cortex 46 (2010) 858–868

available at www.sciencedirect.com

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journal homepage: www.elsevier.com/locate/cortex

Special issue: Review

The cerebellum and language: Historical perspective and review

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ARTICLE INFO

Article history:
Received 26 March 2009
Reviewed 12 May 2009
Revised 4 June 2009
Accepted 14 September 2009
Published online 24 September 2009

Keywords:
Cerebellum
Cerebellar language disorders

ABSTRACT

Investigation of a possible role for the cerebellum in the mediation of cognitive processes, including language, has historically been overshadowed by research interest in cerebellar coordination of motor control. Over the past two decades, however, the question of a possible participation of the cerebellum in language processing itself has come to the forefront. In particular recent advances in our understanding of the neuroanatomy of the cerebellum combined with evidence from functional neuroimaging, neurophysiological and neuropsychological research, have extended our view of the cerebellum from that of a simple coordinator of autonomic and somatic motor function. Rather it is now more widely accepted that the cerebellum, and in particular the right cerebellar hemisphere, participates in modulation of cognitive functioning, especially to those parts of the brain to which it is reciprocally connected. The present paper reviews the neuroanatomical, clinical and functional neuroimaging evidence suggestive of a role for the cerebellum in 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 described.

1. Introduction

The cerebellum has traditionally been viewed as part of the brain dedicated to the regulation and coordination of motor function, a view held since the early 19th century based on reports of the effects of ablation of the cerebellum in animals and reinforced by the first clinical reports of patients with cerebellar pathology by Babinski (1913) and Holmes (1917, 1922). Consistent with this view, the majority of cerebellar lesion studies reported throughout the 20th century largely focussed on investigations into the nature of associated motor impairments to the exclusion of its broader capabilities. Unfortunately, until recently, this pre-occupation with cerebellar coordination of motor control overshadowed any consideration of a possible role for the cerebellum in cognitive and language processing. This oversight is even more surprising given some of the anatomical and functional features of the cerebellum which include: The population of neurones in the cerebellum exceed that of any other part of the human nervous system, including the cerebral cortex; its speed of operation allows it to respond rapidly to information it receives; its massive neural connections with the cerebral cortex, which sends more fibres to the cerebellum than any other part of the nervous system; the extensive connections of

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0010-9452/$ – see front matter
doi:10.1016/j.cortex.2009.07.018

its output fibres which pass to many other parts of the nervous system, including areas of the cerebral cortex well beyond motor areas.

Since the mid 1980s, however, methodological and conceptual advances of contemporary neuroscience have brought about a substantial modification of the traditional view of the cerebellum as a mere coordinator of autonomic and somatic motor functions. These advances have included: Realization of the importance of parallels in the phylogenetic development of the neocerebellum and association areas of the cerebral cortex; greater understanding of the neuroanatomy of the cerebellum and its connections with the cerebral cortex; introduction of advanced neuroimaging techniques, including functional neuroimaging, capable of detecting activation of the cerebellum during performance of language tasks; and advances in neuropsychological/linguistic testing capable of detection of subtle changes in cognitive/linguistic function in patients with cerebellar pathology. Collectively these advances in neuroscience have established the view that the cerebellum participates in a much wider range of functions than conventionally accepted, including cognitive and linguistic functions among others, in addition to regulation and coordination of motor function.

Bloedel and Bracha (1997) outlined five periods in the conceptual growth and development of insights into cerebellar functioning. Firstly, the role of the cerebellum was considered to be coordination of voluntary movements and orientation of the body and head in space. Next, an additional function of the cerebellum was considered to be the regulation and integration of sensory information for reflex organization. Thirdly, the cerebellum was believed to also be responsible for regulating vestibulo-ocular movements and posture of the head. Fourthly, the cerebellum was recognized as an essential structure for learning conditioned responses. Lastly and most currently, various investigations have indicated a possible role for the cerebellum in the regulation of linguistic, cognitive, and affective functions.

Currently, it is thought that, in addition to its contribution to motor control, the cerebellum (particularly the right cerebellum) is responsible for modulating non-motor language processes and cognitive functions of those parts of the brain to which it is reciprocally connected (Lalonde and Botez-Marquard, 2000; Silveri and Misciagna, 2000; Marien et al., 2001). Thus the particular role of the cerebellum in this domain is to modulate rather than generate language and cognition, the latter function being considered to be specific to supratentorial structures, particularly the cerebral cortex (Silveri and Misciagna, 2000). Silveri and Misciagna (2000) described this role of the cerebellum as representing the interface between cognition and execution, coordinating information coming from the supratentorial structures responsible for the precise cognitive process and its executive level. This proposed role for the cerebellum in modulating language has major implications for the assessment and rehabilitation of patients with cerebellar lesions and challenges conventional localizationist theories which promote cerebral cortical exclusivity in relation to language processing in the brain.

Several reasons possibly underly why the recently recognized role for the cerebellum in language and cognition was overlooked for several centuries. According to some authors, a primary explanation lies in the modulatory role of the cerebellum in language and cognition, which results in linguistic and cognitive impairments that are both qualitatively and quantitatively different from those produced by lesions of supratentorial structures (Silveri and Misciagna, 2000). Akin to models of motor control that define a role for the cerebellum in the refinement and coordination of movement (Fabbro, 2000), cerebellar contributions to cognition have been postulated as high-level in nature (Chafetz et al., 1996; Marien et al., 2001). In relation to language, it has been proposed that cerebellar lesions may evoke a form of linguistic incoordination or crudity, potentially manifesting as high-level language deficits (Cook et al., 2004). Complex or high-level language measures have been described as tasks that demand frontal lobe support in the manipulation of novel situations, lexical-semantic operations, the development of language strategies, and the organization and monitoring of responses (Copland et al., 2000). Detection of these high-level linguistic impairments with routine language tests may have been difficult in previous investigations, as standard language test batteries may not have been sensitive or extensive enough to identify such subtle deficits that may follow cerebellar damage (Cook et al., 2004; Murdoch and Whelan, 2007). Consequently the presence of subtle, high-level language problems although present, would most likely have been masked by the severity of any motor impairment in patients with cerebellar pathology. Based on the findings of Cook et al. (2004), it would appear that linguistic disturbances subsequent to cerebellar lesions may be more accurately detected and characterized by high-level assessments that evaluate the proficiency of more complex language processes beyond single word hierarchies.

The aim of the present paper is to review the neuroanatomical, clinical and neuroimaging evidence suggestive of a role for the cerebellum in language. Further, the possible neuropathophysiological substrates of language impairment associated with cerebellar pathology will be explored and the nature of linguistic deficits caused by disease or destruction of the cerebellum described.

2. Evidence from neuroanatomical studies

The primary factor, and hence the cornerstone, in the development of the concept of a cerebellar role in language was the discovery of major reciprocal neural pathways between the cerebellum and frontal areas of the language-dominant hemisphere, including Broca's area and the supplementary motor area. In particular the work of Leiner et al. (1986, 1987, 1991, 1993) was fundamental to this development in that they were the first to draw attention to the possibility that expanded connections from the cerebellum to the cerebral cortex and from the cortex to the cerebellum present in human brains but not in less evolved species, provided a potential neural substrate for the cerebellum to participate in cognitive/linguistic functions in addition to motor functions. Specifically, Leiner et al. (1986, 1987, 1989, 1991) drew attention to long-neglected evidence that the lateral portion of the cerebellar hemispheres and dentate nuclei (particularly the ventrolateral phylogenetically newer part referred to as the neodentate) had enlarged significantly greater than any other part of the brain with the exception of the cerebral cortex, during the phylogenetic evolution of the human brain. Importantly this expansion in size had not occurred in parallel with the cerebral cortex as a whole, but rather specifically in parallel with the cerebral association areas (Leiner et al., 1986). In the course of human evolution these expanded parts of the cerebellum became linked to newly enlarged areas of the cerebral cortex to form a phylogenetically new cerebro-cerebellar system in humans. Of particular relevance to enabling the cerebellum to contribute to cognitive/linguistic processes, these newly formed links between the neocerebellum and the frontal lobe included not only the frontal motor areas (Brodmann areas 4 and 6) but also other areas of the frontal cortex including Broca's area (Brodmann areas 44 and 45) which in turn send back new connections to the cerebellum. This reciprocal connectivity forms a series of segregated neural loops that are hypothesized to facilitate cognitive/linguistic function in the same way that the cerebellum enhances motor functions (Leiner et al., 1989).

It has been proposed that the cerebrocortico-cerebellar loops that connect the lateral parts of the cerebellar hemispheres to the frontal lobe consist of a feedforward, afferent limb and a feedback efferent limb (Leiner et al., 1986; Schmahmann, 1996). The feedforward limb is comprised of two pathways, one of which passes from the cerebral cortex to the pontine nuclei in the brainstem (cerebrocortico-pontine pathways) and from there connects via mossy fibre projections to the cortex of the lateral portion of the cerebellar hemispheres (ponto-cerebellar pathways). The second feedforward limb passes from the cerebral cortex to the red nucleus, from where the central tegmental tract leads to the inferior olivary nucleus and then via climbing fibres to the lateral cerebellar cortex (Schmahmann, 1996). The feedback limb passes from the dentate nucleus, the primary outflow nucleus of the cerebellum to the nucleus ventralis intermedius and nucleus ventralis anterior of the thalamus via the cerebello-thalamic pathways and from there to various areas in the contralateral frontal lobe (including Brodmann areas 6, 44 and 45) via the thalamo-cortical pathways (Schmahmann, 1996; Engelborghs et al., 1998). Therefore, although the cerebellum is a relay for many circuits involved in the control process of several physiological functions (e.g., vestibulo-cerebellar-vestibular loops regulate equilibrium and ocular motility; reticulo-cerebello-reticular loops are involved in muscle tone, control of posture and regulation of several vegetative functions; spino-cerebello-rubro-spinal loops participate in regulation of motor function at the spinal level; hypothalamo-cerebello-hypothalamic loops regulate visceral functions) the primary loops involved in the regulation of voluntary movements and cognitive/linguistic functions are the cerebrocortico-ponto-cerebellocortico-dentato-thalamo-cerebrocortical loops (Bloedel and Bracha, 1997; Middleton and Strick, 1997; Schmahmann and Pandya, 1997) and the cerebrocortico-rubro-olivo-neodentato-cerebrocortical loops (Leiner et al., 1991, 1993). Importantly, in both loops each cerebellar hemisphere sends information to, and receives it from the contralateral cerebral hemisphere. Therefore the right cerebellar hemisphere is connected to the left cerebral hemisphere and conversely. A diagramatic representation of major cerebrocortico-cerebellar loops in the human brain proposed by Leiner et al. (1989) is shown in Fig. 1.

Several neuroanatomical studies of the cerebellum have provided critical evidence that the proposed circuits connecting the cerebellum and non-motor cortical areas do exist. For example, Middleton and Strick (1994) reported retrograde transneuronal transport of a retroviral tracer from the dorsolateral prefrontal cortex to the dentate nucleus. More recently, the same authors also using a retrograde transneuronal transport technique demonstrated the presence of cerebello-thalamo-cortical pathways in primates (Middleton and Strick, 2000).

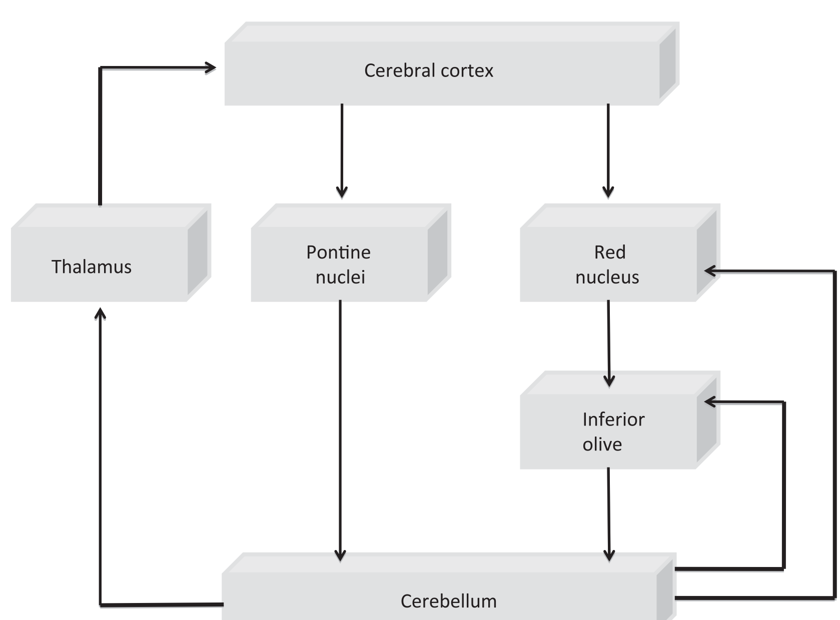

Fig. 1 – Modified schematic diagram of major cerebro-cerebellar loops in the human brain. Adapted from Leiner et al. (1989).

In summary, anatomically cerebello-cerebrocortical pathways lend themselves to a neuroregulatory role apropos non-motor and motor functions, via associative as well as motor cortex terminations. More specifically, the prefrontal, parietal, temporal, and paralimbic cortices demonstrate topographically organized feedforward projections to the cerebellum which are siphoned through cortico-pontine and cortico-rubro-olivary pathways and transmitted via deep cerebellar nuclei (particularly the dentate nucleus) to thalamic nuclei and then back to the cerebral cortex (Schmahmann, 1996; Middleton and Strick, 2000). It has been proposed that this configuration provides a neural substrate whereby the cerebellum may be actively and directly involved in the organization, construction and execution of higher order behaviours, including language.

The reciprocal neuroanatomical connections between the cerebellum and cerebral cortex that are proposed to enable cerebellar input into cognitive linguistic functions have a number of parallel features to equivalent pathways involved in the coordination and modulation of motor function. Indeed, models of motor control have been lent in the translation of cerebellar cognitive disturbances. The term "cerebellar cognitive affective syndrome" was coined by Schmahmann and Sherman (1998) to describe a syndrome typically characterized by impaired executive function, spatial cognition, linguistic processing and affective regulation, and has been operationally defined as "dysmetria of thought" (Schmahmann, 1991, 1996; Gottwald et al., 2003). Analagous to the overshooting and undershooting of ataxic limb movements, dysmetria of thought has been hypothesized to involve either the inadequate or overly elaborate planning or misinterpretation of stimuli. In relation to cognition, the intact cerebellum has been described as capable of detecting, preventing, and correcting mismatches between the intended outcomes and the perceived outcomes of an organism's interaction with the environment (Schmahmann, 1998). Therefore, in the same way as the cerebellum regulates the rate, force, rhythm and accuracy of movement, it may also control the speed, capacity, consistency and appropriateness of cognitive and linguistic processing.

3. Evidence from clinical studies

Further evidence for a role for the cerebellum in language has been derived from the evaluation of the performance of patients with various cerebellar pathologies (including cerebellar atrophy and focal lesions caused by strokes or tumours) on a range of linguistic and neuropsychological tests. The results from several clinical studies converge with the evidence from neuroanatomical and neuroimaging studies to implicate the cerebellum in various aspects of language function. Fiez et al. (1992) examined a patient with a vascular lesion of the right cerebellar hemisphere on a word generation task. Although the patient had high-level conversational skills and normal performance on standard neuropsychological assessments, he had difficulty storing information and failed in various semantic word generation tasks. For instance when asked to generate verbs in response to nouns, he produced many associated but incorrect errors (e.g., although associated many errors were not verbs such as "red" in response to "brick") and failed to learn the task normally. Fiez et al. (1992) theorized that the deficits evident in this case indicated that the right cerebellar hemisphere was involved in error detection tasks and control of some semantic and syntactic aspects of language production. Patients with cerebellar lesions have also been reported to have difficulty learning new verbal associations by other researchers. For instance, Bracke-Tolkmitt et al. (1989) reported that a group of patients with cerebellar damage were significantly impaired compared to matched controls at learning random associations between six words and six colours.

Three aetiologically distinct patient groups with cerebellar pathology were studied by Leggio et al. (1995) using both phonological and semantic fluency tests. The phonological tasks required the subjects to produce as many words as possible with the initial phonemes F, A, and S within 1 min. The semantic verbal fluency tasks consisted of the generation of as many words as possible belonging to the semantic categories "birds" and "furniture". Two of the groups had restricted focal lesions (lateral part of the left or right cerebellar hemisphere) while the third group had atrophic lesions (mainly involving the vermis or paravermal region). Leggio et al. (1995) reported that as a group the subjects with cerebellar lesions performed at a lower level than matched controls on both the phonological and semantic fluency tasks. In addition the atrophic patients obtained better results than those with focal lesions despite having more severe ataxic impairments. The patients with atrophic lesions performed significantly poorer than controls only on the phonological task and patients with lesions involving the right lateral cerebellum performed slightly worse than those with focal lesions to the left cerebellar hemisphere. Overall these findings provided further evidence in support of a functional role for the cerebellum in language and suggested a strong association, firstly between damage to the lateral cerebellum, especially the right cerebellar hemisphere and verbal fluency deficits and secondly between medial cerebellar lesions and the prevalence of motor deficits. These findings were later confirmed by Leggio et al. (2000) who also demonstrated that the observed deficits in verbal fluency were not the outcome of motor speech impairment. These latter authors also proposed that cerebellar lesions affect phonological processes to a greater extent than semantic processes because phonological tasks depend on unusual novel and less automatized search strategies than semantic tasks.

According to Silveri and Misciagna (2000), patients with cerebellar damage show differing degrees of impairment in the various cognitive domains. In fact, different impairments are recognized at different levels of linguistic organization, from the articulatory level to sentence production. The cerebellum is active, according to Silveri and Misciagna (2000), in tasks requiring single word selection and production. However, as noted in the findings of neuroimaging studies discussed above (e.g., Silveri et al., 1994), one of the most interesting findings in patients with cerebellar lesions is agrammatic speech (a disorder in speech production characterized by simplification of the syntactic structures, reduced sentence length and omission and substitution of grammatical morphemes) (Silveri and Misciagna, 2000). Several other researchers have also reported agrammatism in association with right cerebellar lesions (Zettin et al., 1997; Gasparini et al., 1999; Justus, 2004). Justus (2004) reported that individuals with cerebellar lesions are less able to discriminate grammatical and ungrammatical sentences than controls suggesting that damage to the cerebellum can result in subtle impairments in the use of grammatical morphology. Occasionally, production of content words is impaired to different degrees, such that verbs, for example, may be produced with more difficulty than nouns (Silveri and Misciagna, 2000).

The language abilities of four patients with focal cerebellar lesions of differing aetiologies and localized in different areas of the cerebellum were investigated by Fabbro et al. (2000) to determine if linguistic difficulties existed and whether these deficits were stable or evolved following surgery. All four patients exhibited mild language impairments, particularly affecting morphosyntactic features and lexical access. The first patient, who presented with an arachnoid cyst compressing the superior portion of the vermis, exhibited some morphosyntactic errors in pre-operative spontaneous speech, while a few months post-surgery no errors were found. While propositioning had reportedly improved from the pre-surgical assessment, the most compromised linguistic level was found to be syntax. Difficulties in some word generation tasks were also reported, particularly synonym and attribute generation. The second case presented with a hemangioblastoma compressing the right cerebellar hemisphere. While spontaneous speech remained fluent, some of the morphosyntactical errors exhibited pre- and post-surgery resolved ten months following surgery, as did deficits in syntactic comprehension, reading and writing. Improvement of propositionizing skills and morphological and syntactic levels also occurred, although difficulties in mental arithmetic and synonym generation did not change. The third patient was diagnosed with an astrocytoma in the vermis and exhibited cerebellar dysarthria, nonfluent spontaneous speech, and morphosyntactic errors following surgery. An assessment of language revealed difficulties in grammatical comprehension, antonyms, morphological opposities, reading and writing, with the most compromised tasks including propositionizing and lexical access. Of most significance were impairments in morphology, syntax, and semantics. Fabbro et al. (2000) suggested that findings from this case particularly supported involvement of both the right cerebellar hemisphere and the vermis in language processing. The final patient, with an astrocytoma involving the left cerebellar hemisphere, exhibited fluent spontaneous speech with some morphosyntactic errors, poor grammatical comprehension and arithmetic, significantly poor performance in both propositionizing and reading, and significantly impaired syntax. While two of the patients (one with an arachnoid cyst compressing the superior portion of the vermis, and the other with a hemangioblastoma compressing the right cerebellar hemisphere) showed partial recovery of linguistic deficits following surgery, the remaining two (both with cerebellar tumours) did not experience an improvement in language function.

In contrast, based on administration of standard aphasia tests to children and adolescents with acute focal cerebellar lesions following surgery for the treatment of posterior fossa tumours, Frank et al. (2008) reported no statistically significant difference in the language abilities of children with right and left-sided lesions and controls. These authors did, however, note the presence of mild signs of language disturbance, primarily related to reduced performance on written language tasks, in two subjects with right-sided cerebellar lesions.

Fabbro et al. (2000) believed that the mild linguistic deficits evidenced by their four cases with focal cerebellar lesions demonstrated an alteration of language control processes rather than to a structural impairment of specific components of the language system. In their view, the vermis and portions of the cerebellar hemispheres operate within a large functional language network as an organizational control mechanism via the frontal lobe system. The rapid recovery of linguistic disturbances noted in two of the four patients following acute cerebellar damage was attributed to partial functional reactivation of linguistic centres after regression of diaschisis phenomena. The recognition that linguistic deficits may be compensated for over time prompted Frank et al. (2007) to examine language function in children and adolescents in the acute stage (a few days) after surgically induced cerebellar lesions when maximal disruption of language function could be expected. Although their findings suggested that acute cerebellar lesions do not significantly impair verb generation to picture objects, the authors recommended confirmation of their results in a larger cohort of subjects, in particular in children and adolescents with acute right-sided cerebellar lesions.

While the findings of Fabbro et al. (2000) generally supported the view that the cerebellar structures involved in language are essentially the right cerebellar hemisphere and some structures of the vermis, one of their four cases demonstrated linguistic deficits subsequent to a tumour in the left cerebellar hemisphere that were similar to those observed in the three cases with right cerebellar lesions. Although the concept of “crossed aphasia” in relation to cortical-based language disorders is well documented, to date only two other studies in addition to Fabbro et al. (2000) have reported the occurrence of language problems in right-handed individuals in association with left cerebellar hemisphere lesions (Cook et al., 2004; Murdoch and Whelan, 2007). Cook et al. (2004) outlined the linguistic profiles of five individuals with left primary cerebellar lesions of vascular origin. All five of their participants demonstrated deficits on measures of word fluency, sentence construction within a set context, producing word definitions and producing multiple definitions of the same words. Cook et al. (2004) also reported deficits for several of their participants on measures of understanding figurative language, forming word associations, identifying and correcting semantic absurdities and producing synonyms and antonyms.

The findings of Murdoch and Whelan (2007) supported those of Cook et al. (2004) that left cerebellar lesions may disrupt language processing, particularly in the area of complex or high-level language skills, including phonemic fluency, sentence formulation and lexical-semantic manipulation tasks. Such tasks, involving the manipulation of novel situations, lexical-semantic operations, the development of language strategies and the organization and monitoring of responses, have been hypothesized to demand frontal lobe support in their manipulation (Copland et al., 2000). Murdoch and Whelan (2007) therefore suggested that frontal lobe hypoperfusion as a consequence of ipsilateral cortical diaschisis provided one plausible explanation for the language deficits exhibited by their 10 patients with primary left cerebellar vascular lesions. Ipsilateral cerebellar-cerebral diaschisis has been reported as a consequence of cerebellar lesions (Beldarrain et al., 1997). In an investigation of the relationship between neuropsychological deficits (including language) and single photon emission computed tomography (SPECT) scan perfusion patterns in the cerebral hemispheres subsequent to cerebellar lesions, Beldarrain et al. (1997) noted that of the nineteen participants in their study who underwent a SPECT scan, six showed contralateral diaschisis and seven ipsilateral diaschisis with the remaining six subjects showing no evidence of diaschisis. On the basis of their findings, Murdoch and Whelan (2007) suggested that cerebellar involvement in language may be bilateral. Collectively the findings of Fabbro et al. (2000), Cook et al. (2004), and Murdoch and Whelan (2007) highlight the need for further investigation of language disorders associated with both left and right cerebellar lesions in order to further elucidate the extent and nature of language lateralization in the cerebellum.

4. Evidence from functional neuroimaging studies

In addition to the neuroanatomical and clinical evidence outlined above, data supporting participation of the cerebellum in language has also, in recent years come from a number of functional neuroimaging studies that have utilized techniques such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI) and SPECT. These techniques are important because they represent the only relatively non-invasive means of monitoring neuronal activity in humans by directly measuring associated changes in blood flow and oxygenation. In general these studies have shown that the right lateral cerebellum (neocerebellum) is activated during cognitive processing of words, while anatomically distinct from areas activated during performance of motor tasks.

Petersen et al. (1988, 1989) were among the first to report cerebellar changes in blood flow as measured by PET during a word generation task. Specifically these authors reported right lateral cerebellar activation when subjects were asked to produce appropriate verbs in response to visually presented nouns (e.g., ‘‘bark’’ in response to ‘‘dog’’) but not when they read the nouns aloud. Since their subjects produced spoken words in both tasks, the increase in blood flow observed in the right lateral cerebellum, which projects to the left prefrontal language areas, was interpreted as support for the hypothesis of cerebellar involvement in non-motor language. Although subsequent studies have varied the original task design, activation of the right lateral cerebellum during word generation tasks has been consistently reproduced (Raichle et al., 1994; Martin et al., 1995; Grabowski et al., 1996). Leiner et al. (1989) interpreted the simultaneous activation of the right lateral cerebellum and Broca’s area during word generation as a reflection of accelerated transmission of signals between these two centres during word finding.

In an examination of human visual information processing, Shulman et al. (1997) analyzed nine PET studies to determine the consistency of brain blood flow increases during active relative to passive viewing of the same stimulus array. While no consistent blood flow increases were found in the cerebral cortex outside of the visual cortex, increases were observed in the thalamus and cerebellum. More specifically, a left cerebellar and a medial cerebellar focus reflected motor-related processes, whereas blood flow increases in the right cerebellar region were considered to be not motor related. The right thalamic focus exhibited sensitivity to variables related to focal attention, suggesting involvement of this region in the attentional engagement of visual stimuli (Shulman et al., 1997). The left thalamic focus, however, was completely uncorrelated with the right region, indicating involvement in separate functions. The results of the study indicated that both the left thalamus and right cerebellum yielded larger blood flow increases when subjects performed a complex rather than a simple language task which, according to Shulman et al. (1997) possibly reflected a language-related pathway. Based on their observations, Shulman et al. (1997) concluded that the left-frontal cortex, left thalamus and right cerebellum may form a circuit in certain language tasks. In support of this suggestion, based on a PET activation study of naming-related brain activity, Grönholm et al. (2005) also implicated the cerebellum in a left-lateralized network, that also included the left-dominant frontotemporal areas of the cerebral cortex, that is recruited during naming of newly learned objects. The right dorsolateral prefrontal cortex and the right cerebellum have also been suggested to form part of the syntactic analysis network involved in prosodic segmentation and pitch processing (Strelnikov et al., 2006).

In contrast to the several PET studies suggesting a contribution of the lateral aspects of the right cerebellar hemisphere to the cognitive aspects of speech production, Ackermann et al. (1998) report that in their study of eighteen subjects who underwent fMRI during continuous silent automatic speech (recitation of names of the months of the year), that observed cerebellar activation appeared to be related to the articulatory level of speech. During the study, activation in the right cerebellar hemisphere together with an asymmetric activation pattern occurred towards the left side at the level of the motor strip in the cerebral cortex. These authors argued that this was attributable to the fact that highly overlearned word strings supposedly posed few demands on the controlled response selection, together with the fact that the projections of the right cerebellar hemisphere to the left precentral gyrus also participate in motor control.

Desmond et al. (1998) used fMRI to examine the distinctive contributions of the right cerebellar regions and left-frontal cerebral cortex using a word stem completion task. Subjects were asked to complete three-letter word stems that had either many possible completions (e.g., STA-) or few possible completions (e.g., PSA-). Findings revealed that conspicuous increases in activation were observed in the left middle frontal gyrus and left caudate nucleus in the condition which had many word stem completions, compared to the condition with few possible word stem completions. Conversely, portions of the right cerebellar hemisphere (posterior quadrangular lobule and superior semilunar lobule) and cerebellar vermis exhibited increases in the "few" condition, in comparison to the "many" condition. The authors believed that this double dissociation suggested that the frontal and cerebellar regions make distinctive contributions to cognitive performance, with left-frontal (and striatal) activations reflecting response selection (which increases in difficulty when there are many appropriate responses), and right cerebellar activations illustrating the search for responses (which increases in difficulty when even a single appropriate response is hard to retrieve). Desmond et al. (1998) concluded that these results did not challenge previous findings that the left-frontal and right cerebellar regions regularly interact in verbal performance, but rather believed that such findings demonstrated that these two regions make distinctive contributions to that interaction, providing insight into the nature of such unique contributions. In addition to the increased need for working memory resources required for the search for responses, the "few" condition may also require more error correction in order to reject similar but incorrect matches that would likely occur more often for the "few" condition. Desmond et al. (1998) therefore suggested that the right cerebellar activations may also reflect such error correction operations.

Further support for a role for the right cerebellar hemisphere in the non-motor aspects of language was provided by the work of Schloesser et al. (1998), Papthanassiou et al. (2000), Xiang et al. (2003) and Frings et al. (2006). Using fMRI, Frings et al. (2006) provided evidence for involvement of the right lateral cerebellar hemisphere in linguistic functions during verb generation. Xiang et al. (2003) used fMRI to examine cerebellar activation in six healthy Chinese speakers during performance of three semantic tasks with differing loads of discrimination. They reported activation in distributed brain areas, including the right posterior-inferior cerebellum, during performance of all three semantic tasks leading them to conclude that cerebellar activation is involved in semantic discrimination. Importantly, stronger cerebellar activation was observed during performance of more difficult semantic tasks indicating that the level of cerebellar activation is modulated by discrimination difficulty. Based on a PET study, Papthanassiou et al. (2000) reported right cerebellar cortex activation during both speech comprehension and production, which was particularly evident during a verb generation task. These authors believed that the findings were indicative of a cerebellar control of the neural computations involved during word semantic processing. Using fMRI, Schloesser et al. (1998) reported areas of activation in the left prefrontal cortex and right cerebellum in subjects during performance of a verbal fluency task.

Neurological evidence to support a role for the left cerebellar hemisphere in language was provided by Pillai et al. (2004). These latter authors examined language-related differences in bilateral fMRI cerebellar activation in speakers of Spanish and English. Specifically, they reported the presence of left-lateralized cerebellar activation during language processing in both languages, with greater contribution of the left cerebellar hemisphere to overall cerebellar activation in the non-native language (English) than the native language (Spanish). More recently Connor et al. (2006) using fMRI provided evidence that cerebellar activity switches from the right cerebellar hemisphere to the left cerebellar hemisphere in parallel with recruitment of putative compensatory right homologous frontal regions in patients post-stroke. These latter findings support the suggestion that right frontal and left cerebellar circuits may be relevant to recovered/residual verbal function following stroke. Consistent with this suggestion, Lidzba et al. (2008) have recently demonstrated that individuals with congenital focal lesions in the left cerebral hemisphere reorganize their entire language network into the right cerebral and left cerebellar hemispheres to create a mirror-image organization of the cerebro-cerebellar network engaged in language.

Based on a review of functional neuroimaging studies reporting changes in cerebellar activation during cognitive tasks, Desmond and Fiez (1998) concluded that the cerebellum is involved in basic cognitive processes such as working memory, implicit and explicit learning and memory, and language. These authors also concluded that unlike damage to the left-hemisphere perisylvian regions, damage to the cerebellum is not firmly related to central disturbances of language and reading as in the acquired aphasias and dyslexias, suggesting rather that the cerebellum is not integral to the access and representation of orthographic, phonological, semantic and syntactic information, and that it exerts a more indirect influence. For example, the verb generation task often used to highlight involvement of the cerebellum in language processing [e.g., in studies such as Petersen et al. (1988, 1989)] has features associated with implicit learning tasks, such that performance improves rapidly with practice (Desmond and Fiez, 1998). Additionally, the cerebellum may participate in the search for valid responses from semantic memory, possibly forming the basis for improved performance observed with repeated exposure of the same items (Desmond and Fiez, 1998).

Functional neuroimaging studies have also provided support for neuroanatomical data that suggests crossed reciprocal connections between the cerebellum and higher order cortical association areas (Silveri et al., 1994; Marien et al., 1996, 2000; Hubrich-Ungureanu et al., 2002; Jansen et al., 2005). Hubrich-Ungureanu et al. (2002) used fMRI to examine one left- and one right-handed volunteer during performance of a silent verbal fluency task. Their findings indicated that cerebellar activation is contralateral to the activation of the frontal cortex even under conditions of different language dominance. Similar findings were reported by Jansen et al. (2005). These latter authors used fMRI to determine the association between language-related lateralized activation of the frontal cortex with lateralized activation of the cerebellum in 14 healthy subjects, seven of whom displayed typical left-hemisphere dominance while the remaining seven subjects displayed atypical right-hemisphere language dominance. Results of the fMRI analysis performed during a letter-cued word generation task demonstrated activation of the cerebellar hemisphere contralateral to the language-dominant cerebral hemisphere in each subject. On the basis of these findings, Jansen et al. (2005) suggested that crossed cerebral and cerebellar language dominance is a typical characteristic of brain organization.

Silveri et al. (1994) described a 67-year-old right-handed patient who presented with a right-sided cerebellar syndrome, ataxic dysarthria and transient expressive agrammatism subsequent to a right cerebellar stroke. Although repeated structural neuroimaging examinations were unable to identify any supratentorial abnormality to account for the observed language deficits, a SPECT examination evidenced a relative hypoperfusion in the entire left cerebral hemisphere, but particularly involving the left posterior temporal region. During follow-up examinations, the perfusion defects were noted to parallel the clinical course of improvements in motor and linguistic symptoms.

Silveri et al. (1994) ascribed the agrammatism of their patient to a delay in the processes underlying sentence construction. More specifically, they proposed that the cerebellum has no direct influence on linguistic processing but rather plays an important role in the timing of linguistic functions represented at the level of the cerebral cortex. According to this ‘‘timing hypothesis’’, patients with cerebellar damage will experience great difficulty in temporal modulation, required for several linguistic processes such as phonological processing, sentence construction and comprehension and application of syntactic rules. They proposed that in the case they presented, the online application of syntactic rules may have been slowed, causing the representation of morphemes to decay from working memory leading to a disturbance in sentence integration. According to Silveri et al. (1994) therefore, language deficits following right cerebellar lesions are not really aphasic disorders but are due to the impairment of some cognitive components (e.g., working memory) that are involved in language processing.

A different hypothesis was proposed by Marien et al. (1996) who maintained that cerebellar lesions may provoke an aphasic syndrome. Marien et al. (1996, 2000) also reported the case of a 73-year-old right-handed patient who presented with a predominantly expressive aphasic syndrome and agrammatism subsequent to an ischaemic infarct in the territory of the right arteria cerebellaris superior. Specifically the aphasic disorder resembled a transcortical motor aphasia and was characterized by an impairment of syntax, reduced spontaneous speech, reduced verbal output, perseverations, word-finding difficulties, reduced speech rate, lack of content words, disturbances in mental spelling and comprehension of oral spelling, as well as an expressive and receptive agrammatism. Although the neuroanatomical correlates of this type of aphasia are reported to focus on the frontal lobe of the dominant cerebral hemisphere, repeated structural neuroimaging examinations involving computed tomography (CT) or magnetic resonance imaging (MRI) were unable to identify a lesion in the expected supratentorial areas. Repeated SPECT studies did, however, yield positive findings to account for the language symptoms. In addition to a marked hypoperfusion of the right cerebellar hemisphere, SPECT revealed a left frontoparietal hypoperfusion which involved the gyrus frontalis medius and inferior as well as the gyrus precentralis and postcentralis. As in the case reported by Silveri et al. (1994), improvements in linguistic performance paralleled reduction in the level of hypoperfusion.

Marien et al. (2000) believed that the co-occurrence of a right cerebellar lesion and an aphasic syndrome possibly illustrated the pathophysiological hypothesis of a deactivation of prefrontal left cerebral hemisphere language functions due to loss of excitatory impulses passing via the cerebello-ponto-thalamo-cerebrocortical pathways. This phenomenon called ‘‘crossed cerebello-cerebral diaschisis’’ was first documented in a patient with cerebellar infarction by Broich et al. (1987). If, as proposed by Marien et al. (1996, 2000) that the possible explanation for language disturbances following right cerebellar damage is a reduction of excitatory impulses through the cerebello-ponto-thalamo-cerebrocortical pathways (Sönmezoglu et al., 1993), it would follow that aphasia in cerebellar pathology does not imply representation of language functions at the level of the cerebellum but rather reflects a diaschisis phenomenon involving diminished or abolished function of the supratentorial ‘‘language zones’’ due to reduced input via cerebellocortical pathways (Marien et al., 2001).

The case of a 17-year-old left-handed man with a right cerebellar hemisphere infarction associated with ataxic dysarthria and subtle language dysfunction was described by Hassid (1995). Moderate anomia was demonstrated in all modalities along with mild difficulties in auditory reception and reading, with severe difficulties in writing and mathematics. Although structural neuroimaging by way of CT and MRI scans only revealed a right-sided wedge-shaped cerebellar infarction, a SPECT scan indicated reduced blood flow in the right cerebellum and the left temporal, frontal and parietal lobes consistent with right cerebellar infarction induced crossed cerebello-cerebral diaschisis. Hassid (1995) suggested that complex cerebellar-cerebral connections are therefore capable of influencing both motor and cognitive functions, with the anatomic substrates of each of these functions distinct, both in the cerebellum and thalamus. In support of this suggestion, disruption of the cerebellar-encephalic pathways connecting the cerebellum to the frontal supratentorial areas which subserve attentional and planning processes has been implicated as the cause of the cognitive and linguistic deficits reported in a 58-year-old, right-handed man subsequent to right superior cerebellar artery infarction (Marien et al., 2009). In this latter case, a SPECT study demonstrated hypoperfusion in the right cerebellar hemisphere and the left medial frontal lobe in the absence of any structural damage in the supratentorial brain regions. Crossed cerebello-cerebral diaschisis involving reduced perfusion of the left prefrontal cortex subsequent to a right cerebellar haemorrhage has been suggested as the cause of an apraxic agraphia and minor aphasia in a 72-year-old engineer (Marien et al., 2007). Further, based on functional neuroimaging data, Marien and Verhoeven (2007) have hypothesized that crossed cerebellar diaschisis may play a role in the pathogenesis of motor speech planning disorders such as apraxia of speech and foreign accent syndrome. In a study of two patients, Marien and Verhoeven (2007) reported a close parallel between clinical recovery of the symptoms of foreign accent syndrome and improvement of right cerebellar hypoperfusion.

Following an extensive review of contemporary investigations, Marien et al. (2001) concluded that the cerebellum is topographically organized in subserving a wide range of cognitive, linguistic and affective functions. These authors proposed that within a framework of topographical functional representation, a substantial amount of clinical and experimental evidence supported that the specific modulatory role of the cerebellum in language processes, such as lexical retrieval, syntax and language dynamics, are represented in a highly restricted way in the fourth cerebellar area Marien and colleagues termed the ''lateralized linguistic cerebellum''. Marien et al. (2001) also outlined that the right hemisphere of the cerebellum is crucially involved in the integrated subsystem of working memory that subserves several language processes, articulatory planning, a variety of linguistic operations implicated in semantic and phonological word retrieval, syntactic processing, and the dynamics of language processing. Thus Marien et al. (2001) advanced the concept of a functionally lateralized linguistic cerebellum with a modulatory role in apraxia of speech, classic aphasia syndromes, and aphasia in atypical populations. Additionally, these authors postulated that linguistic deficits following cerebellar pathology do not imply representation of linguistic functions at the cerebellar level, but reflect functional deactivation of the supratentorial language areas due to reduced input via cerebello-cerebrocortical pathways, thereby placing emphasis on diaschisis processes as the relevant neuropathological mechanism for cerebellar induced language disorders.

5. Summary

In summary, the results of recent neuroanatomical, clinical and neuroimaging studies have demonstrated that the role of the cerebellum is not limited to motor functions but appears to be involved in the modulation of a broad spectrum of linguistic functions such a verbal fluency, word retrieval, syntax, reading, writing and metalinguistics abilities. Based on neural evidence and information processing theory, Leiner et al. (1986) showed that the phylogenetically newest part of the cerebellum (particularly the lateral portions of the cerebellar hemispheres and dentate nuclei) might interact with the frontal association cortex to allow for skilled manipulation of information or ideas. In support of this proposal, neuroanatomical studies have demonstrated reciprocal connections linking the cerebellum with centres in the cerebral cortex, including areas crucially involved in high-level linguistic functions (Middleton and Strick, 2000). The existence of a reciprocal functional connectivity has been clearly demonstrated by functional neuroimaging studies that show cerebellar activation during a range of linguistic tasks which require no motor response (e.g., Petersen et al., 1989). Further clinical investigations of patients with cerebellar pathology using sensitive linguistic tests capable of detecting subtle, high-level language impairments (e.g., Murdoch and Whelan, 2007) have demonstrated the presence of a variety of linguistic impairments in association with cerebellar pathology.

Several different theories have been proposed relating to possible neuropathological mechanisms involved in the occurrence of language disorders subsequent to cerebellar lesions. Firstly, it has been suggested that crossed cerebello-cerebrocortical diaschisis reflecting a functional depression of supratentorial language areas due to reduced input to the cerebral cortex via cerebello-cerebrocortical pathways may represent the neuropathological mechanism responsible for linguistic deficits associated with cerebellar pathology (Broich et al., 1987; Marien et al., 2001). In support of this suggestion, functional neuroimaging studies based on SPECT, PET or fMRI have consistently revealed regions of contralateral cortical hypoperfusion in relation to the orientation of the cerebellar lesion (e.g., Silveri et al., 1994; Beldarrain et al., 1997). According to the cerebello-cerebrocortical diaschisis model, therefore, the cerebellum is not involved in the generation of language (which remains a supratentorial activity) but rather modulates language function via segregated, multi-component neural circuits the major pathways of which include the cerebrocortico-ponto-cerebellocortico-dentato-thalamic-cerebrocortical loop and the cerebrocortico-rubro-olivo-neo-dentato-cerebrocortical loop. In this way the cerebellum acts as an important relay in the neural circuits responsible for language in much the same way as other subcortical structures such as the basal ganglia form important components of the segregated, multi-component neural circuits that enable those structures to also influence frontal-lobe activities.

A second theory proposed to explain cerebellar involvement in linguistic function is the timing hypothesis which proposes that the cerebellum has no direct influence on linguistic processes but plays an important role in the timing of linguistic functions represented on a supratentorial level (Keele and Ivry, 1991; Silveri et al., 1994). A third hypothesis relating to the role of the cerebellum in language proposes a direct cerebellar contribution via the topographically organized reciprocal connections with the cerebral cortex. According to this theory, the cerebellum does not act as a sole modulator of language but is actively involved in the organization, construction and execution of linguistic processes. As yet, however, the precise role of the cerebellum in language is not clear. Further studies that rely on a combination of neuroanatomical, neuroimaging, and neurolinguistic investigations are needed to further elucidate the nature of the role of this complex and somewhat neglected and underestimated part of the brain in language function.

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