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Special issue: Research report

Functional activation in the cerebellum during working memory and simple speech tasks

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ARTICLE INFO

Article history:
Received 20 December 2008
Reviewed 22 July 2009
Revised 22 August 2009
Accepted 1 September 2009
Published online 23 September 2009

Keywords:
Verbal working memory
Cerebellum
Speech production

ABSTRACT

Verbal working memory is the ability to temporarily store and manipulate verbal information. This study tested the predictions of a neuroanatomical model of how the cerebellum contributes to verbal working memory (Desmond et al., 1997). In this model, a large bilateral region in the superior cerebellum is associated with articulatory rehearsal and a right-lateralized region in the inferior cerebellum is associated with the correction of errors within the working memory system. The Desmond et al. (1997) model was based on neuroimaging findings using item recognition tasks and comparisons between working memory and covert rehearsal tasks, whereas in this functional magnetic resonance imaging (fMRI) study we used a delayed serial recall (DSR) task because it relies more heavily on articulatory rehearsal, and our comparison tasks included both overt and covert speech tasks. Our results provide some support for the Desmond et al. (1997) model. In particular, we found multiple activation foci within the superior and inferior sectors of the cerebellum and evidence that these regions show different patterns of activation across working memory and speech tasks. However, the specific patterns of activation were not fully consistent with those reported by Desmond et al. (1997). Namely, our results indicate that activation in the superior sector should be functionally subdivided into a medial focus involved in speech processing and a lateral focus more specific to verbal working memory; the results also indicate that activation in the inferior sector is not uniquely right lateralized. These complex findings speak to the need for future studies to consider the speech-motor aspects of tasks, to investigate the functional significance of adjacent peaks of activation within large regions of cerebellar activation, and to use analysis procedures that support regional distinctions through direct statistical tests. Such studies would help to refine our understanding of how the cerebellum contributes to speech and verbal working memory.

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0010-9452/$ – see front matter
doi:10.1016/j.cortex.2009.09.009

1. Introduction

Working memory is the ability to actively maintain a limited amount of information in a readily available state, even in the absence of continued sensory input. This capacity for internal representation is central to complex cognition and thus it is not surprising that working memory has been an important interdisciplinary topic of research. One of the most prominent theoretical models has proposed the use of a 'phonological' component that is composed of two subsystems: a short-term store that contains phonologically-based representations of the to-be-remembered items, and a rehearsal loop that acts to prevent the decay of verbal information in the phonological store (Baddeley, 1986; Salamé and Baddeley, 1982). The model developed by Baddeley and colleagues was initially intended to account for patterns of behavioral performance in the normal population and in participants with brain damage. A number of neuroimaging researchers adopted this model in an attempt to explain patterns of brain activation observed during the performance of working memory tasks. For instance, Smith et al. (1998) proposed that the left inferior parietal cortex is the site of phonological storage for verbal material and a set of regions associated with speech production are involved in articulatory rehearsal.

One of the speech-related regions associated with articulatory rehearsal is the left inferior frontal gyrus (i.e., Broca's area) (Chein et al., 2002); such a mapping is consistent with neuropsychological findings that have found rehearsal-related deficits in verbal working memory in individuals with Broca's aphasia (Benson, 1979; Damasio and Damasio, 2000; Dronkers et al., 2004). Motor-related speech areas have also been associated with articulatory rehearsal, including regions within the medial and lateral portions of premotor cortex and the cerebellum (Cabeza and Nyberg, 2000; Fiez, 1996; Fiez et al., 1996; Henson et al., 2000). The involvement of these areas raises interesting questions about the nature of the coding that is used in articulatory rehearsal: specifically, whether the coding is restricted to the language system, or whether it also involves the use of motor representations in brain regions that are outside of the language system *per se*. The neuroimaging results favor the latter interpretation, since activation during verbal working memory tasks is found in both language and motor-related brain regions. However, prior neuropsychological results favor the former interpretation. For instance, Bishop and colleagues (Bishop and Robson, 1989) examined the verbal working memory performance of individuals with cerebral palsy. These investigators found that verbal working memory performance was not different for those individuals whose motor symptoms included disturbances of speech versus those whose speech was normal. The authors concluded that the inner speech processes that are involved in working memory are at a relatively abstract level of representation since they appeared to be unaffected by difficulties in motoric aspects of speech production.

The apparent discrepancy between neuroimaging and neuropsychological findings may reflect the fact that activation in motor areas during verbal working memory tasks is incidental: that is, motor activation could be an irrelevant by-product of speech processing in the inferior frontal gyrus. This possibility has yet to be ruled out for cortical motor regions (e.g., medial and lateral premotor cortex). However, recent neuropsychological findings suggest that this account does not hold in the cerebellum. Across a relatively large number of neuropsychological studies, it has been found that individuals with damage to the cerebellum exhibit mild-to-moderate working memory deficits (Timmann and Daum, 2007), especially for verbal material (Ravizza et al., 2006).

More recent work in neuroanatomy, neuronal tracing, neuropsychology, and neuroimaging lend further support to the idea that the cerebellum is highly influential not only for motor processing, but also for cognitive processes. The cerebellum and the cerebrum are reciprocally connected through multi-synaptic closed-loop circuits (Strick et al., 2009) and the cerebellum appears to exhibit a functional topography that is consistent with specific patterns of cerebral connectivity (Stoodley and Schmahmann, 2009). The recent use of functional connectivity magnetic resonance imaging (fcMRI) has provided a new tool for the delineation of non-motor cerebro-cerebellar circuitry. For instance, Krienen and Buckner (2009) found a set of four closed cerebro-cerebellar loops linking both motor-based and cognition-based regions in the frontal cortex with distinct loci in the cerebellum. This account of frontal–cerebellar connectivity is corroborated in another fcMRI study by Allen et al. (2005), who also found parietal–cerebellar connectivity.

Neuroimaging studies have also examined the role of the cerebellum in working memory, with the work of Desmond and colleagues best reflecting a particular focus on the cerebellum. In a series of four studies (Chen and Desmond, 2005a, 2005b; Desmond et al., 1997; Kirschen et al., 2005), they used an item recognition procedure to examine cerebellar activation during verbal working memory. The size of the memory set used in these tasks varied (1 letter or 6 letters) so that load-dependent changes in activation could be detected. The authors used a relatively brief delay (5 sec) between item presentation and the recall probe, to which participants responded by squeezing a pneumatic response bulb if the probe matched an item in the memory set. As one comparison condition, activation was monitored during a rehearsal condition, in which participants silently and repeatedly read either a low (1) or high (6) number of the letters in the display image. As a second comparison condition, activation in one study was monitored during a simple finger-tapping task, in which subjects sequentially touched their right thumb to each finger in a sequence. The findings from these studies collectively support a neuroanatomical model of the cerebellum and working memory introduced by Desmond et al. (1997).

Desmond et al. (1997) identified a set of bilateral regions in the superior cerebellum (in lobule VI and the superior portion of lobule VIIA) that were more active for a high- versus the low-load working memory contrast, and also for a high- versus low-load rehearsal contrast. This observation, coupled with evidence that this portion of the cerebellum is likely to be connected with the inferior frontal gyrus, led the authors to propose that the identified superior cerebellar regions