*Michael G. Paulin*

Department of Zoology
University of Otago, New Zealand

# The Role of the Cerebellum in Motor Control and Perception

● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● ●

**Abstract**

The cerebellum has an important role in control and coordination of movements, but in some species, notably weakly electric fish of the family *Mormyridae*, anatomical, electrophysiological and behavioural evidence indicates that parts of cerebellar cortex are concerned with tracking movements of objects around the animal, rather than with controlling movements of the animal itself. The existence of such anomalies suggests that the cerebellum may not be exclusively, or even primarily, a structure for motor control. Evidence reviewed in this paper shows that the cerebellum is associated with sensory systems used for tracking movements of targets in the environment, as well as movements made by the animal itself, in all vertebrates, not just in a few isolated cases. The evidence indicates that the standard theory that the function of the cerebellum is control and coordination of movements only partially characterizes cerebellar function. The cerebellum may be better characterized as a tracking system, with an important role in control and coordination of movements because of an animal's need to track moving objects, to track its own movements, and to analyze the sensory consequences of movements in order to control movements. This theory not only predicts the known motor consequences of cerebellar dysfunction, it also predicts a specific kind of perceptual deficit caused by cerebellar dysfunction, namely an inability to accurately follow and predict trajectories of objects moving in the environment. A variety of behavioural and perceptual tasks in addition to motor control and movement tracking may require dynamical state estimation, and therefore may involve the cerebellum.

● ● ● ● ● ● ● ● ● ● ● ●

## Introduction

Willis (1621-1675) claimed that the firm consistency of the cerebellum implies that it 'imparts strength to the muscles' [Dow, 1970]. More recently it has been said that because cerebellar dysfunction causes obvious deficits in control and coordination of movements, but no obvious deficits in sensation or perception, the function of the cerebellum is to control and coordinate movements [e.g. Ito, 1984;

Ghez and Fahn, 1985; Llinas, 1985]. This reasoning, which equates the function of a part of a system with the deficits, which appear when the part is damaged or removed, is logically unsound and potentially misleading.

For example, when a stone shatters the windscreen on a car there may be obvious effects on the car's movements, but it would be a mistake to call the windscreen a 'motor control' device on this basis.

Under normal conditions the windscreen permits the driver to obtain sensory information, which is essential for controlling the vehicle. The motor deficits that arise from the damage are partly due to loss of this information and partly due to other effects of the damage. Occupants of the vehicle experience sensory and perceptual deficits that are not obvious to an outside observer.

An analogous mistake has not necessarily been made in understanding cerebellar function, but the possibility of such a mistake must be given serious consideration. Current widespread acceptance of the motor control theory is based on an impressive accumulation of supporting evidence, rather than on a critical evaluation of that theory in the light of all of the evidence. Some evidence, reviewed in this paper, is inconsistent with the motor control theory, and much of the supporting evidence is equivocal when one asks what might be expected on the basis of alternative theories. In recent years a number of researchers have pointed to a growing body of evidence that is not consistent with the idea that the cerebellum is only, or even primarily, concerned with controlling movements [e.g. Bullock, 1986; Liener et al., 1989, 1991; Bower and Kassel, 1990; Schmahmann, 1991].

Developmentally, the cerebellum is an elaborated sensory structure, which arises from the somatic sensory columns of the neural tube. The regions of the developing central nervous system that give rise to the cerebellum also give rise to the nuclei of the acousticolateralis and vestibular systems [Larsell, 1967, 1970]. Acousticolateralis and vestibular signals contribute to the control of movement, but even if they were used only for control of movements we should be reluctant to refer to the associated structures in the medullary wall as 'motor' areas. In fact, they are clearly involved in sensation and perception as well as in motor control. So is the cerebellum. This is particularly striking in *Gnathonemus petersii*, the 'elephant nosed' fish, which has a spectacularly hypertrophied cerebellar cortex associated with the fish's active electric sense [Bell, 1986; Bell and Szabo, 1986]. One of the main aims of this paper is to show that an association of the cerebellum with certain types of sensory systems, analogous to that seen in the weakly electric fish, occurs in all vertebrates including humans.

In this paper I re-examine reports concerning the gross morphology, neuroanatomy and neurophysiology of the cerebellum and behavioural correlates in a wide range of vertebrates. Differences between species, which are striking when viewed in relative isolation (such as a comparison between *Gnathonemus* and *Homo*), can be seen as variations on a theme when viewed in the larger context. In the final section, I will attempt to elucidate that theme and suggest a new approach to understanding cerebellar function, in which the cerebellum is seen as a device for tracking movements, rather than for controlling them *per se*. More generally, I will argue, the cerebellum is capable to tracking and predicting states of dynamical systems. This capability makes it indispensable for fine motor control, accurate tracking of moving targets, and perhaps a variety of other tasks as well.

### The Cerebellum of Cyclostomes

Cyclostomes are unspecialized filter feeders and parasites, with relatively undifferentiated central nervous systems and limited sensory and motor abilities. In hagfishes, the cerebellum is a commissure linking vestibular, acousticolateral and trigeminal sensory areas on each side of the medulla. Johnston [1901; quoted in Larsell, 1967] noted that large neurons in the medial region of the cerebellum in lampreys resemble neurons in the corresponding layer of the lateral line lobes, and both are similar to mammalian cerebellar Purkinje cells at an early stage of development. He recognized other neural elements of the cerebellum in lampreys as being modified from cells in the acousticolateralis area. There is no clear distinction between the acousticolateral area of the medullary wall and the cerebellum in lampreys.

According to Larsell, there are projections from the cerebellum to the ventral medulla and spinal cord in cyclostomes, indicating that the cerebellum contributes to movement control in these animals. There are also projections to midbrain mechanosensory, electrosensory and visual mapping regions, and there is a projection to the forebrain [Larsell, 1967]. Larsell's observations were based on limited normal material and have yet to be confirmed by modern experimental techniques, but they indicate that the major cerebellar input and output pathways found in mammals have homologs in cyclostomes. Differences in relationships of the cerebellum to other parts of the nervous system, between cyclostomes and mammals, may be accounted for largely in terms of expansion or atrophy of pathways in association with expansion and atrophy of sources and targets of fibres during evolution [Deacon, 1990].

The acousticolateralis areas of the medullary wall in cyclostomes mediate the flow of acousticolateralis signals to the midbrain and seem to be sensory filtering structures of some kind. The acousticolateralis areas are not considered part of the cerebellum, but this distinction is apparently based on assumptions about cerebellar function, i.e., that the cerebellum is for motor control and, therefore, structures not directly involved in motor control are not part of the cerebellum. Anatomically and

developmentally, the cerebellum and the acousticolateralis nuclei of cyclostomes are variations on a theme. This is true in other animals as well, as will be pointed out in subsequent sections, but the distinction between the cerebellum and 'cerebellar-like' structures in the medullary wall is less clear in cyclostomes than in other vertebrates. In cyclostomes, circuitry that is almost indistinguishable from cerebellar cortex is able to perform a sensory filtering function of some kind, which is not directly related to motor control. This does not allow a deduction about the general function of cerebellum, but it does indicate the capabilities of the kind of neural circuitry found in the cerebellum.

### The Cerebellum of Elasmobranchs

Elasmobranchs are a diverse group, which includes active predators, sluggish planktivores and sedentary bottom-dwellers that survive by simply waiting for prey to drift by [Kalmijn, 1982; Tricas, 1982]. Elasmobranchs generally have large brains and large cerebellums in comparison to similarly sized teleost fishes and amphibians, and their range of brain-body weight ratios overlaps the range of similarly sized birds and mammals [Northcutt, 1978]. Removing the entire cerebellar corpus in elasmobranchs has little effect on swimming, unless the underlying nuclei are also damaged [Smeets et al., 1983]. There is no correlation between agility and the relative development of the cerebellum among elasmobranchs [ibid.]. Paul [1982] reported that a cerebellectomized dogfish had a 'tendency to stall', and often bumped the sides of its tank because it 'failed to judge its turns accurately'.

Montgomery [1984] found that the dorsal octavolateral nucleus (DON) in elasmobranchs is a filter that rejects noise related to the animal's own activity from incoming electrosensory signals, before transmission to the midbrain. DON is not usually regarded as part of the cerebellum, but it has a cerebellar-like organization with an overlying molecular layer. Parallel fibres in this molecular layer come from a group of granule cells that also provide parallel fibres to the corpus of the cerebellum [Bodznick and Board, 1986]. Thus, the anatomical facts indicate that DON is a specialized part of the cerebellum. Whether this is accepted or not, Montgomery's work shows clearly that the version of cerebellar circuitry in DON acts as a sensory filter. This filtering operation is related to the animal's own movements, but not to control of those movements.

### The Cerebellum in Teleost Fishes

More than half of all vertebrate species are teleosts, and they exhibit exceptional diversity in brain structure [Lauder and Liem, 1983]. The African family *Mormyridae* is of particular interest. Mormyrids have extraordinarily large cerebellums. *Gnathonemus petersii*, for example has a brain-body weight ratio of 1:50 – the same as an adult human – largely due to an extraordinary hypertrophy of the rostral portion of the cerebellum, the valvula. The unfolded valvula of a 10-cm-long *Gnathonemus* is a ribbon about one metre long, the same as the total length of the unfolded cerebellum of a human [Bell and Szabo, 1986]. The valvula is not the only relatively enlarged part of the brain in mormyrids. The electroreceptive lateral line lobe, and the toral region of the midbrain are also enlarged [Bell and Szabo, 1986].

Mormyrids are weakly electric, using electrical pulses for spatial mapping and communication. The valvula, the caudal lobe and the electroreceptive lateral line lobe of the cerebellum in mormyrids are involved in electrolocation. The same brain structures are involved in electrolocation in another family of weakly electric teleosts, the South and Central American gymnotiformes. Many gymnotiformes have enlarged cerebellums, particularly enlarged valvulae, but the trend is not as extreme as in the mormyrids [Bastian, 1986]. Gymnotiformes are not closely related to mormyriformes and must have developed their electric sense independently [Bass, 1986].

A wide variety of modalities and response types is found among cerebellar purkinje cells in weakly electric teleosts. Many cells respond to external stimuli, and their response properties indicate that they monitor trajectories of objects in the surrounding water. In the cerebellum in gymnotids, most Purkinje cells that respond to an electrical stimulus prefer or even require the stimulus to move. Most have preferred target distances and preferred directions of movement. In some parts of the cerebellum, Purkinje cells show similar responses to visual stimuli, and visual and electric fields often coincide [Bastian, 1986]. Similar behaviour is found in cerebellar Purkinje cells in mormyrids [Bell, 1986]. Bullock [1986] notes: '… the cerebellum [of weakly electric teleosts] is working unceasingly, during behavioural rest, keeping track of exteroreceptive as well as proprioceptive input, far more than the truly motor centers of the brain'.

Bombardieri and Feng [1977] found evidence that the cerebellum of the gymnotid *Apteronotus albifrons* is essential for recognizing and/or tracking approaching stimuli. Apteronotus normally prolongs one or two cycles of its opercular breathing cycle if a metal object approaches. The reflex is abolished by local cooling of cerebellar cortex. The response can still be elicited by other stimuli, showing that the

deficit is in detecting or recognizing the approaching target, not in organizing the motor response.

The secondary nucleus of the electrosensory system in mormyrids is called the electrosensory lateral line lobe (ELL). The histology of the ELL resembles that of cerebellar cortex, and granule cells of the dorsal granular ridge provide parallel fibres to the caudal lobe of the cerebellum as well as to the ELL. Bell [1986] observed that the variations on the basic cerebellar circuit found in ELL and other so-called 'cerebellar-like' structures are similar to, and no more extreme than, the variations found in structures that are unquestionably regarded as cerebellar. The basis for regarding ELL as 'cerebellar-like' rather than simply 'cerebellar' seems to be that it is apparently a sensory filtering structure, but the cerebellum is assumed to be involved only in motor control.

The function of ELL in mormyrids is similar to the function of the dorsal octavolateral nucleus in elasmobranches: it filters signals en route to the midbrain. Mormyrids have three different types of electroreceptors, which are the initial stages of three separate but parallel electrosensory pathways. The secondary nuclei on two of these pathways, the ampullary and mormyromast pathways, perform filtering operations that depend on accurate information about the fish's own body position and movements. These nuclei have cerebellar-like anatomy. The secondary nucleus on the third pathway, the knollenorgan pathway, filters signals by simply blocking incoming signals while the fish discharges its electric organ. This nucleus does not receive information about the fish's body position and movements, and it does not have cerebellar cortex-like anatomy [Bell and Szabo, 1986]. These facts indicate that cerebellar cortex-like organization of parts of the medullary wall in these fish is not due to a developmental or evolutionary constraint (because the secondary nucleus of the knollenorgan pathway lacks this organization); rather, it reflects an ability of this kind of circuitry to perform some kind of signal analysis related to movements.

Other aspects of cerebellar function in teleosts have received less attention than cerebellar involvement in electroreception. Cerebellar ablation experiments in teleosts have provided equivocal and sometimes contradictory evidence about the involvement of cerebellum in movement control, with some authors reporting disturbances of equilibrium and others reporting no effect [Paul, 1982]. In fish trained to distinguish sounds of a different frequency, cerebellectomy caused a loss of the ability to locate the source of a particular sound, even though conditioned reflexes that demanded only that a sound be detected were not affected [*ibid*.].

*The Cerebellum in Amphibians*

The cerebellum in terrestrial amphibians is very small and simple, both in gross morphology and neuroanatomy, in comparison to the cerebellum of other vertebrates. Llinas and Hillman [1969] regarded the cerebellum in frogs as primitive on this basis. This is incongruous with the view that the cerebellum is a motor control device. Posture, balance and movement control problems should be compounded in the transition from free-swimming to tetrapod terrestrial locomotion. On the other hand, navigation and orientation are more difficult in a three-dimensional environment, especially where landmark cues are poor. That is, it is easier to control movements in a water environment, but more difficult to determine your position and orientation in that environment. Terrestrial amphibia not only have relatively small cerebellums in comparison to other aquatic vertebrates, they have relatively small cerebella when compared to their own aquatic forms. The cerebellum of the urodele amphibian *Triturus*, for example, shrinks during metamorphosis from the aquatic to the terrestrial form [Larsell, 1967].

*The Cerebellum in Reptiles*

Locomotion in chelonians (turtles, terrapins and tortoises) involves only the appendicular skeleton, as compared to other vertebrates in which the axial skeleton plays a major role in locomotion. The medial region of the cerebellar corpus is greatly reduced in chelonians. This may be because (as some investigators have suggested) the medial region of the cerebellum is generally involved in controlling medial musculature, which is absent in chelonians, but it might also reflect the lack of sensory innervation of the carapace. The Japanese soft-shelled turtle, *Trionyx japonica*, is an instructive anomaly. *Trionyx* has a sensitive carapace, and the medial region of the cerebellar cortex in this animal is hypertrophied, forming a pendular structure which projects into the intracerebral ventricle. Larsell [1967] concluded from his examination of *Trionyx* that this unusual feature of the cerebellum is related to 'massive tactile sensory input' from the carapace, not to the limited motor capabilities of the dorsal musculature.

*The Cerebellum in Birds*

The cerebellum in birds is folded into a series of ten lobules, which Larsell [1967] homologized with the ten primary vermal lobules of the cerebellum in mammals. Birds have a great variety of locomotor styles: from fast, powerful runners incapable of flight, such as ostriches, to agile, rapid fliers, more or less incapable of walking or hopping, such as

hummingbirds. The lobules of the cerebellum differ in relative size in different bird species, and, although Larsell commented that the pattern of differences seems to reflect the importance of various motor systems in different species, his descriptions of individual species belies this. Pearson [1972] commented that the pattern of association between motor systems and cerebellar lobular development seems to have been a theoretical assumption that Larsell used to guide his interpretation of cerebellar anatomy, not a conclusion drawn from his observations.

Flourens' work on pigeons in the 19th century was seminal in the development of current ideas of the motor role of the cerebellum. He observed postural and locomotor disturbances in pigeons after cerebellar ablation. Damage to the outer part of the cerebellum did not lead to marked disturbances, which only became apparent when the deeper layers including the cerebellar nuclei were damaged. Later work by a number of other investigators showed that even the most severe of motor disturbances, which result from complete cerebellar ablations in pigeons, persist for only a few months [Pearson, 1972]. These results indicate that cerebellar output influences motor output in some way, but they do not indicate the normal function of the cerebellum. Acute effects of cerebellar ablation on posture and locomotion could be simply due to alterations in levels of tonic input to motor regions of the CNS.

Hummingbirds are very agile. Larsell [1967] pointed out that cerebellar regions related to the use of the legs are poorly developed in hummingbirds, which use their legs only for perching, and never for locomotion or manipulation. On the other hand, the legs of hummingbirds are not important sensory structures, and the poor development of corresponding regions of the cerebellum might be related to this. Lobule I, related to innervation of the tail, is relatively small in hummingbirds [Larsell, 1967]. The tail in hummingbirds is extremely important for controlling and stabilizing flight, but it does not seem to be an important sensory structure.

### The Cerebellum in Mammals

There is a large body of literature concerning the cerebellum in mammals, but most of this relates to a limited range of species, mainly rats, cats and primates. Mammals vary a great deal, and so does the mammalian cerebellum. My aim in this section is to point out that the 'anomalous' features of cerebellum – i.e. those indicating a direct involvement of cerebellum in non-motor tasks – that are so obvious in animals such as the weakly electric teleosts, are also obvious in mammals. In retrospect,

these 'anomalous' features are present even in the cerebellum of 'ordinary' laboratory animals.

As pointed out in previous sections, the acousticolateralis regions of the medullary wall in fish and amphibians resemble the cerebellum histologically, and in some species are difficult to distinguish from the cerebellum except on the grounds that they are clearly not motor control structures. If these structures are regarded as part of the cerebellum, as Bell [1986] suggested, then their mammalian homolog, the dorsal cochlear nucleus (DCN) should also be regarded as part of the cerebellum. The DCN, often described as having 'cerebellar-like' histology, is a secondary nucleus of the auditory system. Mugnaini et al. [1987] found a monoclonal antibody that uniquely labels cerebellar Purkinje cells and DCN Cartwheel cells. Berribi et al. [1990] reported that DCN has the same embryological origin as the cerebellum, and that the presence or absence of Cartwheel cells is exactly correlated to the presence or absence of cerebellar Purkinje cells in mutant mice. While it is clear that DCN is not 'ordinary' cerebellum, it is equally clear that it is a variation on the cerebellar theme, and a correct theory of cerebellar cortex ought to encompass DCN. The work of Bell and Szabo [1986] on weakly electric teleosts and Montgomery [1984] on elasmobranchs implies that a major role of DCN is to strip self-movement-related noise and distortions from incoming auditory signals.

*Monotremes*: Larsell [1970] noted that monotremes have very large and unusual cerebella, and: 'There are no differences in body form or in sensory or motor equipment of monotremes, as compared with other mammals or with birds, that can be correlated with such disparities in the functional lobes of the corpus cerebelli, if you consider these lobes from the functional point of view'. Monotremes seem to be poorly equipped with sensory systems. They are nocturnal, with small eyes, and they lack auditory pinnae and vibrissae. On the other hand the trigeminal nerve is hypertrophied and the trigeminal sensory nucleus is large. This nucleus sends afferents to the cerebellum and pons. Larsell noted that the large lobule VI of the cerebellum of the platypus, *Ornithorynchus anatinus*, is related to the rich sensory innervation of the beak. This sensory innervation was thought to be tactile, but it is now known that monotremes are electroreceptive and that this sense is mediated by receptors on the beak, which project to the CNS via the trigeminal nerve [Scheich et al., 1986]. The platypus beak is a major sensory accessory structure in these animals, richly endowed with both mechanoreceptors and electroreceptors.

*Rodents*: Physiological mapping of granular layer cerebellar cortex in lightly anaesthetized rats reveals a high proportion of cortex devoted to analysis of light tactile stimulation of the body surface. Crus I and crus II of the ansiform lobe of the cerebellum in rats receive signals from peri-oral structures such as lips, teeth and vibrissae. Responses in these regions of rat cerebellar cortex to peripheral stimulation are mainly rapid, graded information about light tactile cutaneous stimuli. The receptive fields are small, well-defined patches on perioral structures [Welker, 1987]. Topological relationships between receptive field patches in the cerebellar cortex in rats appear to correspond to patterns of sensory input that occur during natural exploratory behaviour [Bower and Kassel, 1990].

A comparison of rats with platypus is informative. Trigeminal sensory inputs are important for both rats and the platypus, and both have enlarged regions of cerebellar cortex, which predominantly receive trigeminal inputs. The mechanoreceptive trigeminal sense in rats is associated with a complex motor system – the jaws, lips and tongue – which is used in intricate, complex movements during exploratory behaviour, while the trigeminal sensory system in platypus is linked to a rigid beak which is incapable of complex configurational changes and is used rather clumsily as a probe in exploring for food. Enlarged regions of the cerebellar cortex in both animals relate mainly to exteroreceptors, not to the muscles that control the movements of these receptors. The snout regions of these distantly related animals are vastly different in terms of motor capacity and motor behaviour, but in both groups sensory structures of the snout region form major channels for acquiring sensory information from the environment. Organisation of cerebellar cortex in these animals reflects the importance of these sensory channels, not of the complexity of associated motor behaviour.

*Marine Mammals*. When pinnipeds (seals and sea lions) are compared with terrestrial relatives, three regions of the cerebellum are relatively expanded. These are the dorsal paraflocculus, the ventral paraflocculus and the paramedian lobule. The same is true of cetaceans (whales and dolphins). Compared to terrestrial mammals, whales and dolphins have large cerebellums, with expanded parafloccular and paramedian lobules. The agile, carnivorous odontocetes (toothed whales), including dolphins, who are among the fastest and most agile swimmers in the sea, and whose gymnastic capabilities are well known, have small cerebellums compared to other cetaceans'. The more sedate, planktivorous baleen whales have, on both relative and absolute terms, the largest cerebellums of any

mammal [Jansen, 1969]. The fin whale *Balenoptera sulphurea* has a very large cerebellum, due mainly to a massively expanded ventral paraflocculus, which makes up about half the cerebellar volume. Marine mammals have highly specialized locomotor systems, but the expanded regions of their cerebellums are not related to these. The expanded areas are homologous to the auditory regions initially identified in the cerebellar cortex in cats (see below).

Vermal lobule VIII is more highly developed in echolocating cetaceans than in the non-echolocating baleen whales, and it is also expanded in echolocating bats and insectivores (see below). This suggests that lobule VIII in cetaceans is involved in echolocation. The anterior lobe of the cerebellum, lobule I in particular, tends to be poorly developed. Larsell [1970] expressed surprise at this, because in other animals these regions were thought to be associated with medial, caudal musculature involved in locomotion. Cetaceans have reduced limbs and massive development of the medial musculature of the tail, which is the main source of thrust and control for movements.

To summarize, in cetaceans regions of the cerebellum with sensory inputs from the major sensory system used in navigation, spatial mapping, prey detection and communication are greatly expanded, while regions related to the main motor system are not.

*Bats*. There are two major groups of bats. Microchiropterans (microbats) have brains resembling those of insectivores, probably their nearest living relatives, while megachiropterans (megabats) have brains resembling those of certain primates [Henson, 1970] and may be more closely related to them [Pettigrew, 1986]. Megabats are fructivores and rely mainly on vision for navigating and finding food. Microbats, on the other hand, have a wide variety of habitats, habits and diets, and they rely almost entirely on active echolocation.

In birds, a relatively large cerebellum has been described as an adaptation related to flight: 'When a bird winds through the branches of trees, survival depends on temporal coordination of complex movements. It is perhaps because of this that birds have such a large cerebellum' [Kornhuber, 1974]. However, microbats are very agile in flight: "Many bats remain continuously on the wing while catching and eating insects in the confined spaces between the trees and shrubs of a forest … The remarkably manoeuverable flight of bats is unequalled by birds' [Vaughan, 1970]. Microbats have small cerebellums by mammalian standards, but certain lobes are relatively enlarged. These are the parafloccular lobes and the medial lobe, which is homologous to vermal lobules VI-VIII in other mammals [Larsell, 1967;

44

Henson, 1970]. That is, the expanded regions in the cerebellum in microbats are the same as those areas that are enlarged in the cerebellums of echolocating marine mammals. These lobes are not expanded in non-echolocating megabats.

Neurons in these auditory regions of cerebellar cortex in bats are sensitive to position and velocities of acoustic targets [Kamada and Jen, 1990; Sun et al., 1970]. Lobes related to the forelimbs are relatively small in microbats. Cerebellotectal projections are prominent. Crus I of the ansiform lobe is enlarged, and this is accompanied by an enlarged trigeminal nerve innervating the tactile sensilla of the face [Henson, 1970].

In summary, when the cerebellum of microbats is compared to the cerebellum of other mammals, the pattern of relatively enlarged areas is almost exactly the opposite of what would be expected under the assumption that cerebellum is dedicated to control and coordination of movements. The organization of cerebellum in bats reflects the importance of the auditory system, the main sensory modality for identifying and tracking prey, and for locating and avoiding obstacles.

The involvement of the cerebellum in echolocation may be related to the control of orienting responses [Ito, 1984], but if the role of the cerebellum is in organizing the motor response to acoustic targets, it is surprising that the pattern of cerebellar development is similar in echolocating bats and cetaceans. The motor apparatus and locomotor style of microbats and cetaceans are opposite extremes, not just among mammals but among vertebrates. Bats move using only their forelimbs, even on the ground. Cetaceans, on the other hand, have greatly reduced forelimbs and a massive development of the medial dorsal musculature of the tail, which provides all of the thrust and much of the steering during movements. Microbats and odontocete cetaceans are highly specialized mammals with very different morphology, locomotor styles and motor capabilities. However, they share an unusual (i.e. derived – not shared by relatives) pattern of cerebellar lobular development and an unusual system for spatial orientation, navigation, prey detection and tracking. The major component of cerebellar organization in these animals is directly related to echolocation and only indirectly related to motor control (i.e. because echolocation provides information necessary for target-directed movements).

*Carnivores*. Snider and Stowell [1944] found auditory responses in a region covering lobules VI, VII and VIII of the cerebellar cortex in cats. Tone-evoked potentials and unit responses to tone stimuli in this auditory region are sensitive to movement, particularly to the direction of movement, of the tone generator [Wolfe, 1972; Aitken and Boyd, 1975]. The location of a frontal sound source is represented in domestic cat cerebellar cortex [Aitken and Rawson, 1983], and two-thirds of the neurons in the auditory region are sensitive to interaural time and intensity difference. One-third of the neurons have a preference for acoustic targets moving along a specific trajectory [Ito, 1984].

*Primates*. The hemispherical parts of the anterior lobe, as well as the simplex and ansiform lobules are expanded in primates, especially humans. These regions receive signals from distal parts of the forelimbs and are commonly assumed to be involved in controlling 'skillful movements of fingers and hands' [Ito, 1984]. On the other hand, primate hands and fingers are important tactile sensory structures, and cerebellar regions related to them could be involved in processing sensory signals that occur during movements.

Spider monkeys (*Ateles*) are extremely agile, moving among branches using their prehensile tail as a 'fifth hand'. They have large cerebellums, as do primates in general. The tail region of the spider monkey's cerebellum, lobules I and II, are particularly large. Larsell [1970] described lobule I of a spider monkey cerebellum, related to the distal part of the tail, as the largest that he found in any mammal and an example of cerebellar enlargement in association with a motor system. However, as Larsell noted, spider monkeys have sensitive, glabrous skin on the underside of their tails near the tip. They use this sensory region for '… exploring the ground, fissures and other features of the environment. Frequently, the distal tip of the tail is carried over the head, projecting beyond it in exploratory fashion' [Larsell, 1970].

Holmes claimed that 'in man even extensive lesions of the cerebellum involve no form of conscious sensations' [Dow and Morruzzi, 1958], and according to Dow and Morruzzi [*ibid*.], this '… may be taken as a condensed account of the conclusion reached by most leading physiologists and clinicians … to our times'. However, Holmes reported perceptual deficits in human cerebellar subjects, and Dow and Morruzzi report more. Holmes found deficits in estimating and comparing weights held in the hands, and several other investigators have found this also [Dow and Morruzzi, 1958]. This can be explained if motor output required to hold a weight is used as a cue for weight estimation, but other sensory deficits reported in cerebellar patients cannot be accounted for in this way. For example, patients with cerebellar lesions are not able to accurately locate tactile stimuli on the affected side [Dow and Morruzzi, 1958].

45

Perhaps the most remarkable report of a perceptual problem associated with cerebellar damage is Sasaki's [1985] account of a patient with a cerebellar lesion localized to the left posterior lobe. The patient was a physician who briefly lost consciousness, and tried the finger-to-nose test when he regained consciousness. He reported that as soon as he initiated the movement to place his finger on his nose he was unable to visualize the target. This phenomenon accompanied all targeted movements for the next few days. Hypometria continued for about a month. Sasaki's interpretation of this result is that the cerebellum '… transmits information for personal orientation'.

In recent clinical reviews, Liener et al. [1989, 1991] and Schmahmann [1991] show that there is a body of literature, stretching back over a century, indicating cerebellar involvement in nonmotor aspects of perceptual and cognitive tasks. The older literature has recently been bolstered by evidence from advanced techniques that measure regional blood flow and metabolism during mental activity. Many, but not all, of the mental activities that have been shown to involved the cerebellum are related to visuospatial tasks or mental rehearsal of movements. Cerebellar patients have impaired perception of time intervals and velocity of moving stimuli.

## Conclusion

The idea that the cerebellum is dedicated to control and coordination of movements is based on several lines of evidence: (1) There is a correlation between the relative size and histological and morphological complexity of the cerebellum and the agility of an animal [e.g. Pearson, 1976]. (2) Particular cerebellar lobes are expanded in relation to important fine motor control systems in humans and other animals. (3) Cerebellar damage or disease causes major deficits in motor control and coordination, but not in perception. (4) The activity of neurons in the cerebellum is related to movement patterns. (5) Outputs from the cerebellum travel to known motor and premotor regions of the central nervous system.

On the basis of this evidence, there can be no doubt that the cerebellum does play a role in controlling and coordinating movements. But the strength of a scientific theory does not depend on the amount of evidence accumulated to support it, unless such evidence rules out alternatives, and it is important to raise and discuss evidence that does not seem to support the theory. Current cerebellar theory can only be improved by challenging it, even if it is basically correct. I will argue that it is not (basically correct).

(1) The correlation of cerebellar size and complexity with agility must be interpreted with allowance for allometric scaling effects. In particular, network connectivities cannot be maintained as the size of the network increases, and so changes in the structure of neurons, neural networks and the gross morphology of brain regions are not independent of each other or of changes in size [Deacon, 1990].

When correlations between relative sizes of brain regions and overall brain size are examined in vertebrates, there is a disproportionate increase in cerebral and cerebellar cortical areas, as brains get larger. Therefore, for example, the relatively large and complex cerebellum in primates, compared to that in fishes, is consistent with the null hypothesis that the primate brain is simply a scaled-up version of the fish brain. Similarly, the massive expansion of the lateral hemispheres of the cerebellum in association with the expansion of parts of the cerebrum in mammals cannot be taken to indicate a change in function during evolution as has been suggested by Liener et al. [1989, 1991]. Pathways connecting the forebrain and cerebellum are found in all vertebrates, and the more parsimonious explanation is that there has simply been an increase in demand for cerebellar services (whatever they might be) with elaboration of the forebrain.

Conversely, the hypertrophied cerebellums in fish that electrolocate *does* require an explanation in terms of cerebellar function – specifically, in terms of electrolocation – because the hypertrophy occurs in unrelated groups of weakly electric fish, but not in related fish that lack an electric sense. Similarly, derived (independently evolved) shared cerebellar features in echolocating bats and echolocating cetaceans cannot be explained by allometric scaling effects. These require an explanation in terms of cerebellar involvement in echolocation.

When seeking correlations between cerebellar structure and aspects of sensory-motor performance or behaviour, it must be recognized that motor complexity is correlated to other aspects of vertebrate functional anatomy. Different locomotor styles and skeletal designs evolve in concert with sensory systems and perceptual capabilities. Thus, while there does seem to be a correlation between cerebellar size and complexity, and agility and complexity of motor behaviour in vertebrates, this correlation may be misleading. If we take into account scaling effects and pseudo-correlations, and step beyond the frog-rat-cat-monkey 'scala naturae' of 19th century anatomy and 20th century neurophysiology, it is difficult to sustain the view that there is a specific correlation between any aspect of cerebellar anatomy

and the complexity or accuracy of motor behaviour. The comparative analysis presented in this paper reveals a pattern that is somewhat different from the pattern that might be expected on the basis of the theory that the cerebellum is dedicated to some aspect of motor control. Dow and Morruzzi [1958] noted that data from animal studies are incongruous with data from clinical studies, and they warned that 'the best place to study the cerebellum of man is man [*ibid*. p397]. But if we take evolution seriously, we cannot take seriously the view that the cerebellum is only involved in fine control and coordination of movements.

(2) Expanded cerebellar lobes and lobules are found in association with special motor systems, for example the hands and fingers of primates or the vibrissae and perioral structures of rats. However, these complex motor systems are sensory systems used in active exploration [Welker, 1987]. Bower has suggested that the cerebellum may control movements with the specific purpose of acquiring information about the environment [Bower and Kassel, 1990]. Evidence summarized in this paper shows that the association between cerebellum and motor control systems is more pronounced in relation to those motor systems that can be regarded as having an important role in sensory acquisition than in those motor systems that are primarily concerned with locomotion or manipulation, which supports this view. Theories that attribute to the cerebellum a role in sensation and perception as a secondary consequence of a role in motor control are incongruous with evidence about the kind of sensory information processed through the cerebellum during movements [Bower and Kassel, 1990]. On the other hand, the association of cerebellum with sensory systems that are analogous to the active systems in terms of acquiring sense data, but do not involve movements, notably passive echolocation and passive electrolocation, indicates that the cerebellum is concerned with sensory acquisition even when this does not involve any movement by the animal.

(3) Cerebellar dysfunction does cause perceptual deficits. Such deficits have been reported in clinical studies and animal experiments. The clinical reports are relatively rare and in some cases can be accounted for as a consequence of a motor deficit. Subtle perceptual and cognitive deficits could be due to side effects or general depression of function in brain-damaged subjects. Given that there has been no theory about what kinds of perceptual deficits might occur in cerebellar patients, the absence of tests designed to detect the deficits is understandable, and so is the rarity of reports about such deficits and the lack of attempts to systematically examine them. As reported by Liener at al. [1991] and Schmahmann

[1991], new data are being accumulated, particularly via advanced brain scanning techniques using human subjects, that make it difficult to 'explain away' evidence for cerebellar involvement in sensation and perception in terms of a motor theory of cerebellar function.

Sometimes the cerebellum fails to develop in humans. The motor symptoms may be slight and may not be observed clinically unless the patient presents with some other neurological deficit [Dow and Morruzzi, 1958; Ito, 1984]. This indicates either that other CNS regions can take over the function of the cerebellum (which seems unlikely, given the uniformity and persistence of this structure over more than half a billion years of vertebrate evolution, which has seen spectacular modifications in other structures) or that the normal function of the cerebellum is more subtle than 'coordination of movement', and the emphasis that investigators have placed on the gross acute motor effects of cerebellar dysfunction is misplaced.

(4) Sensory inputs are generally correlated with motor output patterns, so the patterning of cerebellar activity in relation to movement patterns does not tell us whether the cerebellum is interested in controlling movements or in analyzing sense data during movements. The timing of cerebellar activity in relation to movement does not resolve the issue, because information about intended movements and predicted sensory reafference is likely to be useful for analyzing sensory inputs during movements.

On the other hand, there is electrophysiological evidence for direct involvement of cerebellar neurons in following trajectories of targets in the environment. The best such evidence is from electrosensory responses in the cerebellums of weakly electric teleosts, but analogous results have been reported for auditory responses in cats and bats. Lack of more evidence along these lines may be because the well-established theory that cerebellum coordinates movements indicates that it would not be worthwhile to look for such evidence. Because of this bias, we are more likely to see reports of cerebellar activity correlated with movements of the experimental subject than reports of cerebellar activity correlated with movements of targets in the environment, even if the latter is more common.

(5) Anatomical evidence can be criticized on similar grounds. The existence of cerebellar projections to motor regions of the CNS does not imply that cerebellar function is restricted to some aspect of motor control, only that the cerebellum performs some computation which is useful for motor control. The presence of cerebellar projections to other regions of the CNS that are not thought to have a direct role in coordinating movements suggests that

the cerebellum is – at least sometimes – useful for things other than motor control.

*What, then, does the cerebellum do*? As Welker [1987] and others have pointed out, movement and perception are interrelated. Animals are active participants in the world, not passive observers, and therefore it is not surprising to find that a neural structure that is important for fine motor control and coordination of movements is also important for sensation and perception. Elaborations of this idea can neatly explain why a system involved in movement control is also closely involved with sensory systems. This approach seems reasonable in relation to exploratory behaviour in rodents, which Welker's group has studied, but even in this case there are reasons to doubt its validity [Bower and Kassel, 1990]. Some evidence, however, especially that related to cerebellar involvement in electrolocation and echolocation, cannot be accounted for by this kind of theory.

It is easy to explain motor effects of cerebellar dysfunction in terms of a sensory theory of cerebellum. Because the cerebellum projects to motor and premotor regions of the central nervous system, cerebellar dysfunction will disrupt activity in these regions. The acute effects of cerebellar dysfunction - gross deficits in motor coordination – tell us only that cerebellar output is used in motor control. They do not tell us what operations the cerebellum performs, or why these operations are useful in controlling and coordinating movements. As Wiener [1948] and others have noted, the motor symptoms of cerebellar dysfunction in humans resemble performance deficits found in artificial control systems with faulty feedback regulators. Granit was one of the first to suggest that cerebellar dysmetria may arise from disruption of γ-spindle afferent feedback to the CNS during movements [Dow and Morruzzi, 1958].

At the time when these suggestions were made by Wiener and Granit, the importance of accurate state estimation for control of multivariate dynamical systems was not appreciated. Indeed, there was no workable control theory for multivariable systems. Multivariate regulator and state estimator theory was developed in the late 1950's and early 1960's. These theoretical developments were followed, not coincidentally, by rapid advances in control and guidance technology [Bucy and Joseph, 1968]. Classical feedback control theory extends to the multivariate stochastic case, but with the important difference that a system's output cannot be used directly to construct a feedback input. Instead, a particular set of variables called the system's state vector must be estimated from available inputs and outputs and passed to the controller. Without an accurate estimate of the state vector, a controller cannot stabilize the system. Consequently, movements may be too fast, too slow, too compliant or not compliant enough, inaccurate, oscillatory or unstable [Paulin, 1992]. That is, the consequences of state estimator malfunction in a control system resemble the motor symptoms of cerebellar dysfunction.

The problem of computing an optimal estimate of a system's state from measurements of the system's inputs and responses (under certain conditions) was solved by Kalman [1960] and is called the Kalman filter. Although developed initially to solve an important problem in multivariate stochastic feedback regulator theory, Kalman filters are not feedback regulators or controllers. They are devices for tracking and predicting states of dynamical systems. They have a variety of applications including target identification, tracking, prediction, noise rejection and navigation [Bucy and Joseph, 1968].

Breakdown in state estimating subsystems of a communication, command and control system leads to control deficits, due to a lack of information about initial conditions and goals for movements as well as to a lack of accurate feedback for regulating the movements. Although breakdown in these systems may have serious consequences in terms of system outputs, the underlying deficit may not be easily observed. The breakdown is due to a failure in analysis of trajectories but emerges as a breakdown in movement control.

By analogy, Kalman filters are essential for tracking and predicting aircraft movements in modern air traffic control systems. If the Kalman filters failed but the remaining system was robust enough to continue functioning without them, targets might not be where the system predicted them to be. Actions directed using the faulty information would be dysmetric. Air traffic controllers would observe pilots not following instructions accurately. Having no independent way to check their perceptions of the locations and trajectories of aircraft, they would not realize that the pilot's errors were a consequence of instructions based on incorrect perceptions.

The trajectory prediction problem for anti-aircraft fire control, which can be solved by the Kalman filter, is analogous to the head trajectory prediction problem for optimal control of the vestibulo-ocular reflex [Arbib and Amari, 1985; Paulin et al., 1989], which is implemented in the brain by the cerebellum. Kalman filters are used for flight stabilization and control in aircraft and spacecraft [Bucy and Joseph, 1968], and for feedback regulation in industrial plants. More generally, they have a wide variety of applications in filtering and predicting signals generated by dynamical systems.

The evidence presented in this paper shows that the cerebellum appears to be involved in a wide variety of tasks analogous to the technological applications of dynamical state estimators. These include, but are not restricted to, controlling and stabilizing movements.

In drawing an analogy between the cerebellum and a state estimator, I do not intend to imply that the cerebellum implements the Kalman filter algorithm. Rather, the suggestion is that the cerebellum and the Kalman filter are instances, respectively biological and artificial, of systems that estimate the state of dynamical systems. No doubt they work in different ways and have different capabilities. Nevertheless the Kalman filter may be as precise a technological metaphor for the cerebellum as is possible, given the present state of the art in dynamical state estimation theory.

Basic mathematical results relevant to the state estimator theory have been outlined by Paulin [1992].

The theory predicts deficits related to target tracking in cerebellar patients, e.g. loss of performance in judging velocities, and predicting when, where and if a projectile will strike a target based on its initial trajectory. Localized damage to (say) auditory regions of cerebellar cortex should lead to loss of accuracy in auditory-evoked orienting behaviour but not in (say) visually-evoked orienting behaviour. Reports of cerebellar involvement in cognitive and associative learning tasks apparently not related to movements [Liener et al., 1991; Schmahmann, 1991] are damaging to the concept of the cerebellum as a device exclusively for motor control. These reports do not undermine the hypothesis that the cerebellum is a neural analog of a state estimator, but in combination with that hypothesis they entail the prediction that these tasks require dynamical state estimation, filtering or prediction as subtasks.

## References

Aitken, L.M. and J. Boyd (1975) Responses of single units in cerebellar vermis of the cat to monaural and binaural stimuli. J. Neurophysiol., *38*: 418-429.

Aitken, L.M. and J.A. Rawson (1983) Frontal sound source location is represented in the cat cerebellum. Brain Res., *265*: 317-321.

Arbib, M.A. and S. Amari (1985) Sensori-motor transformations in the brain (with a critique of the tensor theory of the cerebellum). J. Theor. Biol., *112*: 123-155.

Bass, A.H. (1986) Electric organs revisited: evolution of a vertebrate communication and orientation organ. In: Electroreception (ed. By T.H. Bullock and W. Heiligenberg), Wiley, New York, pp. 13-70.

Bastian, J. (1986) Electrolocation: behaviour, anatomy and physiology. In: Electroreception (ed. By T.H. Bullock and W. Heiligenberg), Wiley, New York, pp. 577-612.

Bell, C.C. and T. Szabo (1986) Electroreception in mormyrid fish: central anatomy. In: Electroreception (ed. By T.H. Bullock and W. Heiligenberg), Wiley, New York, pp. 375-422.

Berribi, A.S, J.I. Morgan and E. Mugnaini (1990) The purkinje cell class may extend beyond the cerebellum. J. Neurocytol., *19*: 643-654.

Bodznick, D. and R.L. Boord (1986) Electroreception in chondricthyes: central anatomy. In: Electroreception (ed. By T.H. Bullock and W. Heiligenberg), Wiley, New York, pp. 225-256.

Bombardieri, R.A. and A.S. Feng (1977) Deficit in object detection (electrolocation) following interruption of cerebellar function in the weakly electric fish Apteronotus albifrons. Brain Res. *130*: 343-347.

Bower, J.M. and J. Kassel (1990) Variability in tactile projection to cerebellar folia crus IIa

of the Norway rat. J. Comp. Neurol. *302*: 768-778.

Bucy, R.S. and P.D. Joseph (1968) Filtering for stochastic processes with applications to guidance. Wiley, New York.

Bullock. T.H. (1986) Significance of findings on electroreception for general neurobiology. In: Electroreception (ed. By T.H. Bullock and W. Heiligenberg), Wiley, New York, pp. 651-674.

Deacon, T.W. (1990) Rethinking mammalian brain evolution. Amer. Zool. *30*: 629-706.

Dow, R.S. (1970) Historical review of cerebellar investigations. In: The Cerebellum in Health and Disease (ed. By W.S. Fields and W.D. Willis), Hilger, London.

Dow, R.S. and G. Morruzzi (1958) The Physiology and Pathology of the Cerebellum. University of Minnesota Press, Mineapolis.

Ghez, C. and S. Fahn (1985) The cerebellum. In: Principles of Neural Science, 2nd edn. (ed. By E.R. Kandel and J.H. Schwartz), Elsevier, New York, pp. 502-522.

Henson, O.W. (1970) The central nervous system. In: Biology of Bats vol II (ed. By W.A. Wimsatt), Academic Press, London, pp 57-152.

Ito, M. (1984) The Cerebellum and Neural Control. Raven Press, New York.

Jansen, J. (1969) On cerebellar evolution and organization from the point of view of a morphologist. In Neurobiology of Cerebellar Evolution and Development (ed. By R.R. Llinas), Institute for Biomedical Research, AMA/ERF, Chicago. pp. 881-894.

Kalman, R.E. (1960) A new approach to linear prediction and filtering problems. J. Basic Eng. ASME *82*: 35-45.

Kamada, T., and P.H.S. Jen (1990) Auditory response properties and directional selectivity of cerebellar neurons of the echolocating bat *Eptesicus fuscus*. Brain Res. *528*: 123-129.

Kornhuber, H.H. (1974) Cerebral cortex, cerebellum and basal ganglia: an introduction to their motor functions. In The Neurosciences, 3rd Study Program (ed. By F.O. Schmitt and F.G. Worden), MIT Press, Cambridge, MA. pp. 267-280.

Larsell, O. (1967) The Comparative Anatomy and Histology of the Cerebellum from Myxinoids through Birds. Ed. By J. Jansen, Univ. Minnesota Press, Minneapolis.

Larsell, O. (1967) The Comparative Anatomy and Histology of the Cerebellum from Monotremes through Apes. Ed. By J. Jansen, Univ. Minnesota Press, Minneapolis.

Lauder, G.V. and K.F. Liem (1983) Patterns of diversity and evolution in ray-finned fishes. In Fish Neurobiology, Vol. I (ed. By R.G. Northcutt and R.E. Davis), University of Michigan, Ann Arbor.

Liener, H.C., A.L. Liener and R.S. Dow (1989) Reappraising the cerebellum: what does the hindbrain contribute to the forebrain? Behav. Neurosci., 103: 998-1008.

Liener, H.C., A.L. Liener and R.S. Dow (1991) The human cerebro-cerebellar system: its computing, cognitive and language skills. Behav. Brain Res., *44*: 113-128.

Llinas, R.R. (1985) Functional significance of the basic cerebellar circuit in motor coordination. In Cerebellar Functions (ed. By J.R. Bloedel, J. Dichgans and W. Precht), Springer-Verlag, Berlin, pp. 170-185.

Llinas, R.R. and D.E. Hillman (1969) Physiological and morphological organization of the cerebellar circuits in

various vertebrates. In Neurobiology of Cerebellar Evolution and Development (ed. By R.R. Llinas), Institute for Biomedical Research, AMA/ERF, Chicago. pp 43-76.

Montgomery, J.C. (1984) Noise cancellation in the electrosensory system of the thornback ray: common mode rejection of input produced by the animal's own ventillatory movement. J. Comp. Physiol. *155A*: 103-111.

Mugnaini, E., A.S. Berribi, A.L. Dahl and J.I. Morgan (1987) The polypeptide PEP-19 is a marker for Purkinje neurons in cerebellar cortex and cartwheel neurons in dorsal cochlear nucleus. Arch. Ital. Biol. *126*: 41-67.

Northcutt, R.G. (1978) Brain organization in cartilaginous fishes. In Sensory Biology of Sharks Skates and Rays (ed. By E.S. Hodgson and R.FR. Mathewson), Office of Naval Research, Arlington, pp. 117-194.

Paul, D.H. (1982) The cerebellum of fishes: a comparative neurophysiological and neuro-anatomical review. Adv. Comp. Physiol. Biochem., *8*: 111-177.

Paulin, M.G. (1992) A model of the role of the cerebellum in tracking and controlling movements. Hum. Movement Sci. *12*: 5-16.

Paulin, M.G., M.E. Nelson and J.M. Bower (1989) Dynamics of compensatory eye movement control: An optimal estimation analysis of the vestibulo-ocular reflex. Intl. J. Neural Systems 1: 23-29.

Pettigrew, J. (1986) Flying primates? Megabats have the advanced pathway from eye to mid-brain. Science *231*: 1304-1306.

Sasaki, K. (1985) Cerebro-cerebellar interactions and organization of a fast and stable hand movement: Cerebellar participation in voluntary movement and motor learning. In Cerebellar Functions (ed. By J.R. Bloedel, J. Dichgans and W. Precht), Springer-Verlag, Berlin. pp 70-85.

Scheich, H., G. Langner, C. Tidemann, R. Coles and A. Guppy (1986) Electroreception and electrolocation in Platypus. Nature (Lond.) *319*: 401-402.

Schmahmann, J.D. (1991) An emerging concept: The cerebellar contribution to higher function. Arch. Neurol. *48*: 1178-1187.

Smeets, W.J.A.J., R. Nieuwenhuys and B.L. Roberts (1983) The Central Nervous System of Cartilaginous Fishes. Springer-Verlag, Berlin.

Snider, R.S. and A. Stowell (1944) receiving areas of the tactile, auditory and visual systems of the cerebellum. J. Neurophysiol. *7*: 331-357.

Sun, D., X. Sun and P.H.S. Jen (1990) The influence of auditory cortex on acoustically evoked cerebellar responses in the CF-FM bat Rhinolophus pearsonii chinensis. J. Comp. Physiol., *166*: 477-488.

Tricas, T. (1982) Bioelectric-mediated predation by swell sharks, Cephaloscyllium ventriosum. Copeia, *4*: 948-952.

Vaughan, T.A. (1970) Flight patterns and aerodynamics. In: Biology of Bats vol I (ed. By W.A. Wimsatt), Academic Press, New York.

Welker, W. (1987) Spatial organization of somatosensory projections to granule cell cerebellar cortex: functional and connectional implications of fractured somatotopy (Summary of Wisconsin studies). In New Concepts in Cerebellar Neurobiology, A.R. Liss, New York, pp. 239-280.

Wiener, N. (1948) Cybernetics, or control and communication in the animal and the machine. MIT Press, Cambridge, MA.

Wolfe, J.W. (1972) Responses of the cerebellar auditory area to pure tone stimuli. Exp. Neurol. *36*: 295-309.