The Cerebellum Plays a Role in Conscious Episodic Memory Retrieval

Nancy C. Andreasen,^{1,2*} Daniel S. O'Leary,^{1,2} Sergio Paradiso,²
Ted Cizadlo,¹ Stephan Arndt,^{1,4} G. Leonard Watkins,³
Laura L. Boles Ponto, and Richard D. Hichwa²

¹*Mental Health Clinical Research Center, University of Iowa College of Medicine, Iowa City, Iowa*

²*Department of Psychiatry, University of Iowa Hospitals & Clinics, Iowa City, Iowa*

³*P.E.T. Imaging Center, University of Iowa Hospitals & Clinics, Iowa City, Iowa*

⁴*Department of Preventive Medicine and Environmental Health, University of Iowa Hospitals & Clinics, Iowa City, Iowa*

Abstract: The cerebellum has traditionally been considered to be primarily dedicated to motor functions. Its phylogenetic development and connectivity suggest, however, that it also may play a role in cognitive processes in the human brain. In order to examine a potential cognitive role for the cerebellum in human beings, a positron emission tomography (PET) study was conducted during a “pure thought experiment”: subjects intentionally recalled a specific past personal experience (consciously retrieved episodic memory). Since there was no motor or sensory input or output, the design eliminated the possibility that cerebellar changes in blood flow were due to motor activity. During silent recall of a consciously retrieved episodic memory, activations were observed in the right lateral cerebellum, left medial dorsal thalamus, medial and left orbital frontal cortex, anterior cingulate, and a left parietal region. These activations confirm a cognitive role for the cerebellum, which may participate in an interactive cortical-cerebellar network that initiates and monitors the conscious retrieval of episodic memory. *Hum. Brain Mapping* 8:226–234, 1999.

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INTRODUCTION

The cerebellum, like the prefrontal cortex, displays a substantial increase in size in human beings, being

one-third larger than in nonhuman primates [Passingham, 1975]. This phylogenetic increase is difficult to explain if the cerebellum is considered to serve only motor functions, as has been conventionally believed until recently [Leiner et al., 1989; Thach, 1992; Glickstein, 1995]. Evidence is now steadily mounting to suggest that the cerebellum coordinates not only motor activity, but also aspects of cognitive activity [Leiner et al., 1989; Keele and Ivry, 1990; Schmahmann, 1991; Ito, 1993]. Anatomical studies suggest the presence of a cortical-cerebellar loop, linked through the pons, dentate, red nucleus, thalamus, and basal ganglia, implicating a possible role for the cerebellum in

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*Correspondence to: Dr. Nancy Andreasen, University of Iowa Hospitals & Clinics, Mental Health Clinical Research Center, 2911 JPP, 200 Hawkins Drive, Iowa City, IA 52242-1057.

E-mail: nancyandreasen@uiowa.edu

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modulating and coordinating both motor and cognitive activities [Brodal et al., 1991; Middleton and Strick, 1994; Schmahmann and Pandya, 1995]. Although cerebellar lesions or diseases do not produce gross cognitive deficits, a variety of subtle abnormalities have been noted in nonmotor tasks such as verbal learning, language production, judging time periods, and cognitive planning [Akshoomoff and Courchesne, 1992; Fiez et al., 1992]. Functional imaging studies have demonstrated cerebellar activations not only in motor and procedural learning, but also in sensory perception, word generation, nonmotor learning, and several types of memory tasks [Decety et al., 1990; Molchan et al., 1994; Andreasen et al., 1995a–d; Buckner et al., 1995; Moscovitch et al., 1995]. Several recent functional magnetic resonance (fMR) studies have demonstrated an activation of the dentate nucleus, the primary output nucleus from the neocerebellum to the neocortex, in a pegboard task and during sensory acquisition and discrimination [Kim et al., 1994; Gao et al., 1996]. An fMR study also has demonstrated a double dissociation between attention and motor performance in distinct cerebellar regions, further supporting a role for the cerebellum in cognitive activities such as anticipation and planning [Allen et al., 1997].

Although often carefully designed to control for motor or sensory activity, previous functional imaging studies have included some form of sensory or motor input or output (including counting silently to oneself), permitting skeptics of “cerebellar cognition” to argue that the cerebellar activations have some type of motor component and, therefore, do not represent “pure cognition.” Consequently, we conducted a positron emission tomography (PET) study that was a “pure thought experiment.” We sought to determine whether cerebellar activation occurred during an episodic memory task that had no motor or sensory input or output of any type.

MATERIALS AND METHODS

Subjects were recruited from the community by newspaper advertising and were screened using a structured interview to rule out psychiatric, neurological, or general medical disorders, including substance abuse. Eleven were male and eight female. Their mean age was 30.8 (SD 8.6), and their mean educational achievement was 14.3 (SD 1.7). All were right-handed.

Cognitive tasks

Two tasks were chosen that differed only with respect to conscious or intentional retrieval of episodic

memories, with episodic memory retrieval common to both tasks. Subjects were studied under two conditions, both of which consisted of lying quietly with eyes closed and thinking. The conditions differed only in the instructions given concerning the nature and content of thought. During the experimental condition (consciously retrieved episodic memory), subjects were asked to lie quietly with their eyes closed and to relax, but also were instructed to think about a specific event experienced in the past. During the comparison condition, subjects were only told to lie with their eyes closed, to relax, and to think about anything that occurred to them (random episodic silent thought, or REST). No motor activity or speech occurred. The form and content of their thought were assessed by a tape-recorded structured debriefing interview conducted immediately after each 100-sec scanning period was completed. This interview included a series of very specific questions, such as the amount of time spent thinking about past vs. future experiences or the percentage of time spent thinking in words vs. images. This interview was subsequently transcribed, and its analysis confirmed that subjects engaged in episodic memory retrieval (i.e., thoughts of past or future personal experiences) during both conditions. The major difference was in the conscious and sequential nature of recall during the experimental condition, as compared to the random (i.e., not sequentially ordered) nature of the recollected events during the comparison condition. The debriefing interview also indicated that subjects were thinking in mixtures of words and visual images, were not “talking to themselves” in a way that would produce subvocal speech, and had equal amounts of visual imagery or memories involving physical activity during both experimental and comparison tasks.

Image acquisition

PET data were acquired with a bolus injection of ^{15}O H_2O in 5–7 ml saline using a GE PC4096-plus 15-slice whole body scanner using methods as previously described [Andreasen et al., 1995a–d]. Apart from the Butterworth filter used in reconstruction, no additional filter was applied to the PET images, as has been done in some previous PET studies to minimize residual anatomical variability. Filtering reduces anatomic resolution, which we wished to maximize in the present study. MR scans, used for anatomic localization of functional activity, were obtained for each subject with a standard T1-weighted 3D SPGR sequence on a 1.5 Tesla GE Signa scanner (TE = 5, TR = 24, flip

angle = 40, NEX = 2, FOV = 26, matrix = 256×192 , slice thickness 1.5 mm).

Image analysis

The quantitative PET blood flow images and MR images were analyzed using the locally developed software package BRAINS [Andreasen et al., 1992]. MR scans were volume-rendered; the anterior commissure-posterior commissure (AC_PC) line was identified and used to realign the brains of all subjects to a standard position. The MR images from the 19 individuals were averaged, so that the functional activity visualized by the PET studies could be localized on co-registered MR and PET images where the MR image represented the “average brain” of the subjects in this study. The co-registered images were resampled and simultaneously visualized in all three orthogonal planes, thereby permitting 3D checking of anatomical localization of activity. Images were resampled to $128 \times 128 \times 80$ voxels using the Talairach Atlas [Talairach and Tournoux, 1988].

Statistical analysis

The data analysis was designed specifically to isolate the conscious or intentional component of episodic memory retrieval during the experimental task. A within-subject subtraction of the two conditions was performed, followed by across-subject averaging of the subtraction images and computation of voxel-by-voxel *t*-tests of the rCBF changes. Significant regions of activation were calculated on the *t*-map images, using an adaption of the Montreal method, which corrects for the large number of voxel by voxel *t*-tests performed, the lack of independence between voxels, and the resolution of the processed PET images [Worsley, 1992]. Since the images were not filtered, the number of resels was greater than in our previously reported studies. In the present study, a *t*-value of 3.92 was used as the statistical threshold for significance ($P < .00004$, one-tailed, uncorrected). Peaks are much smaller than in our previous studies because the data are unfiltered. Visual displays of data show both the significant peaks (using a cutoff of 15 voxels) and the associated *t*-maps. Positive peaks indicate the conscious component of episodic memory retrieval.

RESULTS

The experimental condition, conscious recall of a specific past experience, produced extensive cerebellar activations, as shown in Table I and Figure 1. The

TABLE I. Regions activated during consciously retrieved episodic memory

Region	t	voxels	x	y	z
Right medial cerebellum	5.59	143	10	-75	-23
Right lateral cerebellum	4.89	99	34	-55	-32
Right lateral inferior cerebellum	4.43	41	40	-60	-42
Right lateral superior cerebellum	4.18	15	42	-66	-23
Left lateral cerebellum	4.25	23	-46	-58	-30
Medial frontal	4.48	35	0	18	41
Left orbital frontal	5.35	63	-9	15	-15
Left parietal	4.91	32	-47	-55	42
Anterior cingulate	5.67	121	0	40	27
Left thalamus	4.61	41	-7	-21	7

Data are reported by showing the *t*-value associated with each peak, the volume of the voxels that exceed the *t*-value, and the location of the voxel with the highest value using Talairach coordinates and anatomic names based on visual inspection of the registered images. We report only peaks containing 15 or more voxels.

largest were in the right cerebellar hemisphere, contralateral to the left hemisphere activations seen throughout the cerebral cortex. An extensive network of cortical regions was also activated in a pattern largely consistent with recognized anatomic connectivity: medial frontal and left orbital frontal, left medial dorsal thalamus, left parietal, and anterior cingulate. This network may represent a cerebral cortex-cerebellar-thalamic-cortical circuit (CCTCC), a feedback loop that links cortical regions and the cerebellum. This feedback loop may be engaged by complex cognitive tasks that require ongoing monitoring and coordination of mental activity. In this study the complex cognitive task is conscious initiation and monitoring of retrieval of specific past experiences from episodic memory. Since no motor or sensory activity occurred during the study, these results provide strong support for a role for the cerebellum in cognition and specifically in some aspect of consciously retrieved episodic memory.

The REST condition also includes episodic memory retrieval, as discussed in a previous study [Andreasen et al., 1995] and as determined in this study by the structured debriefing interviews. Activations common to both conditions (i.e., those involving episodic memory retrieval) are removed in the subtraction analysis. Therefore, the regions identified in Table I are limited to those components of episodic memory retrieval that require consciously focusing on a specific personal experience, initiating and monitoring its retrieval in a time-linked sequence, as compared to thinking about such experiences in a random, unfo-

Figure 1.

Three orthogonal views, with transaxial at the top, sagittal in the middle, and coronal on the bottom. Four sets of images (A–D) were selected to illustrate the activations in Table I. Green crosshairs show location of the slice. Images follow radiological convention and show location as if standing at the foot of the bed (transaxial views) or facing patient (coronal views). Statistical maps (*t*-maps) of the PET data, showing regions that are significantly activated, are superimposed on a composite MR image derived by averaging the MR scans from the subjects. The value of *t* is shown on the color bar on the right. Two types of statistical maps are provided. The “peak map” (left side of image) shows the small areas where all contiguous voxels exceed the predefined threshold for statistical significance (3.92). These are small but anatomically precise, since the data were not smoothed (filtered). The “*t* map”

(right side of image) shows the value of *t* for all voxels in the image and provides a general overview of the landscape of changes in blood flow. The planes were chosen to illustrate the location of the relevant activity. **A** shows the right and left lateral cerebellar peaks (transaxial and coronal) and the right superior and inferior cerebellar peaks (sagittal and coronal). **B** indicates superior medial peak (all three planes) and the superior lateral peak (transaxial) in the cerebellum, as well as a tiny portion of the caudal extension of the orbital frontal activation. **C** shows the left thalamus (transaxial), medial frontal and anterior cingulate regions (sagittal), and parietal and right cerebellar activations (coronal). **D** shows the left orbital frontal activations (all three planes) and the left thalamus activation, which may be medial dorsal (sagittal).

cused, and nonsequential manner. Only one small region was found to be significantly higher in REST, the right postcentral gyrus ($t = 4.44$, 33 voxels, $x, y, z = 59, -16, -22$).

Although the debriefing interview indicated that the patients were not “talking to themselves” or producing an internal narrative that could lead to subvocal speech, which in turn might produce a motor compo-

Figure 1.

nent to the task, we felt it was important to rule out this possible explanation for these findings using direct experimental techniques. Consequently, to determine whether rCBF differences between the REST and consciously retrieved episodic memory conditions could have resulted from subvocalization, an independent group of six subjects was assessed while laryngeal movement was recorded using an electroglottalgram (EGG). Testing occurred in the Speech Science Laboratory, Department of Speech Pathology and Audiology (University of Iowa, in collaboration with Dr. Jerald Moon) and 103 sec of EGG activity were recorded during three conditions: REST, consciously retrieved episodic memory, and silent counting without vocalization. During the first two conditions, subjects were read the same instructions by the same researcher as

were used in the PET study. The recordings were amplified, displayed on an oscilloscope, and scored blindly by two independent raters for presence or absence of laryngeal movement. All six subjects showed marked laryngeal movement during the silent counting condition. None of the subjects showed measurable movement during the REST condition, and five of the six subjects showed no measurable activity during the episodic memory condition. One subject had questionable low amplitude activity during the episodic memory condition that exceeded the activity observed during REST, but was of much smaller amplitude than during silent counting. These results suggest that the substantial cerebellar activations observed during the experimental condition cannot be explained as due to subvocal speech.

Figure 1.

DISCUSSION

This experiment has identified the component of the episodic memory system that is required for the conscious initiation and monitoring of episodic memory retrieval. The two conditions in this “pure thought experiment” were very similar, differing only in the instructions given to the subjects. Yet they produced a distinct pattern of activation that appears to reflect the major difference between the two conditions: conscious initiation of retrieval of sequentially ordered memory, as compared to retrieval of memory that is not consciously initiated and more randomly ordered.

The largest and most numerous activations in the experimental condition occurred in the cerebellum and include both corticocerebellar and medial regions.

Although the cerebellar activations are bilateral, they are much larger and more frequent on the right, reflecting cross-hemispheric connectivity with more prominent activations seen in left cortical regions. These may be interpreted to reflect an interactive network between the cerebellum and the prefrontal cortex that is engaged in planning, initiating, and coordinating the conscious retrieval of time-linked memory. The dorsal, ventrolateral, and medial prefrontal cortices have been shown to have corticopontine projections that are presumed to play a role in this putative interactive cognitive network [Middleton and Strick, 1994; Schmahmann and Pandya, 1995]. Presumably, the prefrontal and cerebellar regions play separate but interactive roles in this task. Based on a large body of evidence reported on other PET studies, it is

Figure 1.

likely that the prefrontal cortex initiated the retrieval process [Tulving, 1983, 1987; Buckner et al., 1995].

The large and numerous cerebellar activations in this study of conscious memory retrieval raise interesting questions about the role of the cerebellum in cognition. This topic, as well as the relevant functional imaging literature, has been reviewed in several recent reports [Fiez and Raichle, 1997; Parsons and Fox, 1997; Desmond and Fiez, 1998]. A growing literature suggests that the cerebellum is involved in many types of nonmotor mental activity, including autobiographical episodic memory retrieval [Fink et al., 1996], but also several tasks that are neither memory nor motor, such as attribution or experience of emotion [Lane et al., 1997; Paradiso et al., 1999], visuospatial attention [Nobre et al., 1997], or musical processing in listeners with absolute pitch [Zatorre et al., 1998]. These studies,

in addition to the present one, confirm a role for the cerebellum in nonmotor higher level cognitive tasks, and their diversity suggests that the cerebellum may provide a common stratum that serves many types of mental activity. Several candidates for this common stratum have been suggested, such as operating multiple independent timing processors [Keele and Ivry, 1990] or combining simple cognitive units into larger units and linking them to a triggering context [Thach, 1998]. Edelman [1989] has suggested that the cerebellum may play a key role in the formation of consciousness. The present study confirms that the cerebellum has a specific role in *conscious* retrieval of memories, as opposed to memory retrieval in general. Its role may be initiating and maintaining the coordination or ongoing updating of the entire retrieval process.

Activations were also observed in the left parietal lobe, the anterior cingulate, and the left thalamus during the experimental task. The parietal activations may reflect the referencing of visuospatial associative memories or the recognition of successful retrieval (ecphory) [Kapur et al., 1995; Goldman-Rakic, 1995]. The anterior cingulate is activated in a variety of tasks that require attentional focus or modulation of response [Paus et al., 1993]. The thalamus is the direct output from the cerebellar dentate nucleus and is presumably activated as a component of the putative frontopontine-cerebellar-thalamic-frontal feedback circuit engaged in coordinating memory retrieval. Similar medial frontal and thalamic activations have been noted in other studies of episodic memory [Buckner et al., 1996]. In the present study, the frontal and thalamic activations were predominantly left-sided, whereas the cerebellar activations were on the right. The left cortical activity during memory retrieval contrasts with that predicted by the HERA (hemispheric encoding/retrieval asymmetry) model [Tulving et al., 1994], which suggests that the right hemisphere initiates episodic memory retrieval. However, episodic memory retrieval was common to both tasks and was subtracted out, which prevents visualization of right hemispheric retrieval activations. The remaining left-sided activations appear to reflect the conscious or intentional aspects of retrieval, which may be a predominantly left hemisphere function.

The regions found to be activated by conscious episodic memory in the present study are remarkably similar to those identified in our previous study of episodic memory [Andreasen et al., 1995d]. The interpretation of that study was confounded, however, by the fact that subjects engaged in motor speech during conscious retrieval. The present study eliminates the confound of any type of motor activity. Consequently, this study extends our previous work and provides strong additional evidence supporting a role for the cerebellum in conscious memory retrieval as part of an interactive frontal-cerebellar-thalamic-cortical memory network.

The intentional recall of specific time-linked personal memories, which place an individual within the context of his or her past experience, is the basis for introspection and self-awareness [Tulving, 1983, 1987; Andreasen et al., 1995d]. The findings support the possibility that the "little brain," the cerebellum, may complement the work of the larger cerebral cortex in functions that involve conscious retrieval of memories that are temporally sequenced. It may be part of a corticocerebellar memory network, linked through the thalamus, that forms the basis for complex cognitive functions such as personal consciousness.

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