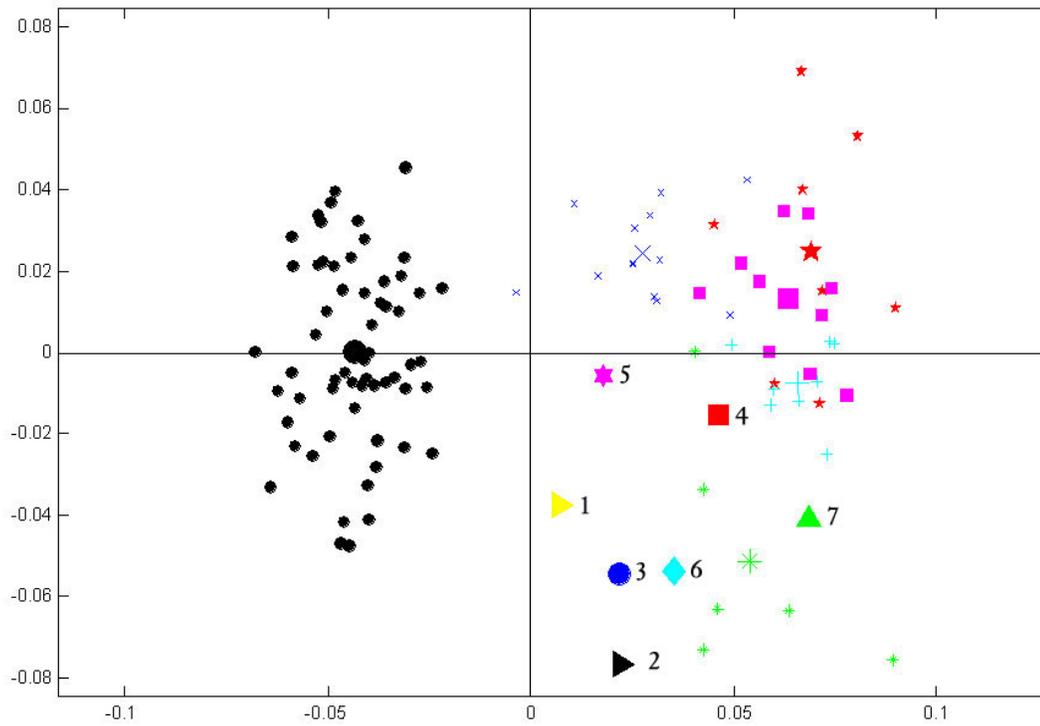


Fig. 5-8 Principal components analysis of all specimens. PC1 graphed on PC2. Fossil hominins are numbered 1-7. 1) Sts5, 2) KNM-ER 1813, 3) KNM-ER 1805, 4) OH5, 5) KNM-WT 17000, 6) LaChapelle-aux-Saints, 7) KNM-ER 3883. Black Dots=*Macaca*, Blue X=*Hylobates*, Red Stars=*Pongo*, Pink Squares=*Gorilla*, Turquoise Crosses=*Pan*, Green Asterisks =modern *Homo*. Large icons represent group means.

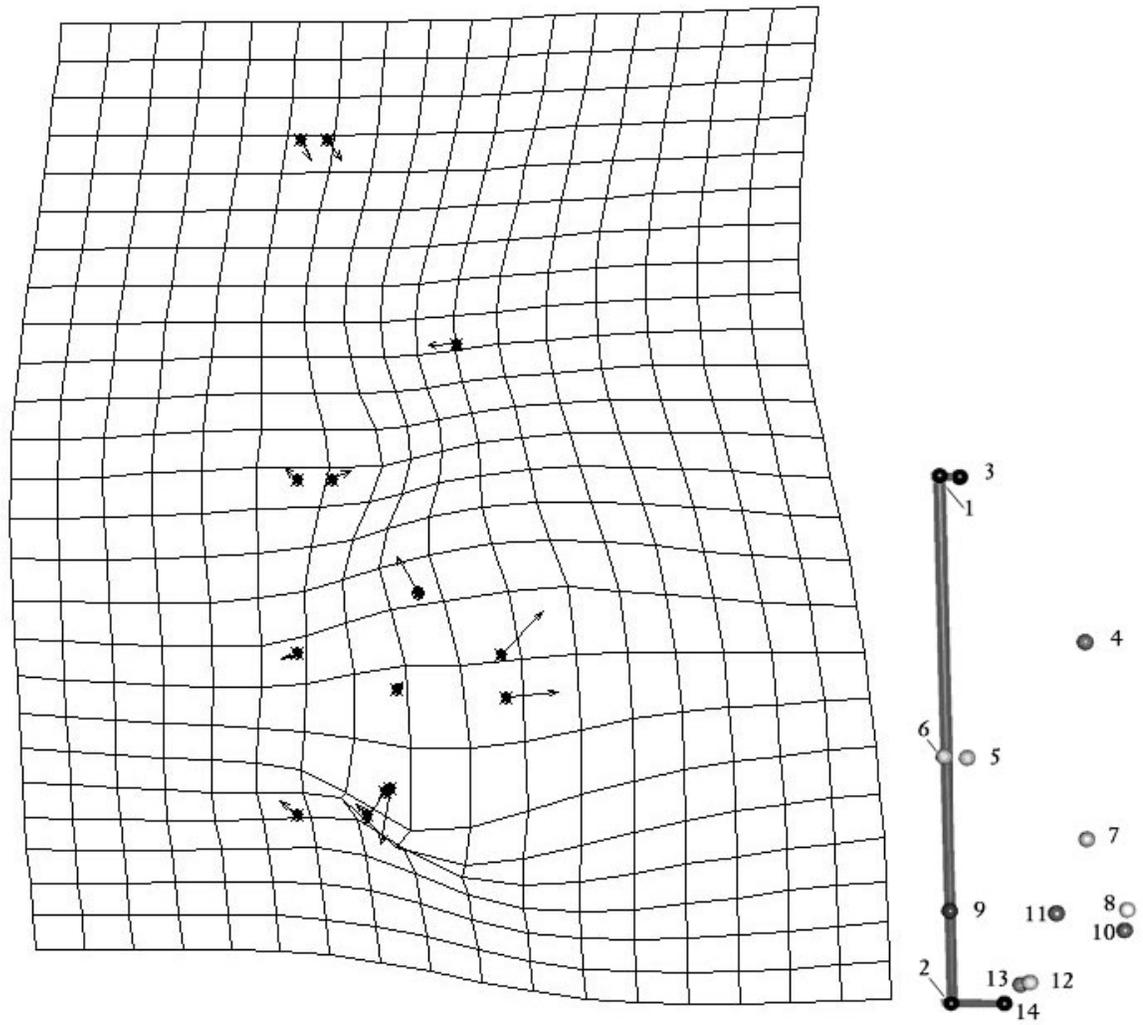


Fig. 5-9 Deformation grid, landmarks and vectors depicting the deformation from the *Macaca* mean on PC1 to *Homo sapiens* mean on PC1. Black dots depict *Macaca* shape and the arrow tips (connected by lines) depict *Homo sapiens* shape. The two shapes are in Procrustes superimposition (centroid size=1.0).

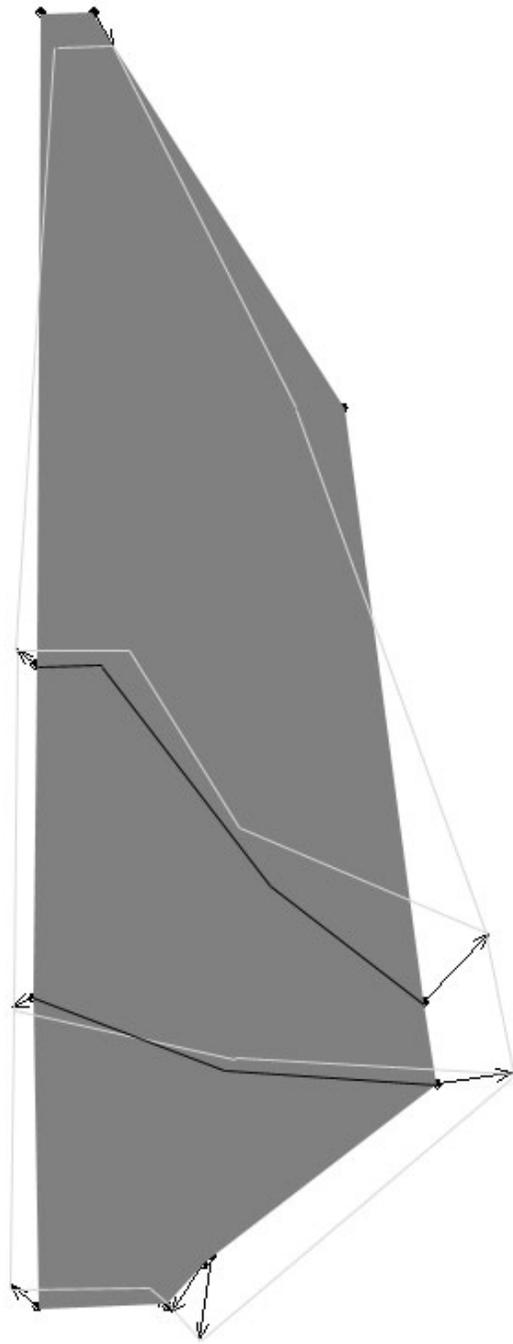


Fig. 5-10 Shape configuration of *Macaca* and *Homo sapiens* along PC1. Colored shape represents *Macaca* and gray lines represent *H.sapiens*.

A clear difference is detected between the macaques, apes, and hominin grades by their relative position in the PCA. Macaques are all grouped in the left (x =negative) quadrants and apes in the right (x =positive) quadrant. Apes and hominins are separated most clearly by the y axis. Macaque basicranial shapes are in general long antero-posteriorly, narrow medio-laterally. Apes and hominins share some aspects of basicranial morphology but differ greatly in the position of the basion. Apes have a more posteriorly located basion, which places them in the upper right quadrant of the PCA. Interestingly, all of the hominin specimens group together and do not reveal the larger morphological differences seen in exo-basicranial morphology (Dean and Wood, 1981, 1982).

Figures 5-9 and 5-10 reveal that the larger-brained species of apes and hominins have antero-posteriorly compressed and medio-laterally expanded posterior cranial fossae. The difference between the hominins and apes along PC1 appears to be the degree to which the cerebellar hemispheres project posteriorly. The lesser ape *Hylobates* and the KNM-WT 17000 are in roughly the same location along PC1 (closer to the origin) than the great apes. Figure 5-8 shows that *Hylobates* and KNM-WT 17000 share a similar posterior cerebellar projection. That is, they are less projecting (underslung) than the great apes.

The apes and hominins differ along PC2 based mainly on the degree to which basion (representing foramen magnum position) is projected anteriorly. Hominins have relatively anteriorly positioned basion landmarks and apes have relatively posteriorly positioned basion landmarks.

Underslung and laterally flaring cerebellums. The relative position of the cerebellum under the cerebral hemispheres and the lateral flare of the cerebellum have been employed to test the progressive or conservative nature of fossil hominins in the past (Connolly, 1950; Holloway et al., 2004; Tobias, 1967). In an effort to quantify these measures I employ Bookstein shape coordinates derived from my sample of endocast landmarks.

Bookstein shape coordinates for my sample are produced using Coordgen6f software (IMP). The length between points 1 (F') and 2 (O') are fixed at 1.0 units and landmarks cl, co, cv are graphed on a Cartesian plane (Figures 5-11 and 5-12).

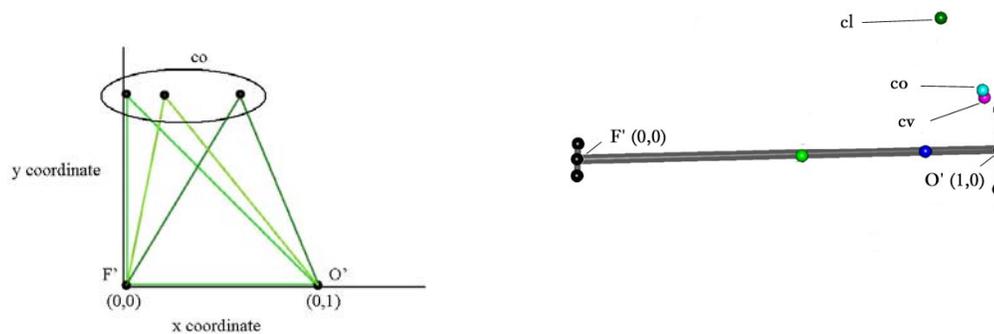


Fig. 5-11 Bookstein shape coordinates. Landmarks F' and O' are constrained to length 1.0 and plotted on a Cartesian plane. The location of the free landmark can then be compared to determine shape differences.

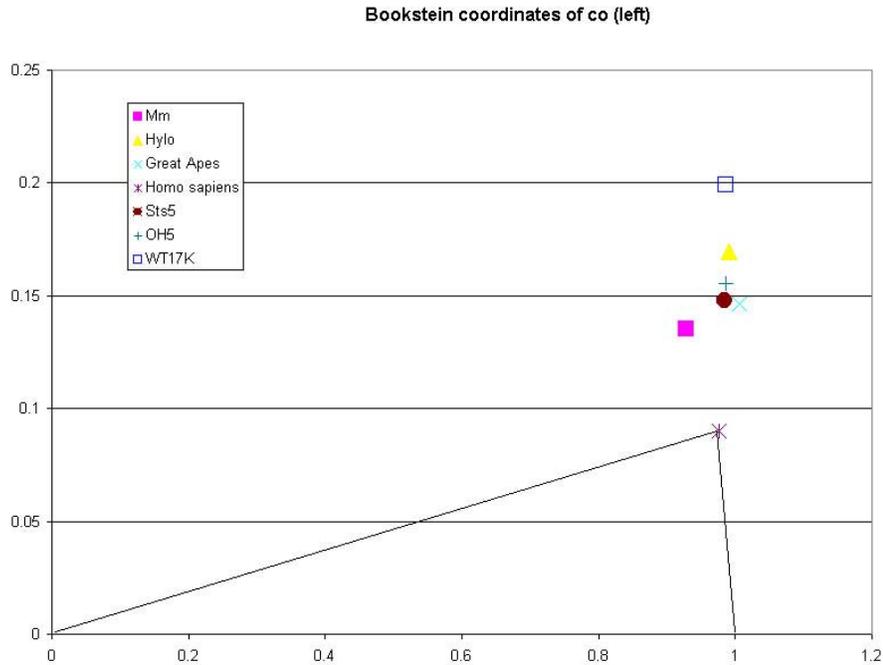


Fig. 5-12 Bookstein coordinates for landmark co (left). Shape triangle drawn for *H. sapiens*.

Figure 5-13 depicts the relationship of landmarks 12 (co-most posterior point on the cerebellar hemispheres) and 13 (cv -most superior points on the cerebellar hemispheres) to the occipital pole. The posterior extension of the occipital pole of the cerebral hemisphere is located at $x=1.0$. Landmarks that surpass 1.0 project beyond the cerebral occipital poles. Landmarks that do not reach the occipital poles are termed “underslung”. Macaques have an extremely underslung cerebellum while great apes have cerebellar hemispheres that, on average, extend beyond the occipital poles. Humans have the most underslung cerebellar hemispheres of all of the hominoids (fossil and living) in our sample.

Holloway et al (2004) describe the cerebellar hemispheres of KNM-WT 17000, an early robust australopithecine, as laterally flaring and posteriorly protruded. Figure

5-14 quantifies the position of the left lateral cerebellar hemisphere KNM-WT 17000. Landmark 10 (cl-left) is indeed more laterally flaring than any other fossil or extant primate in my comparative sample (including fossil hominins from this study not included in the diagram). Figure 5-13 and 5-14 demonstrate however that the cerebellum of KNM-WT 17000 does not protrude more posteriorly than Sts 5 (*Australopithecus africanus*) and is less projected than OH 5.

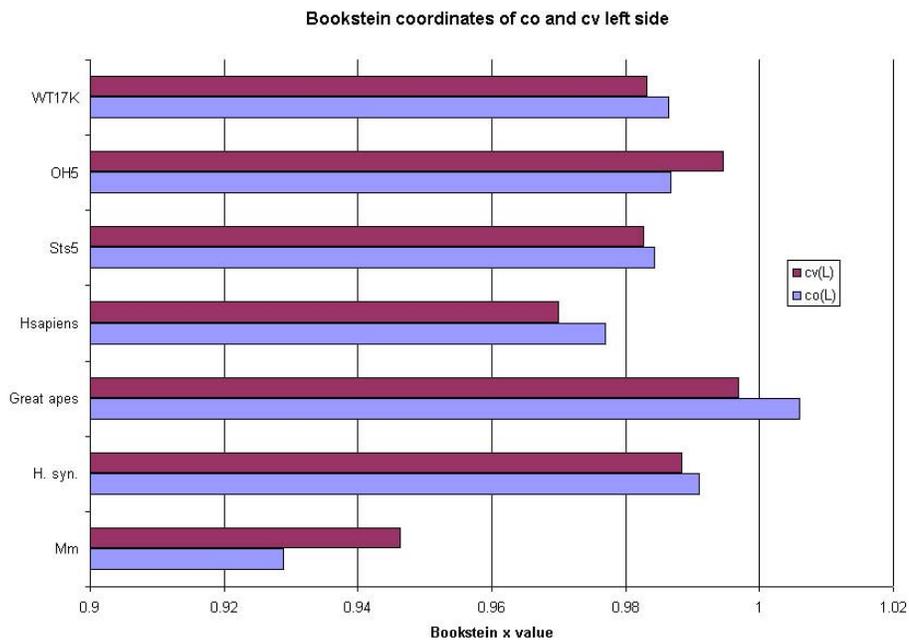


Fig. 5-13 Relative position of landmarks cv and co (left side) in relation to point O' (occipital pole).

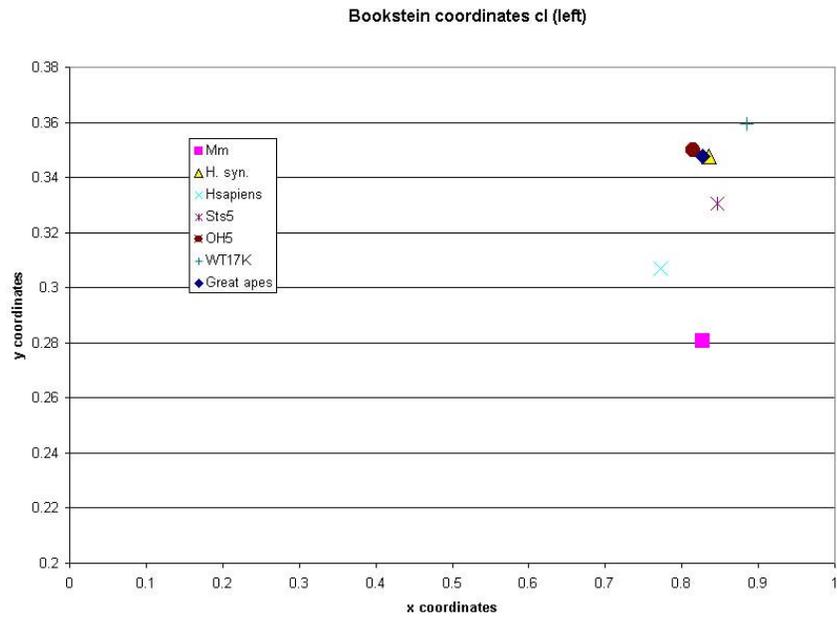


Fig. 5-14 Bookstein coordinates for cl (lateral cerebellum landmark).

Summary of Chapter 5 Results

Similar to the results in Chapter 4, no statistically significant shape lateralizations are revealed in the all-catarrhine samples. Macaques tend to be the most variable group in our sample in both lateralization and sexual dimorphism. It is still unclear whether sexual dimorphism in cerebellum and basicranium shape has any functional correlation in macaques but further work on this subject is warranted.

The analysis of geometric morphometric data by principal components analysis reveals antero-posterior compression and medio-lateral expansion of the basicranium as centroid size increases. These data support the hypothesis that basicranial reorganization (coronal orientation of petrous bones, basicranial flexion, lateral expansion of posterior cranial fossa) occurs as a result of a spatial-packing problem (Gould, 1977).

Fossil hominin and modern *Homo sapiens* specimens tend to be morphologically similar in basicranial organization and distinct from monkeys and apes. *Paranthropus* and *Australopithecus* don't appear to differ in endo-basicranial morphology as much as has been reported from the analysis of exo-basicranium (Dean and Wood, 1981, 1982).

PART 2 SUMMARY

This work uses linear and geometric morphometric techniques to examine the posterior cranial fossa and cerebellum of catarrhine primates and Plio-Pleistocene fossil hominins. The interconnection between the cerebellum and higher cognitive functions reported in Part 1 justifies anthropological and paleoneurological interest in this major and relatively unstudied substructure of the fossil hominin endocast. In this work, novel empirical evidence of cerebellar and basicranial size and *shape* are reported. Previous work has detailed absolute and relative size of the cerebellum in human and nonhuman primates but shape has not been addressed systematically. Lateral asymmetry, sexual dimorphism, and grade differences are examined in a comparative sample of monkeys, apes, humans, and fossil hominins.

The major empirical findings of this work are: 1) analysis of linear cerebellar measurements reveals no statistically significant lateralization or dimorphism in the all-catarrhine sample; 2) linear measurements indicate that macaque males are significantly larger than females in cerebral length, cerebellar breadth, and cerebellar length, 3) absolute measurements of cerebellum size appear to parallel cognitive advancements in catarrhine evolution more closely than relative or index measures; 4) cerebellum shape appears to differ between grades of primates. 5) *Macaca* cerebellum shape and basicrania as determined by landmarks and geometric morphometric techniques are lateralized and sexually dimorphic; 6) principal components analyses of cerebellum landmarks alone and in conjunction with other basicranial landmarks reveal an antero-posterior foreshortening and a medio-lateral expansion in cerebellum and basicranial

shape from monkeys to hominoids; 7) hominins and apes differ mainly in the position of the foramen magnum. Ape foramina magna are more posteriorly oriented and hominin foramina magna are more anteriorly oriented.

CONCLUSION

Paleoneurological discussion of the cerebellum and posterior cranial fossa before the end of the last century can be characterized as a whisper. The cerebellum, although available for study on endocasts, was relatively ignored because it was perceived to be a conservative, motor-only structure. Earlier workers can hardly be blamed for not paying closer attention the cerebellum based on what was known about its function. For a scientist interested in elucidating the process of human brain evolution, a conservative structure that retains primitive functions and does not appear to change dramatically through time is clearly not the ideal structure to study.

As discussed in Part 1 of this dissertation, a substantial amount of experimental and clinical literature in the twentieth century has revealed strong links between cognitive functions in the neocortex and the cerebellum. As the importance of the cerebellum in both motor and cognitive processing became more clear, a new field of endeavor opened up for paleoanthropology. Paleoneurologists began to re-examine evidence from primates and fossil hominins in order to better understand this part of hominin brain evolution.

In this dissertation, I have employed endocasts, the only direct evidence of the brains of extinct species, to analyze size and previously undocumented aspects of cerebellum shape during catarrhine brain evolution. Three general questions were tested: 1) Do cerebellum size and shape show grade level differences in my sample of catarrhine primate endocasts? 2) Are cerebellum size and shape laterally asymmetrical? and 3) Are cerebellum size and shape sexually dimorphic?

The absolute linear dimensions of the cerebellum show differences in size between the different grades of primates in this study. These results are expected based on brain and body size differences in these groups. Taking allometric effects into consideration, I show that the cerebellum size of macaque and ape endocasts differ statistically in linear dimensions. Apes have larger cerebellums than monkeys suggesting that apes use the cerebellum for a greater variety of tasks than monkeys. This versatility in cerebellum function is undoubtedly adaptive in a complex and changing environment.

My analysis does not support the hypothesis that humans and apes have different linear cerebellar dimensions controlled for allometry. However, MacLeod (2000) has shown, convincingly, that the proportions of lateral hemispheres and vermis of the cerebellum in monkeys, apes, and humans are statistically distinct. The lateral hemispheres communicate heavily with the cerebral neocortex and the cerebral neocortex has propelled the cognitive advancements that clearly separate ape and hominin grades.

The principal components analyses in Chapters 4 and 5 also indicate distinct shape patterns in the posterior cranial fossa and basicranium of monkeys, apes, and hominins. The results of both chapters indicate a medio-lateral expansion and an antero-posterior compression from monkeys to humans. The configuration of the internal cranial base changes shape from one group to the next. This reconfiguration is influenced by evolutionary changes that occur in both the supra- and infra-tentorial spaces (i.e. above and below the tentorium cerebelli). The neocortex and cerebellum

have been shown to maintain strong reciprocal connections but it is still unclear how closely adaptive changes in one structure influence the other.

Plio-Pleistocene fossil hominins provide a good example of this problem. In species like *Homo erectus* and *Homo neanderthalensis*, cerebral length is much longer relative to cerebellar breadth than in modern *Homo sapiens*. This proportional difference within the *Homo* phylum may signal an advancement of the neocortex and a slight lag in cerebellar advancement. Conversely, the conservatively sized cerebellum, well adapted for the role it plays, may allow neocortical expansion without concomitant cerebellum size increases. The just-so story may read as follows: A fortuitous mutation in a regulatory gene adds an extra few hours of cerebellum development *in utero* to our early *Homo sapiens* protagonist, which in turn, allows supplementary connections with the neocortex, expanding cognitive and motor abilities alike. Erectoids and neandertaloids were adept at survival and well adapted to their environments but did not possess the cognitive skills evident in modern *Homo sapiens*. A release in cerebellum/cerebrum interconnectedness may have played a part in this cognitive advancement.

Cortical asymmetries have been reported in macaques (Falk et al., 1990), great apes (LeMay and Geschwind, 1975), fossil hominins, and modern *Homo sapiens* (LeMay, 1976). In Chapter 2, I discuss recent neuroimaging research that suggests that the cerebellum of modern *Homo sapiens* is also functionally lateralized. Linear assessment of my catarrhine sample did not reveal statistically significant differences between the left and right lobes of the cerebellum on endocasts. Shape data reveal that macaques and apes have asymmetrical shapes but the pattern of left/right asymmetries

is different in each group. At this stage, it is difficult to interpret what these shape differences may mean, if anything.

My sample of human endocasts is too small to make any statistical assessments but Fig. 4-5 shows that the lateral cerebellum point, the occipital cerebellum and basion are in different locations in the right and left shapes. In a large MRI-based study, Falk et al. (2005) demonstrated significant zones of expansion in the left antero-lateral and right medio-posterior portions of the cerebellum of right-handed males and the right antero-lateral portions of the cerebellum in left-handed females. These expanded zones are part of the neocerebellum, which may have strong interconnections with areas of the neocortex that have strong language and higher cognitive functions.

Macaques are shown to be the most sexually dimorphic species in the data set utilized in this dissertation. Males tend to be larger than females even when cerebellum size is controlled for allometry. Also the shapes of male and female macaque posterior cranial fossae and basicrania are distinct. Females tend to show medio-lateral expansion and antero-posterior compression compared to males. However, it is unclear whether these results reflect any functional differences between the male and female macaque brains. Others have suggested that life in a highly competitive, polygynous environment may influence male and female behavior differently. Falk et al. (1999) suggest that the demands of this type of environment may select for visuospatial processing power in male monkeys. The cerebellum is also, undoubtedly, implicated in these types of behaviors.

Future research on cerebellar lateralization and sexual dimorphism is clearly justified and needed. Larger samples of ape and human endocasts, be they real or

virtual, would greatly improve the power of the statistical studies reported in this dissertation. Adding to both the primate and fossil hominin sample size would allow more fine-grained analyses of evolutionary trends within the catarrhine and more specifically, the hominin lineages.

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