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Editorial

Language, cognition and the cerebellum: Grappling with an enigma

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The part played by the cerebellum in higher cognitive functions has been and remains something of an enigma. Schmahmann and Caplan (2006) maintain that ''The traditional teaching that the cerebellum is purely a motor control device no longer appears valid, if, indeed, it ever was. There is increasing recognition that the cerebellum contributes to cognitive processing and emotional control in addition to its role in motor coordination'' (p. 290). On the contrary, Glickstein (2006) in the same issue wrote: ''Evidence for a critical role for the cerebellum in cognition or emotion remains unconvincing'' (p. 289). Despite the fact that there is a scientific journal (*The Cerebellum*) devoted solely to research on the cerebellum, it appeared to us from discussion with colleagues and others that recent developments in cerebellar research are not widely known outside the field of its practioners. We felt it was appropriate (70 years on from the well-known paper by Holmes, 1939) to bring such research to the attention of a wider audience involved in cognitive neuroscience. We are grateful to the editors of *Cortex* for agreeing to our suggestion to compile a special issue of the journal and to our contributors for their papers.

In a letter dated 18th January, 1661 addressed to Robert Boyle, Dr. Lower, assistant to the celebrated Thomas Willis, refers to the latter's ''opinion of the use of the cerebellum for involuntary motion'', a view subsequently published in his famous text of 1664 (translated into English in 1681). Research on animals by Luigi Rolando (1809) and Pierre Flourens (1824) in the early part of the nineteenth century subsequently confirmed that lesions of the cerebellum produce severe disturbances of co-ordinated movement. More fanciful ideas, however, were propagated by the phrenologists. Franz Joseph Gall (see Gall et al., 1838, translated by Combe) was of the view that the cerebellum was the ''organ of the instinct of reproduction''. He drew a connection between the presumed size of the cerebellum and the apparent propensity for enjoyment of sex, writing:

> ''The lady of whom I have spoken above (...) has a large and beautiful head like a man, and she possesses distinguished talents; but the nape of her neck has very little breadth under the ears, which indicates a small development of the cerebellum. I have hitherto found this conformation in all persons in whom the instinct of reproduction was naturally feeble'' (p. 24).

Gall believed that there was a connection between the testicles and the cerebellum. As a direct test of Gall's notion, the finding of François Leuret (1839), referred to by Pierre Flourens (1846, translated by de Lucena Meigs), that on average the cerebellum was larger in 21 geldings than in 10 stallions and 12 mares should have put paid once and for all to the idea that the cerebellum had anything to do with the presence or size of testicles but, being written in French, appears not to have been read or simply ignored by later English speaking theorists. In any case, it was apparently insufficient to dispose of the idea that the cerebellum was the seat of the amative instinct, an idea which seems to have exercised a tenacious hold on the Victorian imagination. As late as 1892, a follower of Gall, one John William Taylor, wrote (p. 9):

> ''(1) I am led to conclude, apart from co-ordination, according to our leading cerebral physiologists, the main function of the cerebellum is the amative instinct. (2) The

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energy of amativeness bears a constant relation to the development of the cerebellum. (3) The loss of both testicles by castration or otherwise causes a great diminution in the bulk of the cerebellum; and (4) that excessive development of the cerebellum predisposes to erotic mania."

Taylor (p. 9) quotes "David Ferrier, in *Functions of the Brain*, page 432" as follows: "As morbid irritation of the sexual organs may excite a morbid sexual appetite, so, conversely, the sexual appetite may be morbidly excited by pathological irritation of the cerebral paths, and the cerebral centres of the sensations connected with the exercise of generative functions. To the former belong the satyriasis or nymphomania occasionally observed in connection with the middle lobe of the cerebellum; to the latter the various morbid exhibitions of the sexual appetite in insanity, where the centres are functionally or organically diseased".

Other than its supposed role in regard to the sexual instinct, the idea that the cerebellum is involved in some way in control of movement has a long history. The Greek anatomist Erasistratos (310–250 BC) was of the opinion that there was a relation between the size of the cerebellum and the running speed of animals (see Tesak and Code, 2008, p. 7/8).

For a long time exploration of cerebellar function was dominated by experimental work with animals. Luciani's (1891) descriptions of the effect of lesions to the cerebellum in dogs and primates provided the basis for much that was to follow. However, in a discussion of six contributions to a *Symposium on the Cerebellum* published in volume 50 of *Brain*, Francis Walshe (1927) gave as his opinion that "the problem of cerebellar functions remains where Luciani left it nearly half a century ago" (p. 378) (for a modern evaluation of Luciani's work see Manni and Petrosini, 1997). Of the six papers of the symposium, only one, by Theodore Weisenburg (later to publish a celebrated work on aphasia), was based on clinical investigations in humans rather than experimental work with animals.

Although not the only neurologist or physician to be interested in the cerebellum, it was the work of Holmes (1917, 1922) more than anyone that encouraged clinical investigation of the symptoms of cerebellar disease. One of the chief clinical signs of acute cerebellar damage is what Holmes (1917) described in his classic paper on the effects of gunshot wounds in 21 victims of the first world war as 'decomposition of movement'. In this paper, Holmes acknowledges his debt to "Babinski's masterly analysis of the symptoms of cerebellar disease" (p. 463). Indeed, Babinski (1902) coined the term 'adiadochokinesis' to refer to the inability to execute rapidly alternating movements. He believed that the principal function of the cerebellum was to link together simpler movements that make up compound movements (Babinski, 1899, 1906).

In the Tenth Hughlings Jackson Memorial Lecture delivered in December 1938, Holmes (1939) began by pointing out that in the 16 years since his 1922 Croonian lecture "numerous clinical observations have been published and an enormous amount of experimental work has been devoted to the cerebellum, but the conclusions drawn from them are so discordant that it seems wiser to omit reference to them when possible" (p. 1). His own conclusions were interesting in that he dismissed the idea that the cerebellum contained a special centre for co-ordination of movement. Rather, he argued that:

"...in addition to regulating postural tone, the cerebellum reinforces or tunes up the cerebral motor apparatus, including subcortical structures with motor functions, so that they respond promptly to volitional stimuli and the impulses from them which excite muscular contractions are properly graded.

In his classical contributions to the physiology of the cerebellum Luciani (1891) described as the three symptoms of cerebellar defect: atonia [loss of muscle tone], astasia [tremor, oscillation, inco-ordination] and asthenia [muscular weakness]. These three symptoms occur in man as a result of acute cerebellar lesions and by them the irregularities of movement which constitute cerebellar ataxia can be fully explained" (p. 29).

In the years following publication of the Hughlings Jackson memorial lecture, research on the cerebellum moved apace. Giuseppe Moruzzi and his colleagues demonstrated inhibitory cerebellar influences on other parts of the brain, and particularly on the autonomic system (Moruzzi, 1947). Sir Charles Sherrington's dictum that the cerebellum is the "head ganglion of the proprioceptive system" (Sherrington, 1906) emphasised that normal posture and movement requires abundant proprioceptive input. Snider (1967) similarly considered the cerebellum to be a regulator of sensory input, while Brindley (1964) suggested that skills such as playing the piano are first learned consciously under cortical control but with time and practice the cerebellum comes to control the actions subconsciously or automatically.

Marr (1969), well-known for his later contribution to the study of vision, proposed that the cerebellum was important both for learning movements and actions and for learning to maintain balance and posture. Albus (1971) developed a mathematical theory of cerebellar function independently of Marr but saw it as an extension and modification of the latter's theory. Albus regarded the cerebellum as being a site of motor memory. De Schutter and Maex (1996) pointed out that along with the "dogma" that the cerebellum is exclusively involved in motor control, another has been that it is the site of memory storage for motor learning as proposed by Marr and Albus, a view De Schutter and Maex (1996) themselves rejected.

In reviewing non-motor functions of the cerebellum (as revealed very largely by research on animals) Watson (1978) concluded: "A large amount of evidence underscores the insufficiency of strictly postural and motor control concepts." He noted that through its connections with the forebrain, reticular and limbic system structures, "The cerebellum may contribute to sensory processing, learning, performance, emotion, motivation and reward" (p. 960). Watson made no mention of what we would consider cognition but a decade later Leiner et al. (1989) reviewed findings on the human cerebellum which led them to reject the view that this structure is exclusively involved in motor control (see also Leiner et al., 1986). Instead they referred to "the cognitive cerebellum". They argued that the cerebellum is involved in cognitive functions by virtue of the extensive connections between it (especially the lateral cerebellar structures) and frontal and prefrontal areas of the cortex. According to Leiner et al. (1989) cerebellar connections to prefrontal cortex enable the cerebellum to "improve" mental skills, connections to

Broca's area enable it to "improve" language skills and connections to motor cortex enable the cerebellum to "improve" motor skills.

From time to time the view had been expressed prior to publication of the paper by Leiner et al. (1989) that the cerebellum was involved in cognitive functions (e.g., Gowers, 1888) but usually dismissed (e.g., André-Thomas, 1912). Controversy over the role of the cerebellum, what it does and how it does it, has characterised cerebellar research since at least the nineteenth century and has continued to do so. Weisenburg (1927) began his paper with the words "Perhaps there is no subject in neurology today about which there is more controversy than the function of the cerebellum". Almost 50 years later in an attempt to extend the diversity of possible lesion locations in foreign accent syndrome beyond the supratentorial brain regions, Cole (1971) discussed two patients in whom the causative lesion was situated in the posterior fossa. Robert Joynt, former editor-in-chief of *Neurology*, commented on this unexpected finding: "...it doesn't appear unusual that any of the brain mechanisms which are used to integrate motor acts may alter force, prosody, and rhythm of speech. It is well that Dr. Cole has pointed this out with posterior fossa lesions" (p. 153). However, he ironically added: "(...) I am enough of a romanticist to think that these subtle inflections and nuances of speech must ultimately stem from the cerebral cortex. For example, if Juliet had said in a monotone, "Romeo, Romeo, wherefore art thou, Romeo?" I doubt if Romeo would have done himself in for her. But then, I don't think Shakespeare wrote for the cerebellum." (p. 153).

A quarter of a century later, the role of the cerebellum in non-motor functions was still being questioned. The April 26th, 1996 issue of *Science* has an introductory article entitled "The Cerebellum: Movement coordinator or much more?". Ten years after that an invited commentary (Glickstein, 2006) on a paper in *Brain* (Ravizza et al., 2006) appears under the heading "The Cerebellum – motor control or more?" while Glickstein (2007) asks the rhetorical question "What does the cerebellum really do?" In these papers Glickstein takes issue with the emerging view that the cerebellum has a role to play in cognitive and linguistic functions.

In some ways it is not surprising that there remains controversy regarding the role of the cerebellum in cognitive functions. It is a relatively small structure at the bottom of the brain that seems to hide under the occipital lobes as if unwilling to assume a more prominent position in the cranial cavity. Yet the cerebellum contains at least as many neurones than the much larger cerebrum under which it lies. As Glickstein (1993) put it, "The cerebellar hemispheres have more cells than the cerebral cortex. What on earth do they do?" (p. 451).

In a much cited paper, Schmahmann and Sherman (1998) studied 20 patients with disease confined to the cerebellum, concluding that there is a constellation of deficits which they termed the "cerebellar cognitive affective syndrome" characterised by disturbances of executive, linguistic, spatial and affective function. Not all deficits occurred in each case but certain symptoms were particularly prominent. Decreased verbal fluency was said to be present in 18 patients and visuospatial "disintegration" in 19 cases. However, the authors pointed out that "it is impossible on the basis of these cases to distinguish the contribution of the lesioned cerebellum to these abnormal behaviours from that of the cerebral regions newly deprived of their connections with the cerebellum. Furthermore, (...) disruption of behaviour by cerebellar lesions is, to some extent, transient" (p. 576).

In an earlier paper reviewing cognitive, psychiatric and other aspects of research on the cerebellum, Schmahmann (1991) suggested that "The overshoot and inability in the motor system to check parameters of movement may (...) be equated, in the cognitive realm, with a mismatch between reality and perceived reality, and erratic attempts to correct the errors of thought or behavior. Hence, perhaps, dysmetria of thought" (p. 1183).

As with other cerebral structures (see Thach, 1996), claims that the cerebellum has a role to play in cognition or linguistic function derive from three main strands of research: first, the effect of cerebral lesions, second functional neuroimaging studies and third, neuroanatomical considerations. To these might be added investigations of developmental abnormalities of the cerebellum (for general critique and review of cerebellar research in relation to cognition see Stein and Glickstein, 1992; Thach et al., 1992; Leiner et al., 1993; Daum and Ackermann, 1995; Thach, 1996; Paquier and Mariën, 2005; Timmann and Daum, 2007; Strick et al., 2009). Special issues of *Trends in Cognitive Science* (Volume 2, issue 9, 1998) and the companion volume *Trends in Neurosciences* (Volume 21, issue 9, 1998) as well as Volume 13, issues 2–3 (2006) of the *Journal of Neurolinguistics* and Volume 59, issue 4 (2007) of *Folia Phoniatrica et Logopaedica* are devoted to the cerebellum. March 2002 saw the first issue of *The Cerebellum*, a quarterly journal devoted to the science of the cerebellum and its role in ataxia and other disorders. For a review specifically of executive function in relation to the cerebellum see Bellebaum and Daum (2007) and for spatial processing and the cerebellum see Molinari and Leggio (2007). Reviews of the role of the cerebellum in language functions are provided by Gordon (1996), Mariën et al. (2001b), Paquier and Mariën (2005), De Smet et al. (2007b), and Murdoch (2010, this issue). For brief review of history of anatomical research see Glickstein, Strata and Voogd (2009).

Glickstein (2006, 2007; Glickstein and Doron, 2008) is one of the most sceptical opponents of the view that the cerebellum is involved in cognition (for an explicitly contrary opinion to that of Glickstein see Strick et al., 2009). The main thrusts of his arguments are that evaluation of the effects of cerebral lesions is difficult since "Lesions of the cerebellum may not occur in isolation. Traumatic, vascular, developmental anomalies and tumours typically cause damage to brain structures outside of the cerebellum and treatments associated with cerebellar resection, such as chemotherapy and radiation, may themselves produce cognitive deficits" (p. 288). With regard to neuroimaging research, Glickstein (2007; see also Glickstein and Doron, 2008) suggests activation of cerebellar areas may be related to actual or planned movement of the eyes, vocal apparatus or fingers rather than to cognition, a view buttressed by the fact that neuroanatomical connections between cerebellum and cortex largely involve areas concerned with eye movements as opposed to areas known to be involved in cognition.

Seventy years on from publication of Holmes's (1939) landmark paper we are pleased to have the opportunity to bring together for readers of this journal a collection of review articles and reports devoted to current research carried out in to the functions of the cerebellum, together with the associated controversies. One of us (AB) is not directly concerned with cerebellar research but was drawn to consider its functions by an interest in dyslexia and the hypothesis (Fawcett and Nicolson, 1992; Nicolson et al., 1995, 2001; Nicolson and Fawcett, 2007) that a cerebellar deficit is at the root of this developmental condition (for critiques see Beaton, 2002, 2004a; Vlachos et al., 2007; see also Bishop, 2002). In addition, this co-editor among others (Peters, 1995; Snyder et al., 1995; McManus and Cornish, 1997; Jäncke et al., 1999) has suggested that the phenomenon of handedness is intimately associated with the functions of the cerebellum (Beaton, 2003, 2004b), a view lent credence perhaps by the finding that cerebellar damage results in impairment of skilful movements of the fingers (Glickstein et al., 2005). In addition, left and right hands differ in terms of their "steadiness" (Simon, 1964; Annett et al., 1979), or lack of extraneous movement in performing fine motor tasks, and in the degree to which each is associated with cerebellar activation (Jäncke et al., 1999). Furthermore, cerebellar volume is related to measures of fine motor dexterity (Paradiso et al., 1997). The second co-editor (PM) has been much more intimately involved in research on the cerebellum for a number of years (Baillieux et al., 2006, 2007; De Smet et al., 2007a, 2007b, 2009; Mariën et al., 1996, 2000, 2001a, 2001b, 2006, 2007, 2009; Mariën and Verhoeven, 2007; Paquier and Mariën, 2005).

As we see it, there are three main issues relating to the question "Does the cerebellum contribute to cognitive and linguistic functions and, if so, how?"

1. Does the cerebellum have a single *modus vivendi* or does it operate in a multiplicity of ways?

A number of authors have proposed that the cerebellum operates according to some single principle or is dedicated to a relatively restricted set of functions. Bloedel (1992) was struck by the functional heterogeneity of the cerebellum in the face of its structural homogeneity. According to Bloedel, "cerebellar function involves a characteristic operation that is performed across its various components. (...) this operation includes integrating sensory information about execution space, the target, peripheral inputs, and the body scheme with inputs reflecting the properties of the movement being executed. Although the fundamental characteristics of this operation are likely to be similar across the subdivisions of the cerebellum, the organization of cerebellar afferent and efferent systems will result in differences in the behavioral consequences of the processing in various cerebellar regions. This heterogeneity reflects the multiple systems with which the cerebellum interacts rather than a multiplicity of functional operations within the cerebellum itself" (p. 678).

As noted above, Snider (1967) thought the role of the cerebellum is to modulate sensory input. More recently, Gao et al. (1996) suggested that the cerebellum is specialised more for acquisition of sensory data than for movement per se. They argued that "cerebellar deficits in voluntary movement, such as incoordination and ataxia, may reflect disruption of the sensory data (from the medial cerebellum-controlled muscle spindle system) on which the motor system depends, rather than disruption of cerebellar computations of smooth motor performance per se" (p. 547).

The concept of "'control augmentation', based on the computer action of cerebellar circuits" was proposed by Ito (1986). He regarded the cerebellum (Ito, 1990) as "an organ dedicated to endow adaptive control abilities to all kinds of bodily functions, through reflexes to voluntary movement to mental activity" (p. 569) and pointed out that "Dysmetria can be regarded as impairment of predictive control, for which a computer is indispensable. Incoordination may be related to multivariable control in which plural inputs and outputs are manipulated at the same time" (p. 564). Through a process of error learning the cerebellum develops and updates internal models of the dynamics of body parts which allow performance of precise movements without the need to refer to feedback from the moving part. This applies to manipulation of mental representations of the cerebral cortex as much as to adaptive control of motor activity (Ito, 1993, 2008). This kind of view has much in common with others that see the cerebellum as essentially a predictive device (Miall et al., 1993; Courchesne and Allen, 1997).

One role for the cerebellum that has been emphasised, in particular by Ivry and his colleagues, is that of timing (Ivry and Keele, 1989; Ivry, 1993; Ivry and Fiez, 2000). A problem in timing the temporal relation between antagonist muscles would explain the dysmetria and adiadochokinesia that is seen following cerebellar damage although "The timing functions of the cerebellum are not limited to motor control" (Ivry et al., 2002, p. 304).

Raymond et al. (1996) agreed with Marr (1969) and Albus (1971) that "the idea that the cerebellum is a primary site of motor learning (...) is one of the most appealing hypotheses of cerebellar function". On the basis of similarity of neural mechanisms used in eye-blink conditioning and learning in relation to the vestibulo-ocular reflex (VOR), both of which are cerebellum-dependent, they suggested that the cerebellum is a "neuronal learning machine". Such learning is seen, for example, in prism adaptation experiments. Raymond et al. (1996) suggest that the neural mechanisms used in these two behaviours may "represent general principles that apply to all forms of cerebellum-dependent learning, including motor learning in saccadic eye movements and reaching arm movements" (p. 130).

Schmahmann (2004) argues that "because cerebellar anatomy is essentially uniform throughout the structure, the basic work that the cerebellum does in the nervous system should be constant as well. This we have referred to as the universal cerebellar transform, characterized as the cerebellar modulation of behaviour, serving as an oscillation dampener maintaining function automatically around a homeostatic baseline and smoothing out performance in all domains" (p. 374–5).

One way in which the cerebellum might influence different cognitive functions in brain damaged patients is through the influence of diaschisis. A number of studies have shown that damage to the cerebellum can lead to reduced metabolic activity in the contralateral cerebral hemisphere (see e.g., Botez et al., 1990; Sönmezoglu et al., 1993; Mariën et al., 1996) and elsewhere due, perhaps, to the loss of excitatory cerebellar input to thalamus and forebrain structures, that is, to a reverse cerebellar diaschisis (Anderson et al., 1988). The opposite effect can also occur (diminished activity in the contralateral cerebellum as a result of a cerebral infarction) as found, for example, in studies by Baron et al. (1981), Broich et al. (1987), Mariën et al. (2006) and Mariën and Verhoeven (2007).

Crossed cerebellar diaschisis was not seen in three cases with lesions restricted to the parieto-occipital region in a PET study by Martin and Raichle (1983) although they noted that cerebellar hypometabolism was a general finding in their patients with cerebral infarction. Cerebellar asymmetry of metabolism was seen in every one of their patients with frontal lobe lesions, the side of lowest metabolism being contralateral to the cerebral lesion in all six cases. In another study of 43 patients (Metter et al., 1987) crossed cerebellar diaschisis was found to occur in all eight cases of Broca's aphasia. The level of motor disability (functioning of arm and leg) in cases where there was a cerebellar asymmetry in glucose metabolism was greater than when there was no such asymmetry.

Even in the absence of brain damage there may be a close correspondence between activity in certain areas of one cerebral hemisphere and activity in the opposite cerebellar hemisphere. In a PET study carried out with young normal adults to address this possibility a significant inverse correlation was found between relative left–right asymmetry of glucose metabolism in frontal cortex and relative asymmetry of activation in the cerebellum (Junck et al., 1988).

It seems to us self-evident that the putative role of the cerebellum as applied to cognitive functions cannot be considered in isolation from concurrent supratentorial activity. Indeed, the concept of a functionally "lateralised" cognitive (Allin et al., 2001; Gottwald et al., 2004; Hokkanen et al., 2006) and linguistic cerebellum (Mariën et al., 2001b; Jansen et al., 2005; Stoodley and Schmahmann, 2009a), which is becoming increasingly accepted by researchers, is predicated upon the importance of the crossed connections between cerebellum and cerebral cortex.

2. Extent of movement artefact in fMRI studies (and how interpreted)

One problem in interpreting the results of fMRI studies is that rarely does one have full experimental control over what a participant is thinking. Decety et al. (1990) showed that the cerebellum is activated along with the frontal cortex when subjects merely imagine making tennis movements or count silently. These authors suggested that the cerebellum therefore "participates in pure mental activity" and "may be involved in motor programming which precedes motor acts" (p. 316). (They also suggested that it possibly plays a role in the temporal organisation of neural events related to cognition). Similarly, instructions to participants simply to imagine producing speech are sufficient to induce activation in the cerebellum (Ackermann et al., 1998). Since experimental protocols require participants at some point to initiate an overt spoken or manual act, merely thinking of it can introduce the possibility of unwanted activation.

It has been argued by some that language deficits seen in patients with cerebellar disease or injury concern purely the motor aspects of speech although it is difficult to conceive of what motor deficits could produce symptoms such as anomia (Akshoomoff et al., 1992) or agrammatism that have been reported. For example, Silveri et al. (1994) described the case of a man who sustained a right cerebellar infarct. This patient was said not to be aphasic in his native Italian language, nor to show any syntactic defect; rather he exhibited an impairment in the use of uninflected verbs and in the use of clitics amounting to an agrammatism. Similarly, Mariën et al. (1996, 2000) described the case of a patient with an ischaemic infarction in the vascular territory of the right superior cerebellar artery who developed aphasic symptoms, including "full-blown agrammatism".

A patient with right cerebellar damage reported by Fiez et al. (1992) was asked to generate a verb in response to a visually presented noun. He tended to provide an unusually high number of non-verb responses (e.g., "sharp" in response to "razor" where control subjects gave "shave") without realising that his responses were in any way abnormal (but see Richter et al., 2004). He produced a large number of errors on other word generation tasks, namely synonym, category and attribute generation. The patient was impaired at selecting a synonym from two alternatives and in almost all tasks he failed to show the normal improvement with practice seen in the control subjects. It is difficult to see how this pattern of results can be brought about by purely motor impairment. Conversely, the (right lateral inferior) cerebellum has been shown to be active in response to participants being asked to generate a verb to a given noun after subtraction of a repetition condition in which the noun was repeated (see Petersen and Fiez, 1993). Leiner et al. (1993) argued that such findings demonstrate that the cerebellum cannot have a purely motor function, as traditionally thought, but participates in cognitive operations.

Nor is it easy to conceive how motor deficits can explain impaired cognitive associative learning in cerebellar patients (see Timmann et al., 2002, 2004) although slowed or inefficient motor function arguably might contribute to impairment on certain attentional (see e.g., Gottwald et al., 2003) or visuospatial tasks (see e.g., Bracke-Tolkmitt et al., 1989; Akshoomoff et al., 1992; Molinari and Leggio, 2007). Of course, a strict differentiation between cognitive and motor functions cannot be sustained (Bloedel, 1993). Most action or movement is made in the service of some end and in relation to an existing cognitive framework.

3. Localisation within the cerebellum

The first serious attempt at localisation within the cerebellum was apparently that of Bolk (1906) who concluded that there was some degree of functional localisation in motor control (see also Manni and Petrosini, 2004). Holmes (1917) discussed the question of localisation of function but came to no definite conclusion: "But though my observations lend no support to the theory of focal localisation of function in the cerebellar cortex they cannot be accepted as proof that such localization does not exist'' (p. 534).

On the basis of studies of over 50 patients with cerebellar lesions Weisenburg (1927; see also Mills and Weisenburg, 1914) came down firmly in favour of localisation. He concluded: ''In the vermis are represented the synergic activities of the trunk; in the superior vermis the movements of the shoulder–girdle or the upper trunk; in the inferior vermis the pelvic–girdle or lower trunk. Synergic control of the limbs is in the lateral hemispheres, for the upper limbs in the superior portion, for the lower in the inferior'' (p. 376).

In their classic papers describing the results of ablation and stimulation in the cat, Chambers and Sprague (1955a, 1955b) argued that the cerebellum is longitudinally organised into two functional zones. The medial zone consists of the vermal cortex and fastigial nuclei; the intermediate zone of paravermal cortex and interpositus nuclei. They pointed out that the attributes of each zone correspond to the categories of motor function known as pyramidal and extra-pyramidal respectively. This ''zonal'' characterisation of the functions of the cerebellum stood in contrast to the concept of ''lobular'' organisation.

Schmahmann (2004, 2007) argued from clinical investigations that while the anterior lobe of the cerebellum is largely concerned with motor control, the cerebellar vermis is involved in emotional processing and the posterior lobe in cognitive processing. More recently, Stoodley and Schmahmann (2009b) carried out a meta-analysis of published neuroimaging studies in healthy participants (see also Schoch et al., 2006 for a large scale study). Their results suggested that sensori-motor tasks engaged lobule 5 (along with V1 and VIII) of the anterior lobe and that ''language, working memory and spatial processing were largely localized to lobules V1, Crus 1 and Crus 11. Emotional processing included a midline peak in lobule V11At, and hemispheric activation peaks in lobules V1 and Crus 1. Executive functions showed a distributed pattern, and included bilateral regions in lobule V1, Crus 1, and V11B'' (p. 496).

The question of a possible involvement of the cerebellum in cognitive and affective processes has been overshadowed for more than a century by research interest in the motor role of the cerebellum. However, recent advances in elucidating the neuroanatomical connections of the cerebellum with the supratentorial regions that subserve cognition, combined with evidence from functional neuroimaging, neurophysiological and neuropsychological research, have extended the view of the cerebellum from that of a simple co-ordinator of autonomic and somatic motor function. Yet despite the considerable effort currently devoted to investigating non-motor functions of the cerebellum we do not understand the precise nature of these functions. To do so will require continued investigation of the anatomy and physiology of this structure, together with behavioural and clinical studies of the effects of cerebellar lesions in patients and theoretically driven experimental and neuroimaging investigations with healthy volunteers. Each of these different methodologies and approaches is represented in the papers included in this special issue. As well as providing new data, the collection of papers includes a number of review articles which we believe will be of interest to readers of *Cortex*, especially those for whom this area of research is relatively unfamiliar.

In the first paper of the special issue Cantalupo and Hopkins (2010, this issue) place the development of the human cerebellum within a comparative and evolutionary framework. They point out that great apes show relatively greater size of the cerebellum, especially of the lateral neo-cerebellum known to be involved in planning of reaching and visually guided movements, than do monkeys. Cantalupo and Hopkins (2010, this issue) present data relating cerebellar size and asymmetry in the chimpanzee to evolutionarily significant behaviours, namely tool use and aimed throwing, and show that handedness (or armedness) for throwing is related to asymmetry in volume of the cerebellum.

In the next paper, Stoodley and Schmahmann (2010, this issue) analyse anatomical, functional neuroimaging, and clinical data to test the hypothesis of a topographic organisation of the human cerebellum. Evidence is presented that supports a regional organisation of motor, cognitive, and limbic behaviours. The authors consider this functional topography of the cerebellum to be a consequence of the differential arrangement of connections of the cerebellum with the spinal cord, brainstem, and cerebral hemispheres, reflecting cerebellar incorporation into the distributed neural circuits subserving movement, cognition, and emotion.

Timmann et al. (2010, this issue) compare the results of human cerebellar lesion studies investigating associative learning in the motor, emotional and cognitive domain. The authors show that such studies provide evidence for a role of the cerebellum in motor, emotional and cognitive associative learning. Given its simple and homogeneous micro-circuitry, the authors hypothesise that a common computation may underly cerebellar involvement in these different forms of associative learning and that the overall task of the cerebellum may be to provide correct predictions about the relationship between sensory stimuli.

In his paper Murdoch (2010, this issue) critically reviews the neuroanatomical, clinical and functional neuroimaging evidence suggestive of a crucial role for the cerebellum in various aspects of language processing. The possible neuropathophysiological substrates of language impairment associated with cerebellar pathology are discussed and the nature of the linguistic deficits associated with disease or damage to the cerebellum are described.

Baillieux et al. (2010, this issue) explore the neuropsychological deficits seen in a group of 18 patients with vascular ($n = 13$) and neoplastic ($n = 5$) lesions of the cerebellum. They report finding a wide range of deficits in language, attention, executive function and memory which they relate to lateralised modulation of cognitive functions through the mechanism of crossed cerebello-cerebral diaschisis.

The interaction between the cerebellum and the neo-cortex in regard to executive function and working memory is explored in the contribution by Marvel and Desmond (2010, this issue). Their fMRI findings add to existing data that suggest a functional and anatomical dissociation between dorsal (motor) and ventral (cognitive) regions within the dentate nucleus. Durisko and Fiez (2010, this issue) also examine working memory using fMRI, distinguishing between regions of the cerebellum involved in overt and covert speech tasks on the one hand and verbal working memory tasks on the other. These two papers indicate the complexity of the problem that confronts us in attempting to understand how different cerebellar regions contribute to performance on different experimental tasks.

To investigate the influence of structural anomalies on cognitive, linguistic and emotional development, Tavano and Borgatti (2010, this issue) compared the neurobehavioural profiles of children with Joubert syndrome and children with malformations confined to the cerebellar vermis and one or both cerebellar hemispheres. The overall evidence provides support for an important role of cerebellar structures per se in shaping emotional, cognitive and linguistic development, when vermian lesions are associated with cerebellar hemispheric lesions. Lesions restricted to cerebellar vermis and brainstem, by comparison, appear to have a major impact on motor-related skills, including oro-motor abilities and verbal working memory.

On the basis of a comparative study, Davis et al. (2010, this issue) show that children who receive treatment early in life for a cerebellar tumour are likely to suffer adverse development of both cognitive and motor ability. Type of tumour/treatment and age at diagnosis were found to be the most reliable predictors of subsequent outcome. Catsman-Berrevoets and Aarsen (2010, this issue) analysed the spectrum of behavioural abnormalities, speech and language characteristics in a cohort of 41 children with the posterior fossa syndrome following cerebellar tumour surgery. During recovery all children were dysarthric, but only a few patients presented speech features specific to cerebellar dysarthria. A significant correlation was found between duration of mutism and severity of neurological symptoms. Significant correlations were also found between duration of mutism and abnormalities on SPECT.

It is clear from the papers in this special issue that the role of the cerebellum remains something of an enigma and there is much yet to learn. The Belgian artist Igor Verpoorten hints at this in the artwork on the cover of this special issue, evoking a dark-sided, cerebellar part of the brain, the functions of which remain to be fully elucidated. It is our hope that the papers we have gathered together will not only stimulate further research into the role of this mysterious organ but help to refine the experimental approaches and methodological controls required to do so. Unfortunately, not all the individuals we contacted were able to accept our invitation to contribute within the time frame available, given their other commitments, but we trust that, like us, they would have been pleased to have been associated with the final collection of papers we have assembled. These include not only the papers in the current issue but a number of review papers. The latter cover functional localisation in the cerebellum (Glickstein et al., in press), cognitive repercussions of hereditary cerebellar disorders (Manto and Lorivel, in press), the cerebellum and dyslexia (Stoodley and Stein, in press), developmental disorders more generally (Nicolson and Fawcett, in press), cerebellar involvement in associative learning (Bellebaum and Daum, in press), and the sequencing hypothesis of cerebellar function (Leggio et al., in press). The review papers will appear in the January 2011 issue of *Cortex*, and will provide a forum for discussion.

We wish again to thank all our invited contributors for their manuscripts and for bearing patiently with us in the sometimes protracted matter of editing and revising their papers. We also wish to thank our long suffering referees without whom we could not have produced this special issue. As often happens, referees did not always agree with each other, nor we with them, and we were sometimes obliged to steer a middle course between competing opinions. We hope that in so doing we have not unduly offended any academic sensibilities. Finally, we wish to express our gratitude to the editorial assistants at the *Cortex* office, Mrs. Cheryl Phillips, Mr. Oliver Stewart and Dr. Laura Valkonen who willingly gave of their time and expertise in many ways, not least in helping us to navigate (with a greater or lesser degree of success) the vagaries of the on-line submission system!

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