Cerebellum and Human Evolution: A Comparative and Information Theory Perspective

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C. Huang and Robert E. Ricklefs

Abstract

The cerebral cortex occupies a prominent place in the social brain hypothesis, which posits that human brain evolution has largely been shaped by social interactions in an increasingly more complex group structure and the associated cognitive tasks at the cerebral cortical level. Social interactions are adaptive behaviors in responses to selection pressure and are also the sources of selection pressure. Complex social interactions both require and foster communication. To communicate and transmit information, individual members of the group must acquire a common language of communication, most certainly via imitation. Hurley has recently proposed a shared circuits model for imitation. This model has implicated many cerebral cortical structures, including the mirror neuron system. In this model, a basic element supporting complex behavior leading to imitation is *active perception*. Neuroplasticity mechanisms in the cerebellum and particularly in the neocerebellum may be the major provider of this critical function such that *active perception* constitutes part of the cerebellar function of procedural learning, or vice versa. In this chapter, the role of the cerebellum in the evolution of complex behaviors is examined. Data from fish, amphibian, reptile, bird, and mammal are summarized to show a phylogenetic expansion of the neocerebellum to interact with the neocortex. Within mammals, there is a progressive increase in the capacity of the cerebellum to code and process information from mouse, rat, cat, rhesus monkey, and human. The increasingly expanding interactions between the cerebral cortex and the

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cerebellum operating with a high information coding and processing capacity may uniquely contribute to the acquisition of complex behavior including language and communication for social interaction – a major hallmark of human evolution.

Introduction

Modern humans engage in sophisticated social interactions, including division of labor, long-term planning, and recreation, all of which support human culture and its continued evolution. The influential social brain hypothesis posits that the human evolution has largely been shaped by the increasingly more complex social structure over the course of primate evolution. In particular, the size of the neocortex in social primates increases in direct relation to the number of members in a typical social group for that species (Dunbar and Shultz 2007).

Social interactions require language and communication. The interactive nature of communication dictates that all members in the social group understand and then use the same language to exchange information, implying that imitation is critical. A model for imitation is the shared circuits model (SCM) (Hurley 2008). This model has implicated several cerebral cortical structures including the mirror neuron system (Rizzolatti et al. 1988, 2002). Already prominent as the most basic element of the SCM (layer I in the SCM model), however, is *active perception*. Known functions and patterns of anatomical connectivity of the cerebellum suggest that it may be a critical component, if not the major center, of all types of *active perception*. To assess the role of the cerebellum in the evolution of language and social communication, a comparative study was carried out to examine the evolution of the cerebellum for clues that may address the SCM and in particular *active perception* and its roles in imitation and other complex behaviors. As language and communication are largely supported by the function of cerebral cortical structures and that human communication is uniquely characterized by high information content, the present emphasis is the evolution of cerebro–cerebellar relationship and the information coding capacity of the cerebellum. These findings are discussed with a focus on potential contributions of the cerebellum to human evolution and to complex behaviors as adaptive responses to selection pressure.

Comparative Changes in the Cerebellum and Information Processing

Estimated Comparative Changes in the Volume Fraction of the Neocerebellum

All the data used here have been published previously. Data for cerebellar volume fractions of 95 species of fish with a broad sampling were obtained from Bauchot et al. (1989); Lisney and Collin (2006); Platel et al. (1977); Wagner (2001);

Yopak et al. (2007). Volume fractions of ten amphibian species were obtained from Taylor et al. (1995), and 35 species of reptiles from Platel (1976). Cerebellar volume fractions for 141 species of birds, with broad taxonomic sampling, were obtained from Portmann (1947), who reported the volumes of the brainstem, optic lobes, cerebellum, and striatum. Additional data from Iwaniuk and Hurd (2005); Iwaniuk et al. (2005, 2006); Kalisinska (2005) brought the total to 247 species of birds. Cerebellar volume fractions for mammals were obtained from Stephan et al. (1981) as summarized in Clark et al. (2001). This data set includes 75 species of insectivores and primates, with data on the volume as well as volume fractions of the medulla, mesencephalon, diencephalon, telencephalon, and cerebellum. Additional data were obtained from Knudsen et al. (2002); Marino et al. (2000); Pilleri (1967); Pirlot and Kamiya (1985).

The detailed data analysis have been reported. Briefly, the volume (assumed to be proportional to mass) of a component of the brain can be related allometrically to the volume of the entire brain by a power relationship of the form (e.g., see Barton and Harvey 2000)

$$V_{\text{comp}} = a \cdot V_{\text{brain}}^{b} \tag{59.1}$$

where the value of the exponent [b] describes the rate of increase in the component relative to the whole brain. With a logarithmic transformation, Eq. 59.1 becomes

$$\log V_{\text{comp}} = \log a + b \log V_{\text{brain}} \tag{59.2}$$

In Fig. 59.1, the logarithms of the volumes of the cerebellum and the telencephalon increase approximately linearly as a function of the logarithm of the total volume of the brain in fish, amphibians, reptiles, birds, and mammals. A regression analysis showed that [b] is close to 1 (Table 59.1). Thus, both the cerebellum and the telencephalon remained a constant proportion of the brain over the whole range of size (isometry) and a good approximation for Eq. 59.1 becomes

$$V_{\text{comp}} = a \cdot V_{\text{brain}} \tag{59.3}$$

where [a] equals [$V_{\text{comp}}/V_{\text{brain}}$], or [$F_{\text{comp}}$], the volume fraction of the brain component in question.

An analysis of covariance was next used to determine the relationship of $\log_{10}$-transformed component size to brain size with the different taxonomic groups (fish, amphibian, reptile, bird, and mammal) as fixed effects in the model. To facilitate comparison among animals with widely varying brain volumes, the fractions that the cerebellum and telencephalon constitute of whole brain were also examined (Fig. 59.2).

For the cerebellum, the interaction term between brain size and taxon was significant ($F = 4.0$, df $= 4{,}426$, $P = 0.004$), but it explained less than 0.1% of the total variance and the interaction was deleted from the model. Thus, the

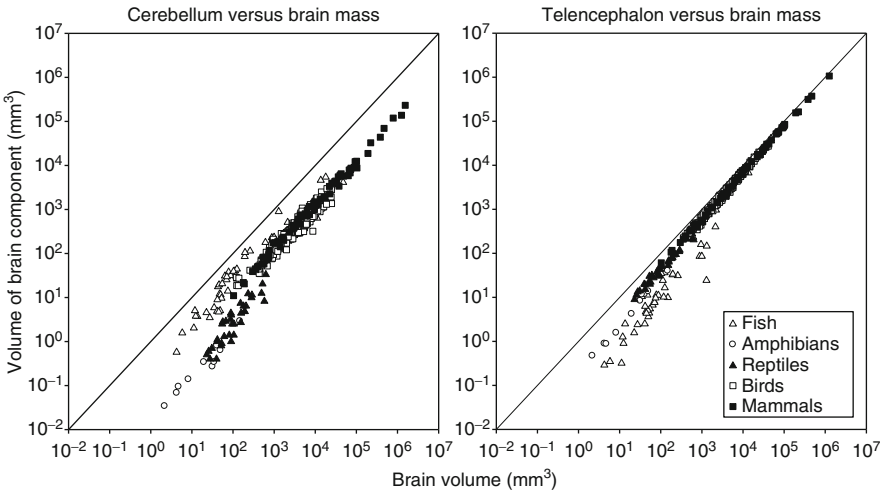

Fig. 59.1 The volume (assumed to be proportional to mass) of the cerebellum (*left*) and the telencephalon (*right*) as a function of the total volume of the brain in fish, amphibians, reptiles, birds, and mammals

Table 59.1 Volume fractions (assumed to be proportional to mass fractions) of the telencephalon, cerebellum, and the neocerebellum in five classes of vertebrates, and the means and standard deviations of [F_{cbl}] and [F_{telen}]. Note: *SE* = standard error of the estimate, *SD* = standard deviation of the distribution of species values. This method of estimation does not allow the determination of values for the SD of f_{neocbl}

	Fish	Amphibians	Reptiles	Birds	Mammals
B	1.220	1.112	0.969	1.047	1.049
SE	0.046	0.035	0.024	0.008	0.004
F_{telen} (telencephalon as a fraction of whole brain)					
Mean	0.185	0.243	0.430	0.631	0.683
SD	0.176	0.049	0.056	0.084	0.085
F_{cbl} (cerebellum as a fraction of whole brain)					
Mean	0.274	0.016	0.029	0.119	0.128
SD	0.141	0.004	0.013	0.034	0.021
f_{neocbl} (neocerebellum as a fraction of cerebellum)	0.0409	–	–	0.1109	0.5805

cerebellum/brain relationship was treated as having parallel slopes within each of the vertebrate classes. The common slope of the logarithmic cerebellum/brain relationship was 0.967 ± 0.010 se ($P < 0.0001$), which was close to but significantly less than 1 (isometry). Thus, the volume fraction of the cerebellum (as a fraction of the whole brain) decreased slightly with increasing brain size. Overall, the analysis of covariance explained 98.1% of the total variance in cerebellar volume ($F = 4460$, df = 5,430, $P < 0.0001$).

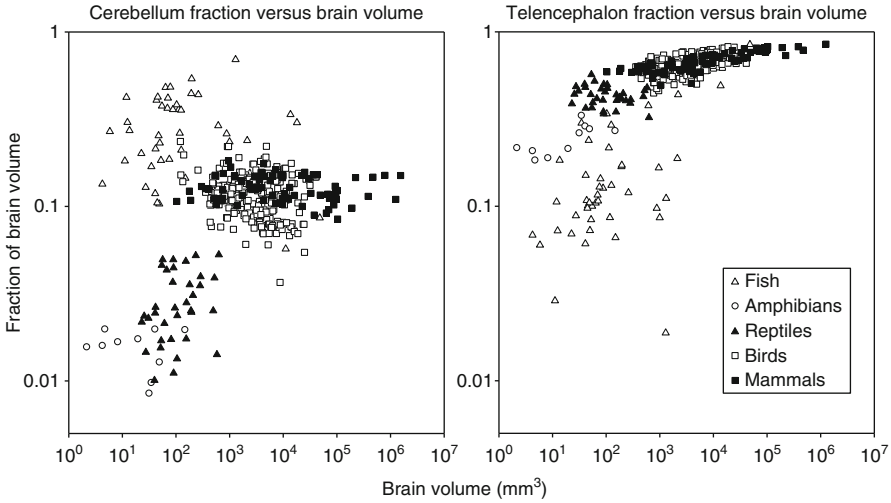

Fig. 59.2 The volume fraction of the cerebellum (*left*) and the telencephalon (*right*, as a fraction of the total volume of the brain) in fish, amphibians, reptiles, birds, and mammals

For the telencephalon (striatum in birds), the interaction term between brain size and taxon was significant ($F = 17.4$, df = 4,319, $P < 0.0001$), but explained only 0.2% of the total variance. An initial analysis of the telencephalon/brain relationship was made assuming parallel slopes for each of the groups. Accordingly, the common slope of the logarithmic telencephalon/brain relationship was 1.088 ± 0.010 SE ($P < 0.0001$), which significantly exceeded 1. Thus, the telencephalon fraction (as a fraction of the whole brain) increased with increasing brain size. Overall, the analysis of covariance explained 99.0% of the total variance in telencephalon volume ($F = 6272$, df = 5,323, $P < 0.0001$).

Table 59.1 is a summary showing that the volume fraction of the cerebellum [F_{cbl}] decreased sharply from 0.274 in fish to 0.016 and 0.029 in amphibians and reptiles, respectively, followed by an increase to 0.119 and 0.128 in birds and mammals, respectively. By contrast, the volume fraction of telencephalon [F_{telen}] increased progressively from fish (0.185), to amphibians (0.243), reptiles (0.43), birds (0.631), and mammals (0.683). Values of [F_{cbl}] were statistically indistinguishable for birds and mammals (Table 59.1). The same was true for [F_{telen}]. In Fig. 59.3, the volume fraction of the cerebellum (as a fraction of the whole brain) in mammals and in birds remained at 10–15% of the overall volume of the brain as the brain increased in size. This observation was consistent with the analysis of (Clark et al. 2001). The invariance of [F_{cbl}] in birds and mammals is remarkable despite the absence of morphologically discernable cerebellar hemispheres in the bird cerebellum (but see Brodal et al. 1950) and despite the variation of the cerebellar hemispherical fraction from ~50–60% in typical mammals to 90–95% in human (Ghez 1991; Ito 1984). In the mammalian cerebellum, the lack of comparative change in [F_{cbl}] contrasts sharply with the findings on the comparative changes at the cellular and synaptic level (see later).

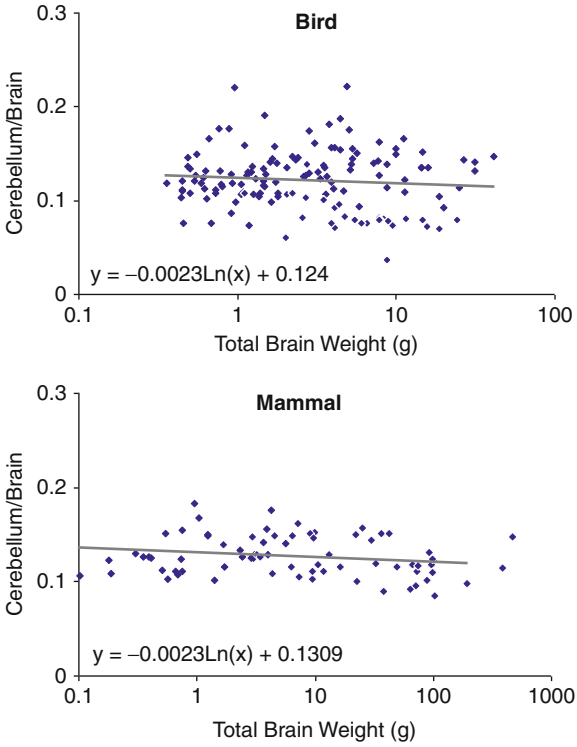

Fig. 59.3 Volume fraction of the cerebellum (as a fraction of the whole brain) remains relatively constant with increasing brain volume

To estimate the size of the neocerebellum as a fraction of the cerebellum, an assumption was made: the volume of the various areas or subdivisions of the cerebellum dedicated to the analysis of information from the telencephalon and those from "other" brain structures should be proportional to the size of afferent projections from the telencephalon and "other" brain structures, respectively, or,

$$F_{cbl} = g_t \cdot F_{telen} + g_o \cdot F_{other} \tag{59.4}$$

In Eq. 59.4, $[F_{cbl}]$, $[F_{telen}]$, and $[F_{other}]$ are the volume fractions, $[g_t]$ and $[g_o]$ are the appropriate proportionality constants with their magnitudes reflecting the influence of the telencephalon and other afferent brain structures, respectively, on the volume fraction of the different subdivisions of the cerebellum. This assumption is supported by several lines of evidence. First, unlike the cerebral cortex, the cerebellar cortex contains no cortico-cortical pathways or cortical regions for the analysis of information from other areas of the cerebellar cortex. A given circumscribed area of the cerebellum is connected with an extra-cerebellar target via dedicated connectivities (Ramnani 2006; Strick et al. 2009; Sturrock 1989). Detailed results from neuroanatomical tracing studies suggest that the cerebral cortical area that is the main target of each output channel from the cerebellum is also the major source of input to that channel. Thus, a closed-loop circuit would best

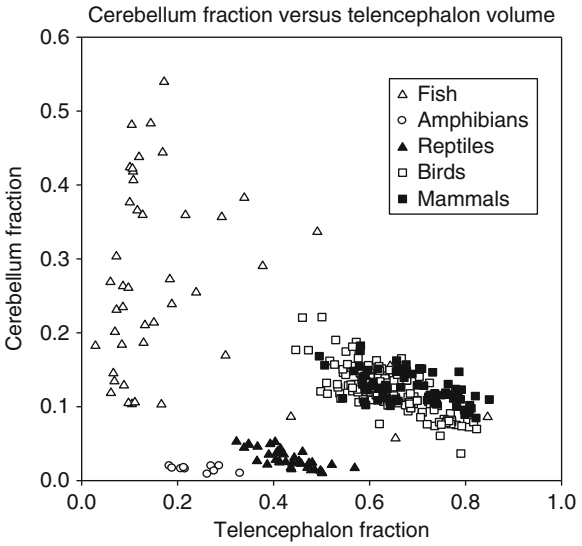

Fig. 59.4 The cerebellar volume fraction (of the whole brain) as a function of telencephalon volume fraction (also of the whole brain) in fish, amphibians, reptiles, birds, and mammals

represent the major architectural unit of cerebro–cerebellar interactions. Second and consistent with the above idea, the local cerebellar cortical synaptic circuitry forms a corticonuclear complex and is everywhere the same within the cerebellum, suggesting that cerebellar function expressed by the input–output transfer function is everywhere the same within the cerebellum (Ito 2006). If these broad assumptions are justified, it follows then that the volume fraction of the neocerebellum (as a fraction of the cerebellum) may be estimated when the proportionality constants $[g_t]$ and $[g_o]$ can be evaluated. This is accomplished first by recalling the normalization statement,

$$F_{cbl} + F_{telen} + F_{other} = 1 \tag{59.5}$$

Substituting (Eq. 59.5) into (Eq. 59.4) to eliminate F_{other},

$$F_{cbl} = [(g_t - g_o)/(1 + g_o)] \cdot F_{telen} + [g_o/(1 + g_o)] \tag{59.6}$$

To estimate $[g_t]$ and $[g_o]$ for each class of animal, a regression analysis of $[F_{cbl}]$ was carried out based on Eq. 59.6 (Fig. 59.4). The slope of the regression yielded estimates of $[(g_t - g_o)/(1 + g_o)]$ and the intercept yielded estimates for $[g_o/(1 + g_o)]$. Values of the slope and intercept were then used to compute $[g_t]$ and $[g_o]$, which, in turn, made it possible to further estimate $[g_t\, F_{telen}]$. This represented the portion of the cerebellum that may be dedicated to the telencephalon, which was, by definition, the neocerebellum (f_{neocbl} in Table 59.1).

For fish, amphibian, and reptile, the values of $[f_{neocbl}]$ were $\leq 4\%$. The cases of the bird and the mammalian cerebellum (particularly the primate) are of interest, as these classes of animals are considered by behavioral scientists to exhibit

considerably more complex behaviors and have been the subjects of various investigations in cognitive function (Briggs et al. 2002; Emery and Clayton 2004). Complex behaviors in birds and mammals are consistent with the relatively high values of [F_{telen}] in mammals and in birds compared with those in amphibians and reptiles (Fig. 59.4). In addition, the slope [$(g_t - g_o)/(1 + g_o)$] and the intercept [$g_o/(1 + g_o)$] in Fig. 59.4 for birds and mammals were generally larger than those in amphibians and reptiles. The value of [f_{neocbl}] was, on average, higher in mammals (~58%) than in birds (~11%). The lower [f_{neocbl}] in birds was consistent with the observation that the bird cerebellum did not have visually noticeable cerebellar hemispheres at the gross morphological level. These results also lend support to the hypothesis that the transformation of the cerebellum toward being a general-purpose computational engine may have begun in a common ancestor of birds and mammals. The higher [f_{neocbl}] in mammals suggest that full attainment as a general-purpose computational engine, however, is most evident in the mammalian cerebellum.

Comparative Changes in the Number of Granule-Cell-Purkinje-Cell (gcPc) Synapses in Mammals

All data used here have been published previously. The detailed data analysis has also been reported. Briefly, the average number of gcPc synapses per single granule cell was estimated by dividing the average parallel fiber length with the average inter-varicosital distance (Huang et al. 1999). This approach entails several assumptions. One, there must be a one-to-one correlation between synapses and synaptic varicosities. This assumption is supported by results from combined Golgi and electron microscope studies of the cerebellar parallel fibers (Harris and Stevens 1988; Palay and Palay 1974; Xu-Friedman et al. 2001). Two, the synapses between granule cells and inhibitory neurons may be ignored by assuming that all the synapses on the parallel fibers are gcPc synapses. This assumption is also well supported (Huang et al. 2006a; Palay and Palay 1974; Palkovitz et al. 1971c). Three, the gcPc synapses in the ascending segments of the granule cell axons may be ignored as they are far fewer (<7%) than those in the parallel fibers (Huang et al. 2006a; Napper and Harvey 1988a, b; but see (Gundappa-Sulur et al. 1999). Four, relatively constant values for inter-varicosital distances have been reported in studies of cerebellar fibers from a number of animal species (Harvey and Napper 1988; Palkovitz et al. 1971a, b, c; Napper and Harvey 1988a, b; Huang et al. 1999, 2006a; Pichitpornchai et al. 1994; Shepherd et al. 2002). This leaves the number of gcPc synapses per granule cell directly proportional to the parallel fiber length. Five, the status of the cerebellar synaptic network may change with age and may not be adequately defined by a snapshot from one single point in time. In general, the ages of the animals used in this analysis were not available in the literature. The number of gcPc synapses per mouse granule cell in Table 59.2 was derived from the 3-month-old mouse, in which this value was at its peak and approximately twice the magnitude at 6 months (Huang et al. 2006b). The data on parallel fiber

Table 59.2 *Comparative changes in cerebellar cellular and synaptic parameters*. The numbers in italics are calculated whereas others are measured data. Although the parallel fiber length of the cat has been estimated stereologically to be from 2 to 4 mm (Palkovitz et al. 1971a), the experimental data from Brand et al. (1976) are preferred. This puts the cat parallel fiber length at 6 mm. This value is longer than that of the rhesus monkey and may represent a special functional adaption. Still, note that the data on human cerebellum often stand out by a factor of ten or more from the rodents

	Mouse	Rat	Cat	Rhesus	Man	Reference
Body weight (g)	25	300	3,000	2×10^4	6×10^4	
Volume of cerebellum (ml)	0.05	0.3	2.4	9	150	
Volume of granule cell layer (ml)	0.0167	0.1	0.79	3	50	Mayhew (1991)
Volume of molecular layer (ml)	0.0167	0.1	0.79	3	50	Mayhew (1991)
Number of granule cells	2.7×10^7	10^8	2.2×10^9	6×10^9	1.1×10^{11}	Bedi et al. (1980), Fox and Barnard (1957), Ito (1984)
Number of Purkinje cells	2×10^5	4×10^5	1.25×10^6	3×10^6	3×10^7	Andersen et al. (1992), Andersen et al. (2003), Fan et al. (2001), Ito (1984), Woodruff-Pak (2006)
Density of granule cells (/ml of gcL)	1.6×10^9	10^9	2.8×10^9	2×10^9	2×10^9	
Density of Purkinje cells (/ml of cbl)	4×10^6	1.3×10^6	5.2×10^5	3.3×10^5	2×10^5	
Mean length of parallel fibers (μm)	2,000	3,000	6,000	5,700	10,000	Huang et al. (1999, 2006a)
Mean inter-varicosital distance (μm)	5	5	5	5	5	Harvey and Napper (1988, Napper and Harvey 1988a, b)
Number of gcPc synapses	1.1×10^{10}	6×10^{10}	2.6×10^{12}	6.8×10^{12}	2.2×10^{14}	
gcPc synapses per granule cell	400	600	1,200	1,140	2,000	
gcPc synapses per Purkinje cell	5.5×10^4	1.65×10^5	2.1×10^6	2.2×10^6	7.3×10^6	Harvey and Napper (1988), Napper and Harvey (1988a, b)
Density of gcPc synapses (/ml)	6.6×10^{11}	6×10^{11}	3.3×10^{12}	2.3×10^{12}	4.4×10^{12}	

Table 59.3 *Comparative changes in cerebellar cellular and synaptic parameters*. The values for the mouse are set at 1. The parameters and numbers in italics are calculated whereas others are measured data

	Mouse	Rat	Cat	Rhesus	Man
Body weight (g)	1	12	120	800	2,400
Volume of cerebellum (ml)	1	6	48	180	3,000
Volume of granule cell layer (ml)	1	6	48	180	3,000
Volume of molecular layer (ml)	1	6	48	180	3,000
Number of granule cells	1	3.7	81.5	220	4,000
Number of Purkinje cells	1	2	6.25	15	150
Density of granule cells (/ml)	1	0.6	1.75	1.25	1.25
Density of Purkinje cells (/ml)	1	0.33	0.13	0.08	0.05
Mean length of parallel fibers (μm)	1	1.5	3.0	2.9	5
Mean inter-varicosital distance (μm)	1	1	1	1	1
Number of gcPc synapse	1	5.5	236	620	20,000
Number of gcPc synapses per granule cell	1	1.5	3.0	2.9	5
Number of gcPc synapses per Purkinje cell	1	3	38	40	133
Density of gcPc synapses (/ml)	1	0.91	5.0	3.5	6.6

length in the human cerebellum were derived from the cerebellar hemisphere of a 50-year-old male with the methods previously described (Huang et al. 1999) and most likely did not represent a peak value but is in good agreement with estimated values reported previously (Smolyaninov 1966, also cited in (Ito 1984). Taken together, uncertainties introduced by variation in age and other factors were not likely to change the estimates in Table 59.2 by a factor of 2, whereas many of the microscopic parameters for the human cerebellum in Table 59.2 were much larger and differed by an order of magnitude or more from those of the other species. Once the number of gcPc synapses per granule cell has been determined, the total number of gcPc synapses was derived by multiplying this number by the number of granule cells. Granule cell counts were obtained from the literature for mouse, rat, cat, rhesus monkey, and human (see references in Table 59.2). Additional data on the mean length of parallel fibers and mean inter-varicosital distances were obtained from data in the literature (Brand et al. 1976; Harvey and Napper 1988; Huang et al. 1999, 2006b; Napper and Harvey 1988a, b).

In Table 59.2, only five primary parameters of the cerebellum must be measured (rather than calculated from other parameters): the volume of the cerebellum, the number of granule cells, the number of Purkinje cells, the length of parallel fibers, and the linear density of synapses along parallel fibers. Comparisons of measured or calculated parameters are facilitated by normalizing the values relative to the mouse (Table 59.3). For example, the body mass ratio from mouse to rat, cat, monkey, and man is 1, 12, 120, 800, and 2,400. This normalization separates the parameters in Table 59.3 into different categories. Category I parameters change proportionately with body mass: the volume of the cerebellum (1, 6, 48, 180, 3,000) and the total number of granule cells (1, 3.7, 81.5, 220, 4,000). The proportional relationship between the volume of the cerebellum and the number of granule cells

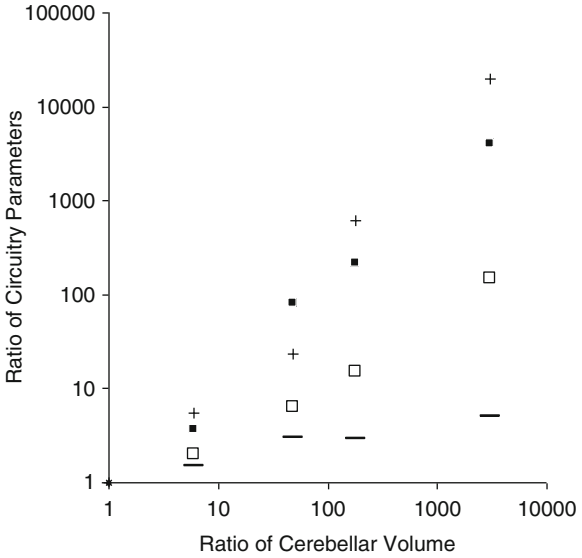

Fig. 59.5 *Ratio of cerebellar circuitry parameters (Y-axis) as a function of cerebellar volume ratio (X-axis).* The values for the mouse are set arbitrarily as one (mouse data as the origin). The other points are rat, cat, rhesus monkey, and man, in that order. Legends: number of gcPc synapses (*crosses*), granule cells (*small solid squares*), Purkinje cells (*larger empty squares*), and length of parallel fibers (*horizontal line segments*). Comparative changes of the parallel fiber length and the number of Purkinje cells are less steep than the number of granule cells, which scales proportionally with the volume of the cerebellum. The number of gcPc synapses varies more steeply than the number of granule cells. Both the X- and the Y-axes are logarithmic

has been noted previously (Fox and Barnard 1957; Ito 1984; Mayhew 1991). Category II parameters also increase with body mass, but less rapidly: number of Purkinje cells (1, 2, 6.25, 15, 150) and number of gcPc synapses per Purkinje cell (1, 3, 38, 40, 133). Category III parameters – ratios, densities, fiber lengths – with no obvious reasons to be related to body or brain volume but nonetheless increase with body mass: length of parallel fibers and the number of gcPc synapses per granule cell (both at 1, 1.5, 3, 2.9, 5), and the density of gcPc synapses per unit volume (1, 0.91, 5, 3.5, 6.6). Category IV parameters remain constant with body mass: density of granule cells per unit volume (1, 0.6, 1.75, 1.25, 1.25). This should be evident as the number of granule cells and the total cerebellar volume are both category I parameters (but see Lange (1975) who has reported a change of ~1/2 order of magnitude over five orders of magnitude of cerebellar volume). Another category IV parameter is the inter-varicosital distance (1, 1, 1, 1, 1) (Harvey and Napper 1988; Huang et al. 1999; Napper and Harvey 1988a, b; Palkovitz et al. 1971a, b, c; Pichitpornchai et al. 1994). One category V parameter, the density of Purkinje cells per unit volume (1, 0.33, 0.13, 0.08, 0.05), decreases with body mass. Finally, one category VI parameter, the number of gcPc synapses (1, 5.5, 236, 620, 20,000), increases faster than the volume of the cerebellum, particularly from monkey to human (Fig. 59.5). The increase from monkey to human (32X) is largely

due to an increase in the number of granule cells (18X), together with an increase in the length of parallel fibers (1.7X). The number of gcPc synapses is of potential interest as the capacity of information storage in brain systems has been suggested to be of the order of 1–2 bits per synapse (Chklovskii et al. 2004).

Summary

Results of experimental measurements at the gross morphological level have shown that amphibians and reptiles have very small cerebellum (<3% of the total brain volume). The volume fraction of the cerebellum increases to 10–15% of the whole brain in mammals and in birds. The neocerebellum in fish, amphibians, and reptiles is likely to be insignificant. Birds (neocerebellum at ~11% of the whole cerebellum, on average) and mammals (neocerebellum at ~58%, on average) have significantly larger neocerebellum fractions compared with all other animals. Even though the volume of the cerebellum largely remains proportional to the telencephalon in mammals such that the volume fraction of the cerebellum remains constant, the number of gcPc synapses increases dramatically according to 1:5.5:236:620:20,000 from mouse, rat, cat, rhesus monkey, to human.

The Role of the Cerebellum in Complex and Adaptive Behavior

Mammals, which as a group have generally larger neocerebellum than birds, also exhibit the largest repertoire of complex behaviors. In mammals, humans exhibit the most complex behaviors and the human neocerebellum accounts for 90–95% of the cerebellar volume (Ghez 1991). Do the cerebellum and its evolution play any important role in adaptive and complex behavior? This question is examined in three sections: (1) the role of the cerebellum in adaptive behavior, (2) the role of information-processing capacity in complex behavior, and (3) the implications of comparative changes of the cerebellum in complex and adaptive behavior.

Adaptive Behavior and the Cerebellum: Action Perception and Learning and Memory

Much of the complexity in human behavior, particularly modern human behavior, is adaptive in nature and is acquired after birth. The emergence of adaptive changes in behavior is dependent upon how the brain responds to novel stimuli from the environment. In *active perception*, the brain may encounter for the first time a novel sensory input from the environment, analyze it, and then make modifications on brain structure and function via intrinsic mechanisms of neuroplasticity. On subsequent encounter with the similar sensory stimuli, a modified and more experienced brain can make better use of the afferent information and generate better responses

in order to improve upon a behavior or action. In the shared circuits model (SCM), active perception forms part of the foundation for more complex behavior such as imitation (Hurley 2008).

In many known cerebellar operations, adaptive cerebellar neuroplasticity allows new behavioral solutions to emerge in response to novel or unexpected stimuli that have become repetitive. Detailed cellular and molecular mechanisms of cerebellar neuroplasticity are known and the part concerning the gcPc synaptic circuitry is particularly well known (Hansel et al. 2001; Ito 2006; Jorntell and Hansel 2006). A generally accepted hypothesis is that cerebellum-bound climbing fibers carry error messages or information about an unexpected event to the Purkinje cell (e.g., see Apps and Garwicz (2005); Bloedel and Bracha (1998)). These messages contribute to associative learning by providing information on timing and other properties of the error message or the unexpected event of interest. An important function of climbing-fiber discharges is to mark the time for Purkinje cells to search for coincidental mossy-fiber events, whose associated gcPc synapses are then subjected to long-term depression (LTD). After many encounters with such events, changes in behavior can occur. The gradual acquisition of newly learned behavior or response to such an event is often accompanied by reduction or absence of climbing-fiber discharges, signaling that error messages are no longer needed. In this way, the cerebellum helps to generate the most appropriate responses to the novel stimuli.

For example, normal vestibulo-ocular reflex (VOR) causes eye movement in a direction opposite to the angular acceleration of the head so that there is no retinal slip and the fovea can better track the visual target of interest. In a subject wearing magnifying or minifying glasses, a "learned" VOR with a different gain can develop with time so that once again retinal slip can be minimized or eliminated (Blazquez et al. 2003). Here the archicerebellum (mainly dedicated to the vestibular system) and the vestibular nuclei, which are phylogenetically related to the cerebellar nuclei, accomplish this feat by learning-related cellular mechanisms which modify the details of the VOR neural circuitry and thereby the equations relating the direction of angular acceleration of the head to the direction of the eye movement. In the paleocerebellum (mainly dedicated to the spinal cord), the cerebellar neuroplasticity similarly modifies the equation relating muscle spindle length to contractile force of the skeletal muscle so that the stretch reflex and other postural reflexes are appropriately and dynamically modulated to make way for, and indeed facilitate, purposeful movement (Ito 1984; Lisberger 1988). In the neocerebellum (mainly dedicated to the cerebral cortex), eyeblink conditioning is another example of such procedural learning in which a tone (as unconditioned stimulus) may have no biological significance at first but can quickly drive the eyeblink (as conditioned response) if the tone is paired in an associative manner with an air puff to the eye (Attwell et al. 2002; De Zeeuw and Yeo 2005; Thomson et al. 1997).

Cerebellar analyses of afferent information are therefore constantly modified in an interactive manner based on climbing-fiber discharges, leading to *active perception* supported by LTD and subsequent functional and structural changes within the gcPc synaptic system of the cerebellar cortex without affecting the peripheral

sensory mechanisms. It is therefore possible to view *active perception* and procedural learning as overlapping, if not identical, concepts. The cerebellum is therefore a major center for *active perception* of signals from the environment in the generation of adaptive behavior.

Complex Behavior and the Cerebellum: Information Coding and Processing Capacity

All animals are exposed to the same information from the environment. They ignore irrelevant signals from the environment, recognize and subsequently utilize biologically significant information in environmental signals, and generate complex behaviors via associative learning or *active perception* in order to avoid extinction. As the mammalian cerebellum evolves, it acquires granule cells at a rate faster than Purkinje cells while it gradually lengthens its parallel fibers (Fig. 59.5). Whenever prompted by a climbing-fiber discharge with an error message, higher granule-cell-Purkinje-cell ratio and longer parallel fiber would allow each Purkinje cell to search more exhaustively for coincidental mossy-fiber events (in reference to a climbing-fiber event) for the purpose of better associative learning. The enhanced sensitivity of the associative learning process leads to greater and more effective behavioral plasticity. The neocerebellum, which has a demonstrated ability to recognize biological significance in environmental stimuli based on associative learning principles (e.g., as in eyeblink conditioning), can be expected to be particularly important to cognitive behavior such as those in social interactions.

Relative to eyeblink conditioning, many other procedural learning processes involve considerably more complex movement sequences which require high information content for their execution. The same can be expected to procedural leaning involving cognitive behavior. Indeed, while social interactions including division of labor, long-term planning, and recreation may be observable in other animal societies such as those of social insects (recreation may be a noticeable exception in social insects but play is common in social mammals and can have social implications (Van Leeuwan et al. 2010)), the foremost feature that characterizes human culture, particularly modern human culture, from all other culture may be in its high information content in complex human behavior.

The mammalian cerebellum contains an enormous number of granule cells. Cerebellar granule cells can reach to >70% of all brain cells in a number of rodents and are likely to be even more in human (Herculano-Houzel et al. 2006). In humans, there is a massive mossy-fiber-granule-cell (mfgc) afferent system from the neocortex to the cerebellum with the collective afferents via the pons containing 40 million fibers (Leiner et al. 1989). Next to the corpus callosum, these fibers constitute one of the largest fiber tracts in the entire central nervous system. This is matched by an equally impressive gcPc synaptic system, estimated to contain 2.2×10^{14} synapses in the human cerebellum (Table 59.2). Marr (1969) has proposed that the massive cerebellar system provides a large capacity to code in detail all kinds of sensory information at the input stage in cerebellar information

processing. Data from eyeblink conditioning studies suggest that the gcPc synaptic system may offer storage for information on motor timing and the coordination of intricate movement sequences available for motor programming at the output stage as procedural or non-declarative memory via immediate recall without further involvement of climbing fibers (Ito 2006). A large cerebellar information coding and processing capacity can therefore improve the analysis and extraction of biological significance from environmental signals on the sensory side and support a more precise (and therefore information-laden) motor response including gesturing and speech motor control. In communication, it is necessary that increases in the information coding and processing capacities for the analysis of subtle sensory cues are matched by appropriate increases in the generation of codes with which to execute movements with a capacity to express equally subtle cues. Comparative increases in the number of gcPc synapses (Tables 59.2, 59.3, Fig. 59.5) suggest, but do not prove, that humans are better supported in terms of information coding capacity which is needed for motor control precision in both the spatial and the temporal dimension. Examples of these high-information-content motor behaviors include the fine and skilled manipulation of voluntary movement sequences in upper limbs and their digits, gesturing and facial expression, the considerable speech motor control, as well as the willful manipulation of abstract symbols in the use of language and logic (think of them as mental gymnastics) (Molinari et al. 1997). With few candidate brain structures rivaling the cerebellum in the scope of its connectivities with other brain structures (Ramnani 2006; Strick et al. 2009), the capacity for information processing (Marr 1969), the ability to provide dynamic neuroplasticity (Hansel et al. 2001; Ito 2006; Jorntell and Hansel 2006), and the unique role serving both sensory analysis and motor programming (Bower 1997; Gao et al. 1996), the cerebellum is an underappreciated but ideal brain center supporting complex behaviors such as language and communication – the foundation of social interaction.

Comparative Changes of the Cerebellum and Behavior

The volume fraction of the cerebellum takes a significant reduction from fishes (~27%) to amphibians and reptiles (<3%). This is accompanied by a reduced role of the lateral-line system in locomotion and perhaps also the role of locomotion in survival (Videler 1993). For amphibians and reptiles, their smaller cerebellum is not likely to bring about significant active perception in behavior, including motor behavior. The volume fraction of the cerebellum jumps to 10–15% in birds and mammals. Although such increase in birds has been attributed to flying (Paulin 1993; Witmer et al. 2003), the increasingly more significant role of the neocerebellum is surely a more important factor leading to the expansion of the mammalian cerebellum. Within major cerebellar subdivisions, the neocerebellum fraction is insignificant in amphibians and reptiles but becomes larger in birds (11% of the cerebellum) and more so in mammals (58%). Indeed, in both birds and mammals, the expansion of the cerebellum is nearly proportional to the

telencephalon (Clark et al. 2001; Sultan 2002, Fig. 3). An interpretation of the constancy of the cerebellar fraction in birds and mammals (~10–15% of the whole brain) may be that the cerebellum serves as a general-purpose computational engine for the whole brain (Herculano-Houzel 2010; Herculano-Houzel et al. 2006, but also see Clark et al. 2001). In view of the role of the cerebellum in *active perception* and procedural learning, it may be further suggested that the nature of cerebellar computation is to provide the dimension of neuroplasticity. The larger neocerebellar fraction in mammals further suggests a role of cerebellar neuroplasticity in cerebral cortical function, including cognition. Comparative changes in the number gcPc synapses are also evident in mammals even though the volume fraction of the cerebellum remains constant. Increased number of gcPc synapses can enhance the sensitivity and effectiveness of climbing-fiber-related learning and neuroplasticity and improve the spatial and temporal precision of motor as well as cognitive behaviors in climbing-fiber-free cerebellar operations. These ideas help to underscore the significance of *active perception* and/or associative procedural learning in brain modeling as well as the role of information-processing capacity of the cerebellum in complex behavior and its acquisition.

Cerebellum and Human Evolution

What aspect of being human is most prominent in human evolution? If complex behaviors in animals are effective to stave off extinction, then they should be interactive, preferably proportional, and adaptive in response to the changing environment. Practically for all species in the animal kingdom successfully surviving extinction, changes in their repertoire of behavior have kept pace with (the relatively slow) changes in environmental complexity over hundreds of millions of years. Humans may represent an exception in that human behavioral complexity has increased at a faster rate compared with most other animals and compared with changes in environmental stimuli since the appearance modern humans about two hundred thousand years ago (for examples in which human culture with advanced language and communication suffered catastrophic failures, see Diamond (2005)). The pace of this change may arguably be quickened in recent times. The reason for such increases in human behavioral complexity is in the relationship between selection pressure and response. Under selection pressure, a basic measure on the potency of a given behavioral response should be defined as how information content of the complex behavior is matched against information content of the environmental complexity. One reason for this exception, therefore, may be that human social interaction generated complex pressure which demands high-information-content responses with human language and communication as a major example. A second reason is that language and communication can also represent sensory stimuli which, in turn, further enrich the sensory world beyond what can be provided by environmental stimuli. The responses to social selection pressure, therefore, can become additional sources of selection pressure. Language

and communication are complex adaptive behaviors in response to the kind of selection pressure described in the social brain hypothesis (Dunbar and Shultz 2007), but they can foster further escalation of social and cultural evolution.

What is the fundamental difference between various adaptive behaviors exhibited in many animal species and complex adaptive behaviors such as human communication and language? Results of behavioral genetic studies in the domestication of fox suggest that adaptive behavior such as aggression can be manipulated significantly by selective breeding over a matter of mere 50–60 years (Kukekova et al. 2008). In the mean time, although many animal species have been domesticated for approximately 8–10,000 years or more and their genes manipulated exhaustively in selective breeding, they do not display complex behavior at the same level as humans. Chimpanzees with a genetic makeup more closely related to that of the humans than any other animals have been exposed to the human environment and even raised with humans since birth apparently are far less likely than humans to recognize and utilize the biological significance in cues from the environment (Smith 2003). The patterns of such limitations in many animal species are consistent with a lack of the required information-processing capacities in hardware. This hardware limitation, possibly manifested by a more limited gcPc synaptic system in the cerebellum, will surely lead to limitations in *active perception*, which, in turn, cast limitations on the types of complex behavior they can acquire, including imitation (but see Tomasello (2006)). Thus, low information capacities can support many types of adaptive behavior, but high information capacities are required for manifestation of complex adaptive behaviors. One such complex behavior may be imitation in which the quality of the imitated behavior may involve functions of error messages and the cerebellar gcPc system. In SCM, the extent in which the repertoire of complex behaviors can evolve is therefore dependent on *active perception* as well as the information coding and processing capacities (Hurley 2008). The human brain may be unlike the brain of many other animals in that it contains elements with significantly higher information coding and processing capacities.

What are the brain structures or systems that are likely to be important for supplying high information coding and processing capacities? The cerebellar information-processing system should rank high as such a brain structure (at least for procedural learning). Among the parameters in Table 59.2, the number of gcPc synapses is the one that shows the most comparative change, implying that the information coding and processing capacities of gcPc synapses are more responsive to selection pressure than other parameters in that table. The comparative expansion of the neocerebellum from fish, to amphibian, reptile, bird, and mammal strongly suggests that the mammalian cerebellum, and human cerebellum in particular, works in close association with cerebral cortical structures including those supporting imitation. As most of the afferent mossy fibers to the neocerebellum are cerebral cortical in origin, it is likely that information conveyed in such afferents are processed at the conscious level (whereas similar operations in the archicerebellum and the paleocerebellum are largely at the subconscious level).

A greatly expanded neocerebellum may be the basis of the ability to be conscious of and, therefore, better able to attend to the generalized "errors" or some unexpected events of interest. The expansion of the human neocerebellum and improved cerebro–cerebellar interaction may have further brought about a blending of cerebellar procedural learning and other mechanisms of declarative learning intrinsic to cerebral cortical structures. The result can be a hybrid memory and learning mechanism that involves both the cerebral cortex and the cerebellum routinely and simultaneously while operating at a high level of information coding capacity (Squire 2004). For example, the skill or lack of it in playing tennis, basketball, music instruments, and in writing this article is most likely the result of such hybrid learning. The tendency toward an ever-increasing information-processing capacity may have helped to elevate the quality of human consciousness in general and facilitated the evolution of human language and communication in particular (Zimmer 2010).

Conclusions and Future Directions

The observations on the coincidental increases in brain volume, social complexity, and cerebellar information coding capacity beg the question whether these increases are related by a causal relationship as have been suggested for the overall brain size and social complexity (Dunbar and Shultz 2007). To establish such a causal relationship would require considerable investigations in the future. In the shared circuits model (SCM), one level above *active perception* is imitation (Hurley 2008). Interestingly, imitation plays an important role in the acquisition of nearly all complex human behaviors. During the course of evolution, humans may have become more likely to imitate on account of a highly elaborated mirror neuron system and other related brain structures. Humans may also be better at imitation on account of a highly evolved cerebellar system that supports *active perception* and/or procedural learning with a large information coding capacity. The resultant impact of these ideas should be relevant to the evolution of the cerebellum as the center piece of the shared circuits model (SCM) and a key structure in imitation and other forms of complex behavior (Hurley 2008).

References

Andersen BB, Korbo L, Pakkenberg B (1992) A quantitative study of the human cerebellum with unbiased stereological techniques. J Comp Neurol 326:549–560

Andersen BB, Gundersen HJ, Pakkenberg B (2003) Aging of the human cerebellum: a stereological study. J Comp Neurol 466:356–365

Apps R, Garwicz M (2005) Anatomical and physiological foundations of cerebellar information processing. Nature Rev Neurosci 6:297–311

Attwell PJ, Ivarsson M, Millar L, Yeo CH (2002) Cerebellar mechanisms in eyeblink conditioning. Ann N Y Acad Sci 978:79–92

Barton RA, Harvey PH (2000) Mosaic evolution of brain structure in mammals. Nature 405:1055–1058

Bauchot R, Diagne M, Ridet JM, Bauchot ML (1989) The brain of rhyacichthys aspro (rhyacichthyidae, gobioidei). Jpn J Ichthyol 36:260–266
Bedi KS, Hall R, Davies CA, Dobbing J (1980) A stereological analysis of the cerebellar granule and Purkinje cells of 30-day-old and adult rats undernourished during early postnatal life. J Comp Neurol 193:863–870
Blazquez PM, Hirata Y, Heiney SA, Green AM, Highstein SM (2003) Cerebellar signatures of vestibule-ocular reflex motor learning. J Neurosci 23:9742–9751
Bloedel JR, Bracha V (1998) Current concepts of climbing fiber function. Anat Rec (New Anat) 253:118–126
Bower JM (1997) Is the cerebellum sensory for motor's sake, or motor for sensory's sake: the view from the whiskers of a rat? Prog Brain Res 114:463–496
Brand S, Dahl AL, Mugnaini E (1976) The length of parallel fibers in the cat cerebellar cortex. An experimental light and electron microscopic study. Exp Brain Res 26:39–58
Briggs NE, Sheeran LK, Shapiro GC, Goodal J (2002) All apes great and small, vol 1, African apes. Kluwer/Plenum, New York, pp 35–53
Brodal A, Kristiansen K, Jansen J (1950) Experimental demonstration of a pontine homolog in birds. J Comp Neurol 92:23–69
Chklovskii DB, Mel BW, Svoboda K (2004) Cortical rewiring and information storage. Nature 431:782–788
Clark DA, Mitra PP, Wang SS (2001) Scalable architecture in mammalian brains. Nature 411:189–193
De Zeeuw CI, Yeo CH (2005) Time and tide in cerebellar formation. Curr Opin Neurobiol 15:667–674
Diamond J (2005) Collapse. Viking Penguin, New York
Dunbar RIM, Shultz S (2007) Evolution in the social brain. Science 317:1344–1347
Emery NJ, Clayton NS (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes. Science 306:1903–1907
Fan H, Favero M, Vogel MW (2001) Elimination of Bax expression in mice increases cerebellar Purkinje cell numbers but not the number of granule cells. J Comp Neurol 436:82–91
Fox CA, Barnard JW (1957) A quantitative study of the Purkinje cell dendritic branchlets and their relationship to afferent fibers. J Anat (London) 91:299–313
Gao J, Parsons LM, Bower JM, Xiong J, Li J, Fox PT (1996) Cerebellum implicated in sensory acquisition and discrimination rather than motor control. Science 272:545–547
Ghez C (1991) The cerebellum. In: Kendel ER, Schwartz JH, Jessell TM (eds) Principles of neural science, 3rd edn. Appleton and Lange, East Norwalk
Gundappa-Sulur G, De Schutter E, Bower JM (1999) Ascending granule cell axon: an important component of the cerebellar cortical circuitry. J Comp Neurol 408:580–596
Hansel C, Linden DF, D'Angelo E (2001) Beyond parallel fiber LTD: the diversity of synaptic and non-synaptic plasticity in the cerebellum. Nat Neurosci 4:407–475
Harris KM, Stevens JK (1988) Dendritic spine of rat cerebellar Purkinje cells: serial electron microscopy with reference to their biophysical characteristics. J Neurosci 8:4455–4469
Harvey RJ, Napper RMA (1988) Quantitative study of granule and Purkinje cells in the cerebellar cortex of the rat. J Comp Neurol 274:151–157
Herculano-Houzel S (2010) Coordinated scaling of cortical and cerebellar numbers of neurons. Frontiers Neuroanatomy 4:1–8 (art 12)
Herculano-Houzel S, Mota B, Lent R (2006) Cellular scaling rules for rodent brains. Proc Natl Acad Sci 103:12138–12143
Huang C, Brown N, Huang R (1999) Age-related changes in the cerebellum: parallel fibers. Brain Res 840:148–152
Huang C, Miyamoto H, Huang R (2006a) The mouse cerebellum from one to thirty-four months: parallel fibers. Neurobiol Aging 27:1715–1718
Huang C, Wang L, Huang R (2006b) Cerebellar granule cell: ascending axon and parallel fiber. Eur J Neurosci 23:1731–1737

Hurley S (2008) The shared circuits model: how control, mirroring and simulation can enable imitation, deliberation, and mindreading. Behav Brain Sci 31:1–58
Ito M (1984) The cerebellum and neural control. Raven, New York
Ito M (2006) Cerebellar circuitry as a neuronal machine. Prog Neurobiol 78:272–303
Iwaniuk AN, Hurd PL (2005) The evolution of cerebrotypes in birds. Brain Behav Evol 65:215–230
Iwaniuk AN, Dean KM, Nelson JE (2005) Interspecific allometry of the brain and brain regions in parrots (psittaciformes): comparisons with other birds and primates. Brain Behav Evol 65:40–59
Iwaniuk AN, Hurd PL, Wylie DRW (2006) Comparative morphology of the avian cerebellum: degree of foliation. Brain Behav Evol 68:45–62
Jorntell H, Hansel C (2006) Synaptic memories upside down: bidirectional plasticity at cerebellar parallel fiber-Purkinje cell synapses. Neuron 52:227–238
Kalisinska E (2005) Anseriform brain and its parts versus taxonomic and ecological categories. Brain Behav Evol 65:244–261
Knudsen SK, Mørk S, Øen EO (2002) A novel method for the situ fixation of whale brains. J Neurosci Meth 120:35–44
Kukekova AV, Trut LN, Chase K, Shepeleva DV, Vladimirova AV, Kharlamova AV, Oskina IN, Stepika A, Klebanov S, Erb HN, Acland GM (2008) Measurement of segregating behaviors in experimental silver fox pedigrees. Behav Genet 38:185–194
Lange W (1975) Cell number and cell density in the cerebellar cortex of man and some other mammals. Cell Tissue Res 157:115–124
Leiner HC, Leiner AL, Dow RS (1989) Reappraising the cerebellum: what does the hindbrain contribute to the forebrain? Behav Neurosci 103:998–1008
Lisberger SG (1988) The neural basis for learning of simple motor skills. Science 242:728–735
Lisney TJ, Collin SP (2006) Brain morphology in large pelagic fishes: a comparison between sharks and teleosts. J Fish Biol 68:532–554
Marino L, Rilling JK, Lin SK, Ridgeway SH (2000) Relative volume of the cerebellum in dolphins and comparison with anthropoid primates. Brain Behav Evol 56:204–211
Marr D (1969) A theory of cerebellar cortex. J Physiol 202:437–470
Mayhew TM (1991) Accurate prediction of Purkinje cell number from cerebellar weight can be achieved with the fractionator. J Comp Neurol 308:162–168
Molinari M, Leggio MG, Silveri MC (1997) Verbal fluency and agrammatism. In: Schmahmann JD (ed) The cerebellum and cognition. Academic, New York
Napper RMA, Harvey RJ (1988a) Number of parallel fiber synapses on an individual Purkinje cell in the cerebellum of the rat. J Comp Neurol 274:168–177
Napper RMA, Harvey RJ (1988b) Quantitative study of the Purkinje cell dendritic spines in the rat cerebellum. J Comp Neurol 274:158–167
Palay SL, Palay V (1974) The cerebellar cortex: cytology and organization. Springer, New York
Palkovitz M, Mezey E, Hamori J, Szentagothai J (1971a) Quantitative histological analysis of the cerebellar nucleus in the cat. I. Numerical data on cells and on synapses, Exp Brain Res 28:189–209. In: Ito M (ed) The cerebellum and neural control. Raven, New York
Palkovitz M, Magyar P, Szentagothai J (1971b) Quantitative histological analysis of the cerebellar cortex in the cat. II. Cell numbers and densities in the granular layer. Brain Res 32:15–30
Palkovitz M, Magyar P, Szentagothai J (1971c) Quantitative histological analysis of the cerebellar cortex in the cat. III. Structural organization of the molecular layer. Brain Res 34:1–18
Paulin MG (1993) The role of the cerebellum in motor control and perception. Brain Behav Evol 41:39–50
Pichitpornchai C, Rawson JA, Rees S (1994) Morphology of parallel fibers in the cerebellar cortex of the rat: An experimental light and electron microscopic study with biocytin. J Comp Neurol 342:206–220
Pilleri GG (1967) The brain and behavior of delphinus delphis. Rev Suisse Zool 74:665–677
Pirlot P, Kamiya T (1985) Qualitative and quantitative brain morphology in the sirenian dugong erxl, Zeitschrift für zoologische. Systematik und Evolutionsforschung 23:147–155

Platel RR (1976) Comparative volumetric analysis of the main subdivisions of the brain in saurian reptiles. Journal für Hirnforsch 17:513–537
Platel R, Ridet JM, Bauchot R, Diagne M (1977) Brain organization of amia, lepisosteus, and polypterus: comparative morphology and quantitative analysis. Journal fur Hirnforsch 18:69–73
Portmann A (1947) Etudes sur la cerebralisation chez les oiseauz: II. Les indices intra-cerebraux. Atauda 15:161–171
Ramnani N (2006) The primate cortico-cerebellar system: anatomy and function. Nat Rev Neurosci 7:511–522
Rizzolatti G, Camarda R, Fogassi M, Gentilucci M, Luppino G, Matelli M (1988) Functional organization of inferior area 6 in the macaque monkey: II Area F5 and the control of distal movements. Exp Brain Res 71:491–507
Rizzolatti G, Fadiga L, Fogassi L, Gallese V (2002) From mirror neurons to imitation: facts and speculation. In: Meltzoff A, Prinz W (eds) The imitative mind. Cambridge University Press, Cambridge, MA, pp 247–266
Shepherd GMG, Raastad M, Andersen P (2002) General and variable features of varicosity spacing along unmyelinated axons in the hippocampus and cerebellum. Proc Natl Acad Sci 99:6340–6345
Smith V (2003) A chimp in the family: the true story of two infants – one human, one chimpanzee – growing up together. Marlowe, New York
Smolyaninov VV (1966) Stricture-functional models of certain biological system. In: Gelfand IM, Gurfinkel VS, Fomin SV, Cetlin ML (eds) Several characteristics in the organization of the cerebellum. Izdatelstvo nauka, Moscow, pp 203–267 (in Russian)
Squire L (2004) Memory systems of the brain: a brief history and current perspective. Neurobiol Learning Memory 82:171–177
Stephan H, Frahm H, Baron G (1981) New and revised data on volumes of brain structures in insectivores and primates. Folia Primatol 35:1–29
Strick PL, Dum RP, Fiez JA (2009) Cerebellum and nonmotor function. Ann Rev Neurosci 32:413–434
Sturrock RR (1989) Changes in neuron number in the cerebellar cortex of the aging mouse. J Hirnforsch 30:499–503
Sultan F (2002) Analysis of mammalian brain architecture. Nature 415:133–134
Taylor GM, Nol E, Boire D (1995) Brain regions and encephalization in anurans: adaptation or stability? Brain Behav Evol 45:96–109
Thomson RF, Bao S, Chen L, Cipriano BD, Grethe JS, Kim JJ, Thompson JK, Tracy JA, Weninger MS, Krupa DJ (1997) Associate learning. In: Schmahmann JD (ed) The cerebellum and cognition. Academic, New York
Tomasello M (2006) Why don't apes point? In: Enfield NJ, Levinson SC (eds) Roots of human sociality: culture, cognition and interaction. Berg, New York, pp 506–524
Van Leeuwan EJC, Zimmermann E, Ross MD (2010) Responding to inequalities: gorillas try to maintain their competitive advantage during play fights. Biol Lett (published online before print 7-14-2010, doi:10.1098/rsbl.2010.0482)
Videler JJ (1993) Fish swimming. Chapman & Hall, London
Wagner HJ (2001) Brain areas in abyssal demersal fishes. Brain Behav Evol 57:301–316
Witmer LM, Chatterjee S, Franzosa J (2003) Neuroanatomy of flying reptiles and implications for flight, posture and behavior. Nature 425:950–953
Woodruff-Pak DS (2006) Stereological estimation of Purkinje neuron number in C57BL/6 mice and its relation to associative learning. Neurosci 141:233–243
Xu-Friedman MA, Harris KM, Regehr WG (2001) Three-dimensional comparison of ultrastructural characteristics at depressing and facilitating synapses onto cerebellar Purkinje cells. J Neurosci 21:6666–6680
Yopak KE, Lisney TJ, Collin SP, Montgomery JC (2007) Variation in brain organization and cerebellar foliation in chondrichthyans: sharks and holocephalans. Brain Behav Evol 69:280–300
Zimmer C (2010) One hundred trillion connections. Sci Amer 304:58–63