

Functional Topography of the Cerebellum in Verbal Working Memory

Cherie L. Marvel · John E. Desmond

Received: 31 March 2010 / Accepted: 4 June 2010 / Published online: 22 June 2010
© Springer Science+Business Media, LLC 2010

Abstract Speech—both overt and covert—facilitates working memory by creating and refreshing motor memory traces, allowing new information to be received and processed. Neuroimaging studies suggest a functional topography within the sub-regions of the cerebellum that subserves verbal working memory. Medial regions of the anterior cerebellum support overt speech, consistent with other forms of motor execution such as finger tapping, whereas lateral portions of the superior cerebellum support speech planning and preparation (e.g., covert speech). The inferior cerebellum is active when information is maintained across a delay, but activation appears to be independent of speech, lateralized by modality of stimulus presentation, and possibly related to phonological storage processes. Motor (dorsal) and cognitive (ventral) channels of cerebellar output nuclei can be distinguished in working memory. Clinical investigations suggest that hyper-activity of cerebellum and disrupted control of inner speech may contribute to certain psychiatric symptoms.

Keywords Cerebellum · Working memory · fMRI · Speech · Addiction · Cognition

Introduction

The cerebellum has been historically linked to the control of posture, gait, and skilled voluntary movement. Yet, as early

as the 1800's, numerous cases of non-motor deficits, such as cognitive impairment, were reported in patients with cerebellar degeneration and atrophy (Schmahmann 1997). Inspired by the work and observations of the Leiners—who anticipated prior to the advent of functional MRI how important neuroimaging would be to the study of non-motor functions of the cerebellum (Leiner et al. 1986)—reports consistent with a cognitive role of the cerebellum began to increase sharply in the early 1990's. This upsurge coincided with an increase in the number of neuroscientists who began to use neuroimaging as a means to examine brain function. Moreover, the neuroimaging results that implicated cerebellar cognitive function converged with the reports of non-motor deficits in cerebellar patients.

In general, cognitive abilities affected by cerebellar damage include working memory (verbal and spatial), executive function, and language (Stoodley and Schmahmann 2009). Verbal working memory, perhaps more than other cognitive processes, has been rigorously studied within the context of cerebellar functions using fairly consistent neuroimaging methods and neuropsychological assessments. For this reason, this review focuses on a description of cerebellar contributions to verbal working memory.

Working memory involves the temporary storage and manipulation of online information, such as computing a tip at a restaurant, following cooking instructions, or dialing a phone number. The core component of working memory is thought to be the “central executive”, which is hypothesized to represent an attention-controlling system for processing phonological information (Baddeley 1992, 2003). This article proposes that the cerebellum generally supports working memory by engaging inner speech mechanisms. The functional topography of sub-regions within the cerebellum, and its relation to working memory, will also be described.

C. L. Marvel (✉) · J. E. Desmond
Department of Neurology, Division of Cognitive Neuroscience,
Johns Hopkins University School of Medicine,
1620 McElderry St., Reed Hall 2205B,
Baltimore, MD 21205, USA
e-mail: cmarvell@jhmi.edu

The Interdependence of Speech and Working Memory

According to a popular model of working memory, the phonological loop provides 1–2 sec of passive storage of verbal information, which can be refreshed via an active rehearsal process (Baddeley and Logie 1999). The phonological loop is thought to have evolved from rudimentary speech systems (e.g., basic phoneme sounds) as a way to enhance language acquisition, such as by combining phonemes into sounds to represent complex meanings (Aboitiz et al. 2006). Moreover, the modern day function of the phonological loop may provide a means for children to form reliable representations of novel speech events (e.g., new words) during language acquisition (Baddeley et al. 1998). For example, it has been shown that phonological memory correlates with vocabulary in young children (Gathercole and Baddeley 1989), and that children with language disorders exhibit working memory deficits (Gathercole and Baddeley 1990). Thus, working memory appears to support language development by providing a temporary holding place for novel sounds, and the larger the working memory capacity, the more efficient the language learning process becomes.

The inverse of this language/working memory relationship has also been described—speech can, in turn, support working memory. For example, it has been demonstrated that speaking information aloud—or merely mouthing or whispering it—while encoding verbal content improves the immediate recall of that information relative to silent reading without mouth movements (Murray 1965). By contrast, producing speech responses that conflict with the primary verbal content (e.g., repeating “the, the, the” while reading) impairs recall performance relative to reading the verbal content aloud (Levy 1971; Murray 1967). It seems, therefore, that engaging speech mechanisms can enhance working memory, as long as the motor behaviors are *consistent* with the production of the phonological form of the content. Internal representations of speech motor sequences (inner speech) may provide similar benefits. For example, a study by Rauschecker et al. (2008) showed that covert repetition of pseudowords became faster when items were presented repeatedly versus when items were presented only once. Post-experimental testing revealed that overt pronunciation of pseudowords was more accurate for items that had been presented multiple times versus those that had been presented once. According to the authors, subjects had learned to articulate pseudowords using inner speech mechanisms in conjunction with the phonological loop. A separate experiment showed that studying a picture of an object speeded subsequent word reading if the object-word pair began with the same phoneme (Roelofs et al. 2007). Thus, covert articulation enhanced word reading as long as the phonological content was consistent between

the two items held in working memory. Internal speech, therefore, may support working memory in the same way that overt speech does, by creating motor memory traces that facilitate the processing of new information (Ackermann 2008; Ravizza et al. 2004).

Cerebellar Support of Overt Speech

The cerebellum is consistently activated in neuroimaging studies of overt speech. These regions include the medial, anterior cerebellum (Lobule IV–V, rostral to the primary fissure) (Bohland and Guenther 2006; Ghosh et al. 2008; Turkeltaub et al. 2002) (see Fig. 1a). Neurological damage to this region of the cerebellum often results in speech and articulatory disruption, or dysarthria (Spencer and Slocomb 2007). Not surprisingly, these same medial-anterior regions of the cerebellum are generally consistent with other forms of motor execution, such as finger tapping (Hulsmann et al. 2003). However, as speech complexity increases (e.g., saying “ta-ta-ta” versus “ka-ru-ti”), activity spreads to lateral regions of the superior cerebellum (superior cerebellar areas Lobule VI and Crus I between the primary and horizontal fissures). These lateral cerebellar activations during complex speech map closely onto those regions that are activated several seconds *prior* to finger tapping (Hulsmann et al. 2003), suggesting that these lateral cerebellar regions support motor planning and preparation, but not motor execution *per se*. The same superior/lateral regions of the cerebellum that are activated during complex speech (presumably as part of speech planning, but not speech execution) are also activated during tasks of working memory (Durisko and Fiez 2010), as described below.

Cerebellar Support of Covert Speech and Working Memory

An item recognition paradigm known as the Sternberg task (Sternberg 1966) has provided a means for systematic study of neural systems that support working memory because of this paradigm’s well defined cognitive components. The Sternberg task consists of three distinct phases: (1) an “encoding phase” to study an array of briefly presented items, (e.g., letters), (2) a “maintenance phase” to maintain these items across a delay interval, and (3) a “retrieval phase” to compare a probe item to the target array and to determine whether there is a match between them.

Neuroimaging research has revealed that the superior/lateral region of the cerebellum (Lobule VI/Crus I) is most active during the encoding phase of the Sternberg task, when the original array of letters are shown at the

comparing speech output (overt or covert) with information contained in online storage (Desmond et al. 1997) or for regulating the timing of motor sequences (Ackermann 2008; Leggio et al. in press). A broader interpretation for the inferior cerebellum's function, however, is that it generally supports phonological storage within working memory (Chen and Desmond 2005a, b; Chiricozzi et al. 2008; Kirschen et al. 2008; Marvel and Desmond 2010; Ravizza et al. 2006).

Functional Dissociation Between the Dorsal and Ventral Dentate

Transynaptic neuroanatomical tracing studies have provided convincing evidence of distinct closed-loop cognitive and motor cerebro-cerebellar circuits. Ventral portions of the cerebellar output dentate nuclei connect with dorsolateral prefrontal regions (BA 9/46) implicated in working memory and executive control (Dum and Strick 2003; Kelly and Strick 2003; Middleton and Strick 2001). A separate circuit connects dorsal portions of the dentate nuclei to primary motor, premotor, and supplementary motor regions of the cerebrum (Akkal et al. 2007; Dum and Strick 2003). Thus an anatomical foundation exists by which cerebro-cerebellar networks can influence higher-level cognition or motor function, depending upon the neural pathway.

The ventral “cognitive” dentate is thought to be evolutionarily younger than the dorsal “motor” dentate and to have evolved in conjunction with the prefrontal cortex (Leiner et al. 1991). Moreover, in humans, the ventral dentate is approximately twice as large as the dorsal dentate, which is a larger ventral-to-dorsal dentate ratio than that observed in great apes (Matano 2001). These observations suggest that the ventral dentate that comprises the “cognitive loop” evolved from a phylogenetically older “motor loop” (involving the dorsal dentate) in order to support higher-order cognitive functions that are uniquely human. In general, the rate of brain development follows a phylogenetic pattern such that evolutionarily older brain regions mature faster than do younger brain regions (Gogtay et al. 2004). Accordingly, the cerebro-cerebellar motor loop matures earlier (by mid-teens) than does the cerebro-cerebellar cognitive loop (by early 20s) (Gogtay et al. 2004; Tiemeier et al. 2010). It therefore seems plausible that throughout development the cognitive loop retains close ties with its evolutionary precursor, the motor loop, which allows both systems to work together, for example by engaging inner speech mechanisms to enhance working memory.

Recent functional magnetic resonance imaging (fMRI) data have demonstrated a functional dissociation between the dorsal and ventral cerebellar dentate that is consistent

with putative functions of the motor and cognitive loops, respectively. Marvel and Desmond (2010) administered a Sternberg variant that asked subjects to count two alphabetical letters forward of the probe letter presented at the end of a trial during the retrieval phase. Subjects were then required to determine a match between the newly identified probe and the original array of encoded letters (Working Memory condition). In the control condition, subjects directly matched the probe letter to the encoded array (Match condition). A direct comparison of cerebellar activity during the Working Memory minus Match conditions revealed phase-specific activity in association with the Working Memory condition, as shown in Fig. 2. During the encoding phase, activity increased in the dorsal dentate. This activity was interpreted to mean that subjects were making a pointed effort to correctly encode letters in the Working Memory condition, a strategy that likely taxed motor-related inner speech mechanisms during the orthographic-to-phonologic translation. During retrieval, activity increased in the ventral dentate. This activity was interpreted as online manipulation (counting two letters forward) of the letter information. Supporting this interpretation, the ventral dentate region was activated in conjunction with the contralateral dorsolateral prefrontal cortex (BA 9). Moreover, a time series analysis indicated that the pattern of activity in the ventral dentate and in BA 9 during the maintenance phase predicted success during the retrieval phase. Thus, activation patterns of the dorsal and ventral dentate of the cerebellum were functionally dissociated in a time-dependent manner that reflected discrete contributions to working memory.

Neuropsychological Studies of Patients with Cerebellar Damage

A convergence of data across multiple studies of patients with cerebellar damage indicates three primary patterns of results. First, in these types of studies, cognitive deficits have been subtle, often falling within the low-normal range (Justus et al. 2005; Leggio et al. 2008; Ravizza et al. 2006). When patients have been compared to well-matched controls, however, deficits become more obvious. Second, verbal working memory is consistently, and sometimes disproportionately, affected in this population (Chiricozzi et al. 2008; Justus et al. 2005; Kirschen et al. 2008; Leggio et al. 2008; Ravizza et al. 2006; Silveri et al. 1998). Third, there appears to be a hemispheric dissociation of function within the inferior lobes of the cerebellum: the left side is more strongly involved in the processing of aurally presented information, and the right side is more strongly involved in the processing of visually presented information. This third point is expanded upon below.

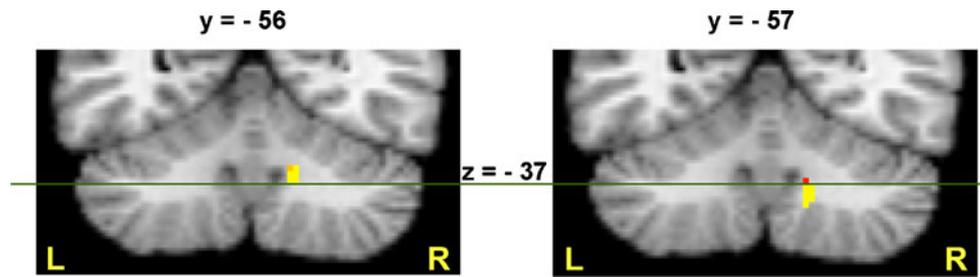


Fig. 2 Peak activations within the right cerebellar dentate are shown for encoding and retrieval phases of the Sternberg task (Working Memory greater than Match conditions), $p < .001$. The green line at $z = -37$ is used to indicate a functional division between the dorsal and ventral dentate, which falls roughly between $z = -36$ to -40 (Dimitrova et al. 2006). This functional division is consistent with

neuroanatomical tracing studies indicating that the dorsal dentate projects to motor regions of the frontal lobe, while the ventral dentate projects to cognitive frontal regions, implicating a “motor” dorsal dentate and a “cognitive” ventral dentate as illustrated in Fig. 1. R = right; L = left. From Marvel and Desmond (2010) with permission¹

Following a stroke localized to the right cerebellar lobule V and the left cerebellar lobule VIIIA, a 54 year old male was given a battery of cognitive tests nine days after the stroke event (Chiricozzi et al. 2008). Performance on many tests fell within the normal range, including tests of intelligence, constructional praxia, frontal lobe function, verbal/visuospatial spans, and verbal recall when information was presented in the visual modality. However, the patient showed a specific deficit for verbal recall (immediate and delayed) when information was presented in the auditory modality. A follow-up battery of tests administered 18 months later indicated that persistent working memory deficits involved an inability to rehearse phonological information held in short-term storage, which was pronounced for information presented in the auditory modality.

A similar link between left inferior cerebellar lobule VIII and auditory working memory performance was found in a study of 12 children (ages 6–19 years) with cerebellar tumors resections (Kirschen et al. 2008). A lobular analysis of the regions of cerebellar damage indicated, after Bonferroni correction for multiple comparisons, that damage to the left inferior cerebellar lobule VIII significantly predicted impairment of auditory digit span. An additional test of working memory was conducted using a phonological similarity paradigm. The phonological similarity paradigm measures one’s ability to hold information in mind despite interference from phonologically similar material (e.g., B, C, D, G, P, T, V) (Baddeley 1966). The presence of interference, known as the phonological similarity effect (PSE), is a healthy effect and is manifested as better immediate recall of dissimilar (e.g., F, K, Q, R, X, W, Z) versus similar material. In this study, three patients showed particularly low performance on the phonological similarity test (more than 3 SD below the mean) for aurally presented material, and three other patients showed similarly low performance for visually presented material. A conjunction analysis of the lesions for each of these three subjects in each modality was performed. All subjects had

in common damage to the inferior cerebellar lobules VIIB/VIII. However, the modality affected was specific to hemisphere: those with deficits in the auditory modality shared damage in the left inferior cerebellum, and those with deficits in the visual modality shared damage in the right inferior cerebellum. These findings of a left inferior cerebellar hemisphere bias for auditory information were consistent with the case report described above. These findings additionally implicated a right inferior cerebellar hemisphere bias for visual information in working memory.

A right-lateralized visual modality effect was further supported in the study of an 18-year-old male with a right inferior cerebellar tumor resection (Silveri et al. 1998). Three days after surgery, the patient showed an advantage of auditory over visual presentation of stimuli in a test of phonological similarity. Thus, the PSE was present for auditory stimuli but not for visual stimuli, and therefore indicated a specific deficit in the visual modality in association with a right inferior cerebellar lesion. Follow-up testing 5 months later showed that plasticity had occurred, and the PSE was intact for both modalities.

Finally, neuropsychological studies of older patients suggest that the hemispheric asymmetry of function in the inferior cerebellum described above is reduced as a function of age. In a study by Ravizza et al. (2006) of fifteen patients (mean age = 60) with cerebellar damage, patients were tested on several working memory paradigms, including auditory digit span. Performance on digit span was negatively correlated with damage to the inferior cerebellar lobe, consistent with the role of the inferior lobe assisting with phonological storage and working memory functions. However, there was no relation between lesion hemisphere and performance: patients with right-sided inferior cerebellar lesions were just as impaired on this auditory working

¹ This figure was published in *Cortex*, 46, Marvel and Desmond, The Contributions of Cerebro-Cerebellar Circuitry to Executive Verbal Working Memory, 880-895, Copyright Elsevier (2010).

memory task as were those with left-sided lesions. It should be noted that a test of visual digit span was not administered, prohibiting a direct comparison of auditory versus visual span performance. A separate study of 10 cerebellar patients (mean age = 67) by Justus et al. (2005) tested phonological similarity, with stimuli delivered aurally and visually. They reported overall reductions in the PSE, but did not find evidence for laterality effects that were associated with stimulus modality. Laterality effects may have been diminished by several factors in this study, including variability of the lesion within the hemisphere (i.e., not specific to the inferior cerebellum), and the inclusion of only one left-hemisphere patient in the visual portion of the study. However, given that both the Ravizza et al. and Justus et al. studies tested older patients (relative to the tumor resection studies described previously), negative laterality effects in older subjects may simply mean that laterality in the cerebellum attenuates with age. A reduction in laterality in the aging cerebellum would be consistent with age-related activation shifts from the left prefrontal cortex to bilateral prefrontal cortex during verbal working memory (Cabeza 2002; Reuter-Lorenz et al. 2000).

Given that processing of language-related stimuli in the neocortex is typically lateralized on the left side, and that cortico-ponto-cerebellar projections have been shown to be predominately (though not exclusively) crossed in animal tracing studies, the dissociation of stimulus modality and hemispheric lateralization observed in verbal working memory deficits is unexpected. That is, verbal working memory impairment for visually presented letters resulting from right cerebellar damage would be predicted based on the crossed cortico-cerebellar connectivity from left-sided language centers. However, similar impairment for aurally-presented letters after left cerebellar damage would not be predicted. Further research on this puzzling pattern is required, but one possible explanation may be that encoding of aurally-presented letters involves greater demand on sensory discrimination than encoding of visually-presented letters, especially for phonologically similar letters (e.g., “P” and “T” are more similar in sound than in appearance). The importance of the cerebellum in sensory acquisition and discrimination has been emphasized in several studies, and left cerebellar hemisphere activations pertaining to sensory discrimination have been reported (Belin et al. 1998, 2002; Bower 1997; Gao et al. 1996; Holcomb et al. 1998; Parsons et al. 1997, 2009).

Functional Topography of the Cerebellum in Working Memory

Given the evidence from neuroanatomical tracing, neuroimaging, and neuropsychology studies, the cerebellum

appears to contain a functional topography for working memory processes that segues from primarily motor to primarily cognitive, as depicted in Fig. 1b: the anterior/medial cerebellum (Lobules IV–V) supports motor execution, including overt speech; the superior/lateral cerebellum (Lobule VI/Crus I) supports the preparation for complex motor patterns and covert speech as part of working memory (but not motor execution per se); and the inferior cerebellum (Lobules VIIIB/VIII) supports working memory independent of motor execution (Durisko and Fiez 2010; Hulsmann et al. 2003; Stoodley and Schmahmann 2009, 2010). Within the inferior cerebellum, the left hemisphere shows a bias for processing auditory information (Chiricozzi et al. 2008; Kirschen et al. 2008). By contrast, the right hemisphere shows a bias for processing visual information (Kirschen et al. 2008; Silveri et al. 1998). In addition, the output nuclei of the cerebellum contain a dorsal/ventral functional topography. The dorsal dentate nuclei support primary and secondary motor functions (including those that may be utilized during certain aspects of inner speech), whereas the ventral dentate nuclei lend support for higher-order cognitive functions (Dum and Strick 2003; Marvel and Desmond 2010).

Clinical Relevance

A recent fMRI study found that when healthy subjects silently manipulated letter stimuli while performing a Sternberg task, cerebellar activity in Lobule VI increased, and accuracy *decreased* (unpublished, see Fig. 3). This pattern of activity suggested that when working memory demands became exceedingly difficult, people continued to

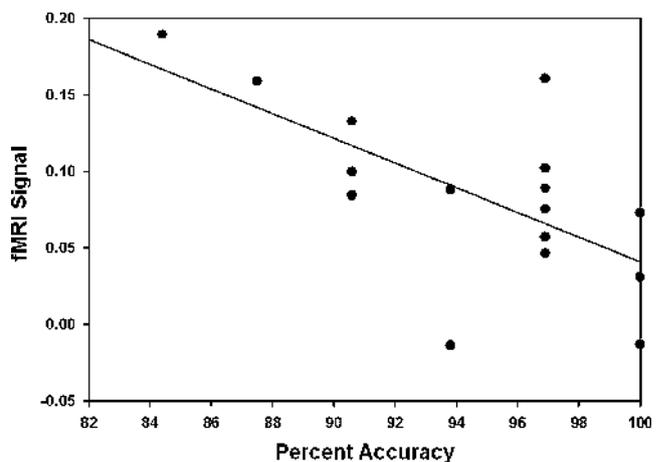


Fig. 3 Correlation between fMRI signal in the right cerebellar Lobule VI and accuracy performance while subjects silently manipulated letters during a Sternberg working memory paradigm. Data represent 16 young, healthy adults, $r = -.65$, $p < .01$. The inverse relationship between these two variables suggests that superior cerebellar activity increased as subjects encountered difficulty with the task

rely on inner speech mechanisms, perhaps intensely so, while struggling to perform the task. It would make sense, then, that clinical populations with known working memory impairments would show a heavy reliance on cerebellar-dependent inner speech mechanisms, and hyper-activity of the cerebellum would be expected.

Working memory impairments are present in a number of psychiatric disorders in which the cerebellum has been implicated, such as addiction, anxiety, obsessive-compulsive disorder, depression, and schizophrenia (Fitzgerald et al. 2008; Ho et al. 2004; Hoppenbrouwers et al. 2008; Kim et al. 2001; Volkow et al. 2003). These disorders consist of psychiatric symptoms that would intuitively involve aspects of inner speech (e.g., craving, ruminations, obsessions, preoccupations, and delusions), which may reflect either a cause or an effect of poor working memory. A thorough review of cerebellar contributions to working memory deficits in psychiatric disorders is beyond the scope of this article, but has been discussed elsewhere (Desmond and Marvel 2009). However, as an example, we focus on the clinical relevance of cerebellar dysfunction and working memory in addiction.

It has been proposed that deficits in working memory and executive function are responsible for the loss of self-control that leads to drug and alcohol addiction (Garavan and Hester 2007). Moreover, decreased gray matter volume in the bilateral inferior lobes of the cerebellum has been observed in drug- and alcohol-addicted populations (Connolly et al. 2009; Sim et al. 2007; Sullivan et al. 2000; Yuan et al. 2009). These findings would suggest, then, that disturbances in cerebellar function may be involved in addiction. When alcohol-dependent subjects and matched controls were tested on a Sternberg task using fMRI, hyper-activity was observed in the alcohol group in a cerebro-cerebellar network that included the right superior cerebellum and left inferior frontal gyrus (BA 44) (Desmond et al. 2003). Similarly, an fMRI study that administered a Sternberg task to opiate users and matched controls revealed hyper-activity in the opiate users in the bilateral superior cerebellum, right inferior cerebellum, and medial prefrontal regions (anterior cingulate) (Marvel et al. 2009). An fMRI study of cocaine users and matched controls performing a Sternberg-like task of response inhibition revealed that the cocaine users increased activity in the left superior cerebellum in association with increased working memory load (i.e., greater number of items to hold in mind) (Hester and Garavan 2004). In the cocaine group, higher cerebellar activity correlated with a higher rate of response errors. This correlation is consistent with the notion that those who found the task the most difficult were more likely to rely on cerebellar-dependent inner speech mechanisms to perform the task. Interestingly, hyper-activity of the superior/lateral cerebellum has also been reported during drug cue-induced craving (Bonson et al. 2002; Volkow et al. 2003; Xiao et al.

2006). Working memory and drug craving, therefore, appear to be intertwined and to share common neural systems, of which the cerebellum is an integral part. Taken together, these findings present the possibility that impairments of working memory and/or cerebellar function may contribute to psychiatric symptoms that involve inner speech disturbances.

Summary

This article proposes that the cerebellum enhances working memory by supporting inner speech mechanisms. This capability emerged from overt speech and motor systems as an evolutionarily adaptive way to boost cognitive processes that rely on working memory, such as language acquisition. The view that the cerebellum is strongly tied to verbal working memory is supported by converging results from neuroimaging studies of healthy subjects and neuropsychological studies of patients with cerebellar damage. Such studies have revealed a topography of cerebellar function. Motor execution, such as speech output, relies on Lobules IV–V in the anterior cerebellum. Motor-related activity, such as planning and preparation, relies on more lateral regions of the superior cerebellum in Lobules VI and Crus I. The inferior cerebellum (Lobule VIII) also contributes to working memory functions, in a way that is independent from motor execution and possibly lateralized by modality of stimulus presentation. In addition, a topography of function exists within the dentate nuclei, with the dorsal dentate supporting motor-related functions, and the ventral dentate supporting higher-order cognitive functions. Clinically, the role of the cerebellum in working memory has broad implications, ranging from disruptions in language acquisition during childhood, to reduced memory span following stroke, to unchecked inner speech involved in a host of psychiatric disorders.

Acknowledgments This work was supported by NIH R01 MH060234.

References

- Aboitiz, F., Garcia, R. R., Bosman, C., & Brunetti, E. (2006). Cortical memory mechanisms and language origins. *Brain and Language*, 98(1), 40–56.
- Ackermann, H. (2008). Cerebellar contributions to speech production and speech perception: psycholinguistic and neurobiological perspectives. *Trends in Neurosciences*, 31(6), 265–272.
- Akkal, D., Dum, R. P., & Strick, P. L. (2007). Supplementary motor area and presupplementary motor area: targets of basal ganglia and cerebellar output. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 27(40), 10659–10673.

- Baddeley, A. (1966). Short-term memory for word sequences as a function of acoustic, semantic and formal similarity. *The Quarterly Journal of Experimental Psychology*, 18(4), 362–365.
- Baddeley, A. (1992). Working memory. *Science*, 255(5044), 556–559.
- Baddeley, A. (2003). Working memory: looking back and looking forward. *Nature Reviews. Neuroscience*, 4(10), 829–839.
- Baddeley, A., & Logie, R. H. (1999). Working memory: The multiple-component model. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 28–61). New York: Cambridge University Press.
- Baddeley, A., Gathercole, S., & Papagno, C. (1998). The phonological loop as a language learning device. *Psychological Review*, 105(1), 158–173.
- Belin, P., McAdams, S., Smith, B., Savel, S., Thivard, L., Samson, S., et al. (1998). The functional anatomy of sound intensity discrimination. *The Journal of Neuroscience*, 18(16), 6388–6394.
- Belin, P., McAdams, S., Thivard, L., Smith, B., Savel, S., Zilbovicius, M., et al. (2002). The neuroanatomical substrate of sound duration discrimination. *Neuropsychologia*, 40(12), 1956–1964.
- Bohland, J. W., & Guenther, F. H. (2006). An fmri investigation of syllable sequence production. *Neuroimage*, 32(2), 821–841.
- Bonson, K. R., Grant, S. J., Contoreggi, C. S., Links, J. M., Metcalfe, J., Weyl, H. L., et al. (2002). Neural systems and cue-induced cocaine craving. *Neuropsychopharmacology*, 26(3), 376–386.
- Bower, J. M. (1997). Control of sensory data acquisition. In J. D. Schmahmann (Ed.), *The cerebellum and cognition*, vol. 41 (pp. 490–513). San Diego: Academic.
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the Harold model. *Psychology and Aging*, 17(1), 85–100.
- Chein, J. M., & Fiez, J. A. (2001). Dissociation of verbal working memory system components using a delayed serial recall task. *Cerebral Cortex*, 11(11), 1003–1014.
- Chen, S. H., & Desmond, J. E. (2005a). Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks. *Neuroimage*, 24(2), 332–338.
- Chen, S. H., & Desmond, J. E. (2005b). Temporal dynamics of cerebro-cerebellar network recruitment during a cognitive task. *Neuropsychologia*, 43(9), 1227–1237.
- Chiricozzi, F. R., Clausi, S., Molinari, M., & Leggio, M. G. (2008). Phonological short-term store impairment after cerebellar lesion: a single case study. *Neuropsychologia*, 46(7), 1940–1953.
- Connolly, C. G., Bell, R., Jones, J., Nierenberg, J., Hoptman, M., Butler, P., et al. (2009). *Neuroimage, changes in grey matter volumes related to cocaine abstinence*. Paper presented at the Organization for Human Brain Mapping 15th Annual Meeting, San Francisco, CA.
- Desmond, J. E., & Marvel, C. L. (2009). Cognition: Cerebellum role. In L. R. Squire (Ed.), *Encyclopedia of neuroscience* (Vol. 2, pp. 1079–1085). Oxford: Academic.
- Desmond, J. E., Gabrieli, J. D., Wagner, A. D., Ginier, B. L., & Glover, G. H. (1997). Lobular patterns of cerebellar activation in verbal working-memory and finger-tapping tasks as revealed by functional MRI. *The Journal of Neuroscience*, 17(24), 9675–9685.
- Desmond, J. E., Chen, S. H., DeRosa, E., Pryor, M. R., Pfefferbaum, A., & Sullivan, E. V. (2003). Increased frontocerebellar activation in alcoholics during verbal working memory: an fmri study. *Neuroimage*, 19(4), 1510–1520.
- Dimitrova, A., Zeljko, D., Schwarze, F., Maschke, M., Gerwig, M., Frings, M., et al. (2006). Probabilistic 3d MRI atlas of the human cerebellar dentate/interposed nuclei. *Neuroimage*, 30(1), 12–25.
- Dum, R. P., & Strick, P. L. (2003). An unfolded map of the cerebellar dentate nucleus and its projections to the cerebral cortex. *Journal of Neurophysiology*, 89(1), 634–639.
- Durisko, C., & Fiez, J. A. (2010). Functional activation in the cerebellum during working memory and simple speech tasks. *Cortex*, 46(7), 896–906.
- Fitzgerald, P. B., Laird, A. R., Maller, J., & Daskalakis, Z. J. (2008). A meta-analytic study of changes in brain activation in depression. *Human Brain Mapping*, 29(6), 683–695.
- Gao, J. H., Parsons, L. M., Bower, J. M., Xiong, J., Li, J., & Fox, P. T. (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science*, 272(5261), 545–547.
- Garavan, H., & Hester, R. (2007). The role of cognitive control in cocaine dependence. *Neuropsychology Review*, 17(3), 337–345.
- Gathercole, S., & Baddeley, A. (1989). Evaluation of the role of phonological STM in the development of vocabulary in children: a longitudinal study. *Journal of Memory and Language*, 28, 200–213.
- Gathercole, S., & Baddeley, A. (1990). Phonological memory deficits in language disordered children: is there a causal connection? *Journal of Memory and Language*, 29, 336–360.
- Ghosh, S. S., Tourville, J. A., & Guenther, F. H. (2008). A neuroimaging study of premotor lateralization and cerebellar involvement in the production of phonemes and syllables. *Journal of Speech, Language, and Hearing Research*, 51(5), 1183–1202.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174–8179.
- Hayter, A. L., Langdon, D. W., & Ramnani, N. (2007). Cerebellar contributions to working memory. *Neuroimage*, 36(3), 943–954.
- Hester, R., & Garavan, H. (2004). Executive dysfunction in cocaine addiction: evidence for discordant frontal, cingulate, and cerebellar activity. *The Journal of Neuroscience*, 24(49), 11017–11022.
- Ho, B. C., Mola, C., & Andreasen, N. C. (2004). Cerebellar dysfunction in neuroleptic naive schizophrenia patients: clinical, cognitive, and neuroanatomic correlates of cerebellar neurologic signs. *Biological Psychiatry*, 55(12), 1146–1153.
- Holcomb, H. H., Medoff, D. R., Caudill, P. J., Zhao, Z., Lahti, A. C., Dannals, R. F., et al. (1998). Cerebral blood flow relationships associated with a difficult tone recognition task in trained normal volunteers. *Cerebral Cortex*, 8(6), 534–542.
- Hoppenbrouwers, S. S., Schutter, D. J., Fitzgerald, P. B., Chen, R., & Daskalakis, Z. J. (2008). The role of the cerebellum in the pathophysiology and treatment of neuropsychiatric disorders: a review. *Brain Research Reviews*, 59(1), 185–200.
- Hulsmann, E., Erb, M., & Grodd, W. (2003). From will to action: sequential cerebellar contributions to voluntary movement. *Neuroimage*, 20(3), 1485–1492.
- Justus, T., Ravizza, S. M., Fiez, J. A., & Ivry, R. B. (2005). Reduced phonological similarity effects in patients with damage to the cerebellum. *Brain and Language*, 95(2), 304–318.
- Kelly, R. M., & Strick, P. L. (2003). Cerebellar loops with motor cortex and prefrontal cortex of a nonhuman primate. *The Journal of Neuroscience*, 23(23), 8432–8444.
- Kim, J. J., Lee, M. C., Kim, J., Kim, I. Y., Kim, S. I., Han, M. H., et al. (2001). Grey matter abnormalities in obsessive-compulsive disorder: statistical parametric mapping of segmented magnetic resonance images. *The British Journal of Psychiatry*, 179, 330–334.
- Kirschen, M. P., Davis-Ratner, M. S., Milner, M. W., Chen, S. H., Schraedley-Desmond, P., Fisher, P. G., et al. (2008). Verbal memory impairments in children after cerebellar tumor resection. *Behavioural Neurology*, 20(1–2), 39–53.
- Krienen, F. M., & Buckner, R. L. (2009). Segregated fronto-cerebellar circuits revealed by intrinsic functional connectivity. *Cerebral Cortex*, 19(10), 2485–2497.

- Leggio, M. G., Tedesco, A. M., Chiricozzi, F. R., Clausi, S., Orsini, A., & Molinari, M. (2008). Cognitive sequencing impairment in patients with focal or atrophic cerebellar damage. *Brain*, *131*(Pt 5), 1332–1343.
- Leggio, M. G., Chiricozzi, F. R., Clausi, S., Tedesco, A. M., & Molinari, M. (in press). The neuropsychological profile of cerebellar damage: the sequencing hypothesis. *Cortex*, doi:10.1016/j.cortex.2009.08.011.
- Leiner, H. C., Leiner, A. L., & Dow, R. S. (1986). Does the cerebellum contribute to mental skills? *Behavioral Neuroscience*, *100*(4), 443–454.
- Leiner, H. C., Leiner, A. L., & Dow, R. S. (1991). The human cerebro-cerebellar system: its computing, cognitive, and language skills. *Behavioural Brain Research*, *44*(2), 113–128.
- Levy, B. A. (1971). Role of articulation in auditory and visual short-term memory. *Journal of Verbal Learning and Verbal Behavior*, *10*, 123–132.
- Marvel, C. L., & Desmond, J. E. (2010). The contributions of cerebro-cerebellar circuitry to executive verbal working memory. *Cortex*, *46*(7), 880–895.
- Marvel, C. L., Ellis, D. A., & Desmond, J. E. (2007). *Cerebellar neural correlates of executive function: An fmri verbal working memory investigation*. Paper presented at the 37th Annual Meeting of the Society for Neuroscience, San Diego.
- Marvel, C. L., Faulkner, M. L., Strain, E. C., Mintzer, M. Z., & Desmond, J. E. (2009). *Brain activation patterns in heroin users as revealed by fmri during an executive verbal working memory task*. Paper presented at the 39th Annual Meeting of the Society for Neuroscience. Chicago, IL.
- Matano, S. (2001). Brief communication: proportions of the ventral half of the cerebellar dentate nucleus in humans and great apes. *American Journal of Physical Anthropology*, *114*(2), 163–165.
- Middleton, F. A., & Strick, P. L. (2001). Cerebellar projections to the prefrontal cortex of the primate. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *21*(2), 700–712.
- Murray, D. J. (1965). The effect of white noise upon the recall of vocalized lists. *Canadian Journal of Psychology*, *19*(4), 333–345.
- Murray, D. J. (1967). The role of speech responses in short-term memory. *Canadian Journal of Psychology*, *21*(3), 263–276.
- O'Reilly, J. X., Beckmann, C. F., Tomassini, V., Ramnani, N., & Johansen-Berg, H. (2010). Distinct and overlapping functional zones in the cerebellum defined by resting state functional connectivity. *Cerebral Cortex*, *20*(4), 953–965.
- Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, *25*(1), 46–59.
- Parsons, L. M., Bower, J. M., Gao, J. H., Xiong, J., Li, J., & Fox, P. T. (1997). Lateral cerebellar hemispheres actively support sensory acquisition and discrimination rather than motor control. *Learning & Memory*, *4*(1), 49–62.
- Parsons, L. M., Petacchi, A., Schmahmann, J. D., & Bower, J. M. (2009). Pitch discrimination in cerebellar patients: evidence for a sensory deficit. *Brain Research*, *1303*, 84–96.
- Rauschecker, A. M., Pringle, A., & Watkins, K. E. (2008). Changes in neural activity associated with learning to articulate novel auditory pseudowords by covert repetition. *Human Brain Mapping*, *29*(11), 1231–1242.
- Ravizza, S. M., Delgado, M. R., Chein, J. M., Becker, J. T., & Fiez, J. A. (2004). Functional dissociations within the inferior parietal cortex in verbal working memory. *Neuroimage*, *22*(2), 562–573.
- Ravizza, S. M., McCormick, C. A., Schlerf, J. E., Justus, T., Ivry, R. B., & Fiez, J. A. (2006). Cerebellar damage produces selective deficits in verbal working memory. *Brain*, *129*(Pt 2), 306–320.
- Reuter-Lorenz, P. A., Jonides, J., Smith, E. E., Hartley, A., Miller, A., Marshuetz, C., et al. (2000). Age differences in the frontal lateralization of verbal and spatial working memory revealed by pet. *Journal of Cognitive Neuroscience*, *12*(1), 174–187.
- Roelofs, A., Ozdemir, R., & Levelt, W. J. (2007). Influences of spoken word planning on speech recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *33*(5), 900–913.
- Schmahmann, J. D. (1997). Rediscovery of an early concept. In J. D. Schmahmann (Ed.), *The cerebellum and cognition* (Vol. 41, pp. 3–27). San Diego: Academic.
- Schmahmann, J. D., Doyon, J., McDonald, D., Holmes, C., Lavoie, K., Hurwitz, A. S., et al. (1999). Three-dimensional mri atlas of the human cerebellum in proportional stereotaxic space. *Neuroimage*, *10*(3 Pt 1), 233–260.
- Silveri, M. C., Di Betta, A. M., Filippini, V., Leggio, M. G., & Molinari, M. (1998). Verbal short-term store-rehearsal system and the cerebellum. Evidence from a patient with a right cerebellar lesion. *Brain*, *121*(Pt 11), 2175–2187.
- Sim, M. E., Lyoo, I. K., Streeter, C. C., Covell, J., Sarid-Segal, O., Ciraulo, D. A., et al. (2007). Cerebellar gray matter volume correlates with duration of cocaine use in cocaine-dependent subjects. *Neuropsychopharmacology*, *32*(10), 2229–2237.
- Spencer, K. A., & Slocumb, D. L. (2007). The neural basis of ataxic dysarthria. *Cerebellum*, *6*(1), 58–65.
- Sternberg, S. (1966). High-speed scanning in human memory. *Science*, *153*(736), 652–654.
- Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. *Neuroimage*, *44*(2), 489–501.
- Stoodley, C. J., & Schmahmann, J. D. (2010). Evidence for topographic organization in the cerebellum of motor control versus cognitive and affective processing. *Cortex*, *46*(7), 831–844.
- Strick, P. L., Dum, R. P., & Fiez, J. A. (2009). Cerebellum and nonmotor function. *Annual Review of Neuroscience*, *32*, 413–434.
- Sullivan, E. V., Deshmukh, A., Desmond, J. E., Lim, K. O., & Pfefferbaum, A. (2000). Cerebellar volume decline in normal aging, alcoholism, and korsakoff's syndrome: relation to ataxia. *Neuropsychology*, *14*(3), 341–352.
- Tiemeier, H., Lenroot, R. K., Greenstein, D. K., Tran, L., Pierson, R., & Giedd, J. N. (2010). Cerebellum development during childhood and adolescence: a longitudinal morphometric mri study. *Neuroimage*, *49*(1), 63–70.
- Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. *Neuroimage*, *16*(3 Pt 1), 765–780.
- Volkow, N. D., Wang, G. J., Ma, Y., Fowler, J. S., Zhu, W., Maynard, L., et al. (2003). Expectation enhances the regional brain metabolic and the reinforcing effects of stimulants in cocaine abusers. *The Journal of Neuroscience*, *23*(36), 11461–11468.
- Xiao, Z., Lee, T., Zhang, J. X., Wu, Q., Wu, R., Weng, X., et al. (2006). Thirsty heroin addicts show different fmri activations when exposed to water-related and drug-related cues. *Drug and Alcohol Dependence*, *83*(2), 157–162.
- Yuan, Y., Zhu, Z., Shi, J., Zou, Z., Yuan, F., Liu, Y., et al. (2009). Gray matter density negatively correlates with duration of heroin use in young lifetime heroin-dependent individuals. *Brain and Cognition*, *71*(3), 223–228.
- Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2001). Neural correlates of simple and complex mental calculation. *Neuroimage*, *13*(2), 314–327.
- Zago, L., Petit, L., Turbelin, M. R., Andersson, F., Vigneau, M., & Tzourio-Mazoyer, N. (2008). How verbal and spatial manipulation networks contribute to calculation: an fmri study. *Neuropsychologia*, *46*(9), 2403–2414.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.