




RESEARCH ARTICLE

Shaky scaffolding: Age differences in cerebellar activation revealed through activation likelihood estimation meta-analysis

Jessica A. Bernard^{1,2}  | An D. Nguyen^{1,3} | Hanna K. Hausman^{1,4}  |
 Ted Maldonado¹ | Hannah K. Ballard² | T. Bryan Jackson¹  | Sydney M. Eakin¹ |
 Yana Lokshina² | James R. M. Goen¹

¹Department of Psychological and Brain Sciences, Texas A&M University, College Station, Texas

²Texas A&M Institute for Neuroscience, Texas A&M University, College Station, Texas

³Department of Cognitive Science, Johns Hopkins University, Baltimore, Maryland

⁴Department of Clinical and Health Psychology, University of Florida, Gainesville, Florida

Correspondence

Jessica A. Bernard, Department of Psychological and Brain Sciences, Texas A&M University, College Station, TX.
 Email: jessica.bernard@tamu.edu

Funding information

Brain and Behavior Research Foundation, Grant/Award Number: NARSAD Young Investigator Award, Donald and Janet; National Institute on Aging, Grant/Award Number: R01AG064010-01

Abstract

Cognitive neuroscience research has provided foundational insights into aging, but has focused primarily on the cerebral cortex. However, the cerebellum is subject to the effects of aging. Given the importance of this structure in the performance of motor and cognitive tasks, cerebellar differences stand to provide critical insights into age differences in behavior. However, our understanding of cerebellar functional activation in aging is limited. Thus, we completed a meta-analysis of neuroimaging studies across task domains. Unlike in the cortex where an increase in bilateral activation is seen during cognitive task performance with advanced age, there is less overlap in cerebellar activation across tasks in older adults (OAs) relative to young. Conversely, we see an increase in activation overlap in OAs during motor tasks. We propose that this is due to inputs for comparator processing in the context of control theory (cortical and spinal) that may be differentially impacted in aging. These findings advance our understanding of the aging mind and brain.

KEYWORDS

aging, cerebellum, compensation, meta-analysis, neuroimaging

1 | INTRODUCTION

Advanced age is accompanied by differences in both cognitive (e.g., Park, Polk, Mikels, Taylor, & Marshuetz, 2001) and motor behavior (reviewed in Seidler et al., 2010). The impact of these differences on quality of life, well-being, independence, and rehabilitation is large. For example, cognitive complaints and deficits in memory, even in cognitively normal older adults (OAs), have broad impacts on quality of life across social and cognitive domains (Parikh, Troyer, Maione, & Murphy, 2016). Motor system differences include those in learning abilities (e.g., Anguera, Reuter-Lorenz, Willingham, & Seidler, 2011) and fall risk. Falls are a major cause of disability in OA, and postural control is associated with cognitive performance (Huxhold, Li,

Schmiedek, & Lindenberger, 2006). Characterizing the neural underpinnings of age-related cognitive and motor behavioral differences is critical for both our basic understanding of the aging process and for the elucidation of new remediation targets to improve quality of life for OA.

To this end, the field of the cognitive neuroscience of aging has greatly advanced our understanding of how brain changes and differences in OA impact behavior. Broadly, we know that in advanced age, the brain is smaller (e.g., Walhovd et al., 2011), there are differences in functional networks at rest (Andrews-Hanna et al., 2007; Langan et al., 2010), and differences in brain activation patterns during task performance (Naccarato et al., 2006; Reuter-Lorenz, Stanczak, & Miller, 1999; Seidler et al., 2010). Patterns of bilateral activation in OA

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. *Human Brain Mapping* published by Wiley Periodicals LLC.

are commonly seen in cases where young adults (YAs) would typically only activate one hemisphere (Cabeza, 2002; Reuter-Lorenz et al., 1999). This bilateral activation, particularly in the prefrontal cortex (PFC), has been suggested to be compensatory (Cabeza, 2002; Reuter-Lorenz & Cappell, 2008) to help maintain performance in advanced age.

While investigating cortical differences in OA has critically informed our understanding of age-related performance differences, cerebellar contributions to performance have been relatively understudied. There is a growing literature which demonstrates age differences in cerebellar volume (Bernard & Seidler, 2013b; Koppelmans, Young, & Sarah, 2017; Miller et al., 2013; Raz et al., 2005; Han et al., 2020) and connectivity with the cortex (Bernard et al., 2013). As our understanding of the functional contributions of the cerebellum has grown, we know now that it contributes to both motor and cognitive task performance (e.g., Balsters, Whelan, Robertson, & Ramnani, 2013; Chen & Desmond, 2005; Stoodley & Schmahmann, 2009). Organized with a distinct functional topography (e.g., Stoodley & Schmahmann, 2009; Stoodley et al., 2012; King et al., 2019) thought to be derived from closed loop circuits connecting the cerebellum to the cortex, via the thalamus (Middleton & Strick, 2001; Strick, Dum, & Fiez, 2009), more dorsal anterior regions contribute to motor task performance (Lobules I–VI), while the lateral and posterior aspects of the cerebellum (Crus I, Crus II, Lobule VIIb) are engaged during cognitive task performance (Stoodley et al., 2012; King et al., 2019). In addition, there is an inferior secondary motor representation in Lobules VIIIa and VIIIb (Stoodley et al., 2012). Because of the consistent cytoarchitecture of the cerebellum across lobules (unlike in the cerebral cortex), it has been suggested that internal model processing which has been well understood may also occur for cognitive tasks (Ramnani, 2006, 2014; Ito, 2008). Though more recent work has questioned the notion of a universal transform, with respect to cerebellar processing and instead suggesting that the same circuit may conduct different computations (Diedrichsen et al., 2019), to date there have been no clear alternative suggestions as to what computation may be.

As such, with these wide-ranging behavioral contributions, understanding how the cerebellum may contribute to performance in OA is of great interest and importance. To date, work in this area has demonstrated that differences in both volume and connectivity of the cerebellum are functionally relevant for both motor and cognitive performance in OA (Bernard & Seidler, 2013a; Bernard et al., 2013; Miller et al., 2013). That is, smaller volume in OA is associated with poorer performance, as is lower functional connectivity (Bernard & Seidler, 2013b; Bernard et al., 2013). In these cases, there is also functional specificity. For example, Crus I and Crus II, which are more associated with cognitive tasks, show volumetric and connectivity correlations with cognitive tasks (Bernard & Seidler, 2013a; Bernard et al., 2013).

Recently, we suggested that differences in connectivity with the cortex and smaller lobular volume in the cerebellum in OA contribute to performance differences in aging due to degraded internal models of behavior (Bernard & Seidler, 2014). As noted above, theories of cerebellar function have suggested that the structure acts on copies of commands for behavior and compares the outcomes of a given command with what is expected based on that initial command (Ramnani, 2006,

2014). Ultimately, internal models of a particular movement or thought process are formed (e.g., Balsters et al., 2013; Imamizu et al., 2000) that allow for greater automaticity. However, due to degraded cerebellar-cortical connectivity and the smaller cerebellar volume in OA, the inputs to this structure may be negatively impacted, resulting in degraded internal model processing and, in turn, performance deficits (Bernard & Seidler, 2014). Furthermore, cerebellar function may provide important scaffolding for behavior in OA (Filip, Gallea, Lehericy, Lungu, & Bareš, 2019). The scaffolding theory of aging and cognition (STAC; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) considers individual differences in brain structure, function, life experience, and the broader environmental context that may allow OA to implement scaffolding of function. This scaffolding can be in a variety of forms (e.g., white matter structure, exercise interventions) that can be relied upon to maintain function in advanced age (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014). We propose that cerebellar function may be one contributor to this general scaffolding. Indeed, it may be the case that the bilateral processing seen in the cortex in OA (c.f., Cabeza 2002) is to compensate for a lessened ability to rely upon cerebellar resources in advanced age. That is, the brain is less able to offload processing and take advantage of more automatic processing via existing internal models, resulting in a greater need for cortical resources. However, there has been limited work investigating the functional activation patterns of the cerebellum in advanced age, which would provide important insight into this hypothesis. Investigating cerebellar functional activation in OA stands to advance our understanding of the neural underpinnings of behavioral differences and changes in advanced age, providing a more complete perspective on the aging mind and brain.

To better understand the functional engagement of the cerebellum in OA, we conducted a meta-analysis of the functional brain imaging literature in OA and YA. We tested two competing hypotheses. Based on our prior work suggesting degraded inputs to the cerebellum and internal model processing in OA (Bernard & Seidler, 2014), decreased convergence of cerebellar activation in OA relative to YA would be expected. That is, we would expect to see less consistent overlap in foci of activation across studies. However, the cortical literature consistently demonstrates an increase in bilateral activation in OA during task performance (e.g., Cabeza, 2002; Reuter-Lorenz et al., 1999). Thus, alternatively, the same pattern may be present in the cerebellum if similar compensatory processes are recruited during task processing. As such, we would expect to see a convergence of foci across studies in both cerebellar hemispheres in OA, while in YA convergence would be limited to one hemisphere (consistent with lateralized findings from prior investigations of the cerebellar functional topography; e.g., E et al., 2014; Stoodley et al., 2012; Stoodley & Schmahmann, 2009).

2 | METHOD

2.1 | Literature search and inclusion criteria

All materials associated with the analysis in the form of text files of foci (for more details see below) are freely available for download at

<https://osf.io/gx5jw/>. To identify papers, we completed two separate and sequential literature searches completed using PubMed (<http://www.ncbi.nlm.nih.gov/pubmed>). The first search used the search term: “cerebell” AND imaging” with the limits “Humans” and “English.” Additionally, we included the limit “Adult 65+” to target the OA literature. Notably, even with this age limit, some manuscripts were included with participants below the age of 65, due to the categorization of papers in our search. However, we carefully investigated the mean ages (when available) as well as the age ranges to ensure that an OA population was studied. As seen in Tables 1–5, the OA in the sample had an average age of approximately 60, though the range was more variable. This resulted in 3,913 articles.

Articles that focused on structural or morphometric analyses, region of interest analysis, and functional connectivity, as well as those that did not report coordinates in the cerebellum, did not report coordinates in standard spaces (Montreal Neurological Institute [MNI] or Talairach), and did not have independent groups contrast analysis were excluded. With respect to this last point, this unfortunately meant that investigations taking a lifespan approach and looking at age effects across adulthood using regression models were not included in this analysis. This is consistent with the exclusion criteria used in recent meta-analyses from our group, and others (Bernard & Mittal, 2015; Bernard, Russell, Newberry, Goen, & Mittal, 2017; Bernard & Seidler, 2013a; E et al., 2014; Stoodley & Schmahmann, 2009). After completion of this search and exclusion of papers based on the aforementioned exclusion criteria, we were left with a very small sample of studies (42 studies) and foci on which to complete our analyses (see Figure 1). However, this was limited, at least in part, to the inclusion of the “cerebell” term in our initial search, as this term may not be in the keywords or abstracts of papers indexed in PubMed. As such, we completed a second search using the terms “aging AND brain imaging” with the same limits as above, which returned 5,982 results as of August 6, 2018. All inclusion/exclusion criteria were identical those for search 1. This second search yielded an additional 73 studies for inclusion. Sixty additional studies were added based on those included in prior meta-analyses (see more below), for a total of 175 studies.

As cerebellar engagement in both motor and cognitive tasks was of interest, we included studies in the following task domains: motor function, working memory, language, and “other cognitive tasks.” Notably, this last category primarily included executive function tasks (such as the Stroop task, tower of London task, etc.), though several tasks assessing spatial processing were also included here. Categorical determination was made to be consistent with the task domains used by both E et al. (2014) and Stoodley and Schmahmann (2009), with the exception of long-term memory as it had not been previously included in past meta-analyses. Tasks included in this category included a memory component with a delay in recall, typically on the order of several minutes. These task domains were chosen for several key reasons. First, we aimed to parallel prior meta-analyses looking at cerebellar function to compare the functional topography in OA to what is known about this topography in YA. Second, these are

domains where there are known age differences in performance and as such are of great interest in the study of motor and cognitive aging. Tables 1–5 include a complete listing of the studies included in our meta-analysis divided by task domain, along with the average age and/or age range of participants when available. This also provides information about the brain imaging modality (PET or fMRI), scanner field strength where applicable, and the number of foci from a given study for each age group.

To complete our analyses of age differences, we used the YA control samples from the OA literature, as opposed to doing an additional search focused on YA alone. To date, there have been several meta-analyses investigating task activation patterns in both the motor and cognitive domains in healthy YA (Bernard & Seidler, 2013a; E et al., 2014; Stoodley & Schmahmann, 2009), and such an analysis would be redundant, and is beyond the scope of the present investigation. Furthermore, we were concerned about considerable differences in the sample sizes that would potentially bias our group comparison analyses, as the YA literature is substantially larger. However, because many of the studies in our OA sample included OA that served as controls for an age-related disease group, we had a limited sample of YA studies. To better equate our groups with respect to the number of studies and foci, we included all the studies and foci from prior meta-analyses investigating cerebellar functional activation (E et al., 2014; Stoodley & Schmahmann, 2009). In defining the tasks of interest in this analysis, we paralleled those used in this prior work, with two exceptions. We included a long-term memory category, and we did not investigate emotion tasks. Additional motor foci were extracted from the studies included by Stoodley and Schmahmann (2009), while those for language, working memory, and cognitive function (categorized as executive function by E et al.) were taken from E et al. (2014). Notably, E et al. (2014) also had substantial overlap with Stoodley and Schmahmann (2009) as they included all of the papers from the prior analysis, as well as new additions to the literature. Notably, we did not gather additional YA papers to specifically match the OA papers for two reasons. First, though we could match based on task type, we were concerned that this could introduce selection bias. For many tasks, there are multiple papers that have similar sample sizes as existing OA studies and additional inclusion criteria could have been biased. Second, though additional YA papers may have cerebellar foci, there would be no guarantee that the number of foci would be matched across studies even when taking this approach.

The literature searches and initial inclusion decisions were completed by T. M., A. D. N., Y. L., J. R. M. G., H. K. B., and H. K. H. Inclusion was confirmed and coordinates for each study were checked, prior to analysis, by J. A. B. After scanning the literature and the inclusion of the studies from both Stoodley & Schmahmann (2009) and E et al. (2014), we had 175 studies, including data from 1,710 YA (403 foci) and 2,160 OA (307 foci) individuals, concatenated across all task domains. Figure 1 provides a flowchart demonstrating our article screening procedure and exclusion regions, broadly defined. The initial search, and secondary broader aging search are presented separately.

TABLE 1 Included studies in the “Other Cognitive/Executive Function” category

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|--|-----------|-----------|--|
| Other cognitive tasks/executive function | | | | | | | |
| Gianaros, Jennings, Sheu, Derbyshire, Matthews (2007). <i>Hypertension</i> , 49, 134–140. | 3T fMRI | — | 46 | Stroop task | — | 1 | YA: N/A OA: 68.04 |
| Hubert, Beauvieux, Chételat, Platel, Landeau, Viader, Desgranges, Eustache (2009). <i>Hum Brain Map</i> , 30, 1,374–1,386. | PET | — | 12 | Tower of Toronto task | — | 6 | YA: N/A OA: 65 (60–73) |
| Luis, Arrondo, Vidorreta, Martínez, Loayza, Fernández-Seara, Pastor (2015). <i>PLoS ONE</i> , 10, e0131536. | 3T fMRI | — | 20 | N-back task combined across spatial and visual domains | — | 2 | YA: N/A OA: 62.2 (58–66) |
| Moffat, Elkins, Resnick (2006). <i>Neurobiol Aging</i> , 27, 965–972. | 1.5T fMRI | 30 | 21 | Spatial navigation | 1 | 1 | YA: 27.07 (21–39) OA: 68.43 (60–78) |
| Belville, Mellah, de Boysson, Demonet, Bier (2014). <i>PLoS ONE</i> , 9, e102710. | 3T fMRI | — | 42 | Dual-tasking using alphabetic equations | — | 1 | YA: N/A OA: Not specified |
| Beauchamp, Dagher, Aston, Doyon (2003). <i>NeuroImage</i> , 20, 1,649–1,660. | PET | — | 12 | Tower of London task | — | 3 | YA: N/A OA: 56.8 (51–69) |
| Harrington, Castillo, Greenberg, Song, Lessig, Lee, Rao (2011). <i>PLoS ONE</i> , 6, e17461. | 3T fMRI | — | 19 | Time perception | — | 14 | YA: N/A OA: 64.6 |
| Drezga, Grimmer, Peller, Wermke, Siebner, Rauschecker, Schwaiger, Kurz (2005). <i>PLoS Med</i> , 2, e288. | PET | — | 10 | Spatial navigation of 3D environments | — | 4 | YA: N/A OA: 68.8 |
| Grönholm, Rinne, Vorobyev, Laine (2005). <i>Cog Brain Res</i> , 25, 359–371. | PET | — | 10 | Object naming | — | 10 | YA: N/A OA: 65.5 (56–77) |
| Ramanoël, Kaufmann, Cousin, Dojat, Peyrin (2015). <i>PLoS ONE</i> , 10, e0134554. | 3T fMRI | 12 | 12 | Spatial scene processing | 0 | 1 | YA: 22.3 (18–26) OA: 64 (61–71) |
| Madden, Langley, Denny, Turkington, Provenzale, Hawk, Coleman (2002). <i>Brain Cogn</i> , 49, 297–321. | PET | 12 | 12 | Visual search | 2 | 7 | YA: 23.58 (20–29) OA: 65.00 (62–70) |
| Geerligs, Maurits, Renken, Lorist (2014). <i>Hum Brain Mapp</i> , 35, 319–330. | 3T fMRI | 12 | 30 | Visual oddball task | 2 | 0 | YA: 24.1 OA: 63.9 |
| Gilbert, Bird, Brindley, Frith, Burgess (2008). <i>Neuropsychologia</i> , 46, 2,281–2,291.** | 3T fMRI | 18 | — | Random generation task | 3 | — | YA: 32 OA: N/A |
| Rao, Bobholz, Hammeke, Rosen, Woodley, Cunningham, Cox, Stein, Binder (1997). <i>NeuroReport</i> , 8, 1987–1993.* | 1.5T fMRI | 11 | — | Conceptual reasoning | 3 | — | YA: 29 (19–45) OA: N/A |
| Dagher, Owen, Boecker, Brooks (1999). <i>Brain</i> , 122, 1973–1987.** | PET | — | 6 | Tower of London task | — | 6 | YA: N/A OA: 58.6 (49–70) |
| Jahanshahi, Dirnberger, Fuller, Frith (2000). <i>NeuroImage</i> , 12, 713–725.* | PET | 6 | — | Random number generation relative to counting | 2 | — | YA: 29.6 OA: N/A |
| Liddle, Kiehl, Smith (2001). <i>Hum Brain Mapp</i> , 12, 100–109.* | 1.5T fMRI | 16 | — | Go no-go task | 15 | — | YA: 30.2 OA: N/A |
| Ernst, Bolla, Mouratidis, Contoreggi, Matochik, Kurian, Cadet, Kimes, London (2002). <i>Neuropsychopharmacol</i> , 26, 682–691.* | PET | 20 | — | Risk decision making | 10 | — | YA: 30.4 (21–45) OA: N/A |

TABLE 1 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|---|-----------|-----------|--|
| Kondo, Morishita, Osaka, Osaka, Fukuyama, Shibasaki (2004). <i>NeuroImage</i> , 21, 2–14.** | 1.5T fMRI | 10 | – | Arithmetic and memory | 6 | – | YA: 23.6 (22–27) OA: N/A |
| Harrington, Boyd, Mayer, Sheltraw, Lee, Huang, Rao (2004). <i>Cog Brain Res</i> , 21, 193–205.* | 1.5T fMRI | 24 | – | Interval timing decision making | 4 | – | YA: 30.6 (21–53) OA: N/A |
| Dreher & Grafman (2002). <i>Eur J Neurosci</i> , 16, 1,609–1,619.** | 1.5T fMRI | 18 | – | Task switching during letter discrimination | 4 | – | YA: 25 (20–31) OA: N/A |
| Schall, Johnston, Lagopoulos, Jüptner, Jentzen, Thienel, Dittman-Balçar, Bender, Ward (2003). <i>NeuroImage</i> , 20, 1,154–1,161.** | PET/1.5T fMRI | 6 | – | Tower of London task | 2 | – | YA: 31.0 (21–41) OA: N/A |
| Daniels, Witt, Wolff, Jansen, Deuschl (2003). <i>Neurosci Lett</i> , 345, 25–28.* | 1.5T fMRI | 8 | – | Random number generation at 1 Hz | 2 | – | YA: 25.4 OA: N/A |
| Blackwood, ffytche, Simmons, Bentall, Murray, Howard (2004). <i>Cog Brain Res</i> , 20, 46–53.* | 1.5T fMRI | 8 | – | Decision making under certain and uncertain conditions | 2 | – | YA: 38 (18–53) OA: N/A |
| Lenzi, Serra, Perri, Pantano, Lenzi, Paulesu, Caltagirone, Bozzali, Macaluso (2011). <i>Neurobiol Aging</i> , 32, 1,542–1,577. | 3T fMRI | – | 14 | Visuospatial attention; line bisection judgments relative to color judgment | – | 1 | YA: N/A OA: 64.3 (50–81) |
| Leshikar, Gutches, Hebrank, Sutton, Park (2010). <i>Cortex</i> , 26, 507–521. | 3T fMRI | 19 | 18 | Relational encoding | 0 | 3 | YA: 20.9 (18–26) OA: 65.7 (60–80) |
| Hartley, Jonides, Sylvester (2011). <i>Brain & Cognition</i> , 75, 281–291. | 3T fMRI | 12 | 12 | Dual-task processing with letters | 1 | 0 | YA: 21.00 (19–25) OA: 70.67 (65–77) |

Note: Notably, while many of the included studies had both YA and OA, in some instances, OA data came from clinical studies wherein the OA served as a control group. Furthermore, additional YA data came from studies included in prior meta-analyses. Cases where there were no cerebellar coordinates are indicated by a 0 in the appropriate foci column. Mean age is provided in years, and the range is also provided when available. N/A: not applicable. “–” denotes studies where a particular age group was not included and as such no coordinates are possible.

*Studies included as part of Stoodley and Schmahmann (2009) and E et al. (2014).

**Studies only included in E et al. (2014).

TABLE 2 Included studies of language tasks

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|--|-----------|-----------|---------------------------------------|
| Language | | | | | | | |
| Rizio, Moyer, Diaz (2017). <i>Brain Behav</i> , 7, e00660. | 3T fMRI | 20 | 20 | Language interference naming | 0 | 2 | YA: 23.7 (18–31) OA: 67.25 (60–79) |
| Provost, Brambati, Chappelle, Wilson (2016). <i>Cortex</i> , 84, 90–100. | 3T fMRI | 16 | 16 | Word reading | 0 | 1 | YA: 27.5 (22–33) OA: 67.0 (60–75) |
| Martins, Simard, Monchi (2014). <i>PLoS ONE</i> , 9, e99710. | 3T fMRI | 14 | 14 | Lexical version of the Wisconsin card sorting task | 6 | 3 | YA: 26 (21–31) OA: 63 (55–71) |
| Whatmough, Verret, Fung, Chertkow (2004). <i>J Cogn Neurosci</i> , 16, 1,211–1,226. | PET | – | 15 | Semantic judgments of word pairs | – | 4 | YA: N/A OA: 74.3 (69–90) |
| Olichney, Taylor, Hillert, Chan, Salmon, Gatherwright, Iragui, Kutas (2010). <i>Neurobiol Aging</i> , 31, 1975–1990. | 1.5T fMRI | – | 17 | Word memory and repetition | – | 3 | YA: N/A OA: 69.7 |
| Daselaar, Veltman, Rombouts, Raaijmakers, Jonker (2003). <i>Neurobiol Aging</i> , 24, 1,005–1,011. | 1.5T fMRI | 26 | 39 | Semantic characterization after shallow or deep encoding | 1 | 1 | YA: 32.4 (30–35) OA: 66.3 (63–71) |

(Continues)

TABLE 2 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|--|-----------|-----------|--|
| Madden, Langley, Denny, Turkington, Provenzale, Hawk, Coleman (2002). <i>Brain Cogn</i> , 49, 297–321. | PET | 12 | 12 | Lexical decision task | 3 | 2 | YA: 23.58 (20–29) OA: 65.00 (62–70) |
| Seki, Okada, Koeda, Sadato (2004). <i>Cog Brain Res</i> , 20, 261–272.* | 3T fMRI | 19 | – | Vowel exchange compared to reading words and non-words | 2 | – | YA: 23.3 OA: N/A |
| Rauschecker, Pringle, Watkins (2008). <i>Hum Brain Mapp</i> , 29, 1,231–1,242.** | 3T fMRI | 14 | – | Listening and cover repetition of non-words | 4 | – | YA: 23.3 (20–34) OA: N/A |
| Daselaar, Veltman, Rombouts, Raaijmakers, Jonker (2005). <i>Neurobiol Learn Mem</i> , 83, 251–262. | 1.5T fMRI | 25 | 38 | Word-stem completion | 1 | 0 | YA: 32.3 (30–35) OA: 66.4 (63–71) |
| Ojemann, Buckner, Akbudak, Snyder, Ollinger, McKinstry, Rosen, Petersen, Raichle, Conturo (1998). <i>Hum Brain Mapp</i> , 6, 203–215.* | PET/1.5T fMRI | 7 | – | Word-stem completion | 7 | – | YA: 24 (19–28) OA: N/A |
| Schlosser, Hutchinson, Joseffer, Rusinek, Saarimaki, Stevenson, Dewey, Brodie (1998). <i>J Neurol Neurosurg Psychiatry</i> , 64, 492–498.* | 1.5T fMRI | 6 | – | Verbal fluency task | 6 | – | YA: 23 (22–26) OA: N/A |
| Lurito, Kareken, Lowe, Chen, Mathews (2000). <i>Hum Brain Mapp</i> , 10, 99–106.* | 1.5T fMRI | 5 | – | Word generation compared to viewing non-letter symbols | 3 | – | YA: 27 OA: N/A |
| Seger, Desmond, Glover, Gabrieli (2000). <i>Neuropsychol</i> , 14, 361–369.* | 1.5T fMRI | 7 | – | Verb generation task | 16 | – | YA: 31 OA: N/A |
| Gurd, Amunts, Weiss, Zafiris, Zilles, Marshall, Fink (2002). <i>Brain</i> , 125, 1,024–1,038.* | 1.5T fMRI | 11 | – | Semantic fluency relative to overlearned sequence fluency (days of the week) | 1 | – | YA: 32 OA: N/A |
| Noppeney & Price (2002). <i>NeuroImage</i> , 15, 927–935.* | PET | 12 | – | Semantic decision task | 2 | – | YA: 24 (20–30) OA: N/A |
| McDermott, Petersen, Watson, Ojemann (2003). <i>Neuropsychologia</i> , 41, 293–303.* | 1.5T fMRI | 20 | – | Word lists of semantic compared to phonological | 3 | – | YA: 22.1 (18–32) OA: N/A |
| Xiang, Lin, Ma, Zhang, Bower, Weng, Gao (2003). <i>Hum Brain Map</i> , 18, 208–214.* | 1.5T fMRI | 6 | – | Semantic discrimination | 1 | – | YA: 21–36 OA: N/A |
| Tieleman, Seurinck, Deblaere, Vandemaele, Vingerhoets, Achten (2005). <i>NeuroImage</i> , 26, 565–572.* | 1.5T fMRI | 22 | – | Semantic compared to perceptual categorization | 3 | – | YA: 29 (22–47) OA: N/A |
| Frings, Dimitrova, Schorn, Elles, Heinkropp, Gizewski, Diener, Timmann (2006). <i>Neurosci Letters</i> , 409, 19–23.* | 1.5T fMRI | 16 | – | Verb generation task | 3 | – | YA: 24.9 (18–35) OA: N/A |
| Callan, Tsytsarev, Hanakawa, Callan, Katsuhara, Fukuyama, Turner (2006). <i>NeuroImage</i> , 31, 1,327–1,342.** | 3T fMRI | 16 | – | Listening to and covert production of singing relative to speech | 2 | – | YA: 26 (19–47) OA: N/A |
| Sweet, Paskavitz, Haley, Gunstad, Mulligan, Nyalakanti, Cohen (2008). <i>Neuropsychologia</i> , 46, 1,114–1,123.** | 1.5T fMRI | 34 | – | Phonological similarity during verbal working memory | 1 | – | YA: 37.24 (18–80) OA: N/A |
| Durisko & Fiez (2010). <i>Cortex</i> , 46, 896–906.** | 3T fMRI | 19 | – | Delayed serial recall task with letters | 2 | – | YA: 23 (19–33) OA: N/A |
| Davis, Kragel, Madden, Cabeza (2012). <i>Cereb Cortex</i> , 22, 232–242. | 3T fMRI | 18 | 16 | Semantic matching task | 0 | 1 | YA: 21.70 OA: 68.06 |

TABLE 2 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|---|------------------|-------|-------|---|-----------|-----------|------------------------|
| Shafto, Randall, Stamatakis, Wright, Tyler (2012). <i>J Cognitive Neurosci</i> , 24, 1,434–1,446. | 3T fMRI | 14 | 16 | Lexical decision task, imageability of high and low competition words | 2 | 0 | YA: 23.86 OA: 75.75 |

Note: Notably, while many of the included studies had both YA and OA, in some instances, OA data came from clinical studies wherein the OA served as a control group. Furthermore, additional YA data came from studies included in prior meta-analyses. “—” denotes studies where a particular age group was not included and as such no coordinates are possible. Cases where there were no cerebellar coordinates are indicated by a 0 in the appropriate foci column. N/A: not applicable.

*Studies included as part of Stoodley and Schmahmann (2009) and E et al. (2014).

**Studies only included in E et al., 2014.

TABLE 3 Included studies of motor tasks

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|---|-----------|-----------|--------------------------------------|
| Motor | | | | | | | |
| Wurster, Graf, Ackermann, Groth, Kassubek, Riecker (2015). <i>Brain Struct Func</i> , 220, 1,637–1,648. | 3T fMRI | — | 10 | Finger tapping | — | 2 | YA: N/A OA: 64.9 |
| Blumen, Holtzer, Brown, Gazes, Verghese (2015). <i>Hum Brain Mapp</i> , 35, 4,090, 4,104. | 3T fMRI | — | 33 | Imagined walking and walking while talking | — | 1 | YA: N/A OA: 73.03 |
| Allali, van der Meulen, Beauchet, Rieger, Vuilleumier, Assal (2014). <i>J Gerontol A Biol Sci Med Sci</i> , 69, 1,389–1,398. | 3T fMRI | 14 | 14 | Motor imagery | 1 | 3 | YA: 27.0 OA: 66.0 |
| Wittenberg, Lovelace, Foster, Maldjian (2014). <i>Brain Imaging Behav</i> , 8, 335–345. | 1.5T fMRI | 12 | 12 | Ecologically valid motor self-care tasks (e.g., buttoning & zipping) and finger tapping | 11 | 6 | YA: 29.0 OA: 61.0 |
| Crémers, D’Ostilio, Stamatakis, Delvaux, Garraux (2012). <i>Movement Disorders</i> , 27, 1,498–1,505. | 3T fMRI | — | 15 | Imagined gait relative to imagined standing | — | 3 | YA: N/A OA: 63.8 |
| Vidoni, Thomas, Honea, Koskutova, Burns (2012). <i>J Neurol Phys Ther</i> , 36, 8–16. | 3T fMRI | — | 10 | Power grip | — | 3 | YA: N/A OA: 73.6 |
| Zwergal, Linn, Xiong, Brandt, Strupp, Jahn (2012). <i>Neurobiol Aging</i> , 33, 1,073–1,084. | 3T fMRI | 20 | 20 | Imagined movement, standing and walking | 0 | 5 | YA: 24–40 OA: 60–78 |
| Askim, Indredavik, Haberg (2010). <i>Arch Phys Med Rehabil</i> , 91, 1,529–1,536. | 1.5T fMRI | — | 15 | Finger tapping – Paced and self-paced | — | 3 | YA: N/A OA: 65.9 (50–75) |
| Allen & Humphreys (2009). <i>Current Biol</i> , 19, 1,044–1,049. | 3T fMRI | — | 7 | Somatomotor tactile stimulation | — | 1 | YA: N/A OA: >74 |
| Eckert, Peschel, Heinze, Rotte (2006). <i>J Neurol</i> , 253, 199–207. | 1.5T fMRI | — | 9 | Opening and closing fist | — | 1 | YA: N/A OA: 60.6 |
| Heuninckx, Wenderoth, Debaere, Peeters, Swinnn (2005). <i>J Neurosci</i> , 25, 6,787–6,796. | 3T fMRI | 12 | 12 | Coordinated hand and foot movements | 8 | 31 | YA: 22.4 (20–25) OA: 64.8 (62–71) |
| Rowe, Stephan, Friston, Frackowiak, Lees, Passingham (2002). <i>Brain</i> , 125, 267–289. | Not specified | — | 12 | Motor sequence learning | — | 3 | YA: N/A OA: 62.0 |
| Kalpouzos, Garzón, Sitnikov, Heiland, Salami, Persson, Bäckman (2017). <i>Cereb Cortex</i> , 27, 3,427–3,436. | 3T fMRI | 22 | 15 | Motor imagery | 1 | 2 | YA: 36.8 OA: 69.7 |

(Continues)

TABLE 3 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|--|-----------|-----------|--|
| King, Saucier, Albouy, Fogel, Rumpf, Klann, Buccino, Binkofski, Classen, Karni, Doyon (2017). <i>Cereb Cortex</i> , 27, 1,588–1,601. | 3T fMRI | – | 26 | Motor sequence learning, initial training only included here | – | 3 | YA: N/A OA: 63.5 |
| Wang, Qiu, Liu, Yan, Yang, Zhang, Zhang, Sang, Zheng (2014). <i>Neurosci</i> , 56, 339–348. | 3T fMRI | 19 | 20 | Motor execution and imagery | 6 | 8 | YA: 36.5 (20–23) OA: 62.5 (52–82) |
| Heuninckx, Wenderoth, Swinnen (2010). <i>Neurobiol Aging</i> , 31, 301–314. | 3T fMRI | 12 | 12 | Externally and internally guided movements | 6 | 8 | YA: 23.5 (21–27) OA: 66.9 (63–73) |
| Riecker, Gröschel, Ackermann, Steinbrink, Witte, Kastrup (2006). <i>NeuroImage</i> , 32, 1,345–1,354. | 1.5T fMRI | 10 | 10 | Motor tapping | 1 | 1 | YA: 23.0 (18–26) OA: 66.0 (58–82) |
| Zapparoli, Invernizzi, Gandola, Verardi, Berlinger, Sberna, De Santis, Zerbi, Banfi, Bottini, Paulesu (2012). <i>Exp Brain Res</i> , 224, 519–540. | 1.5T fMRI | 24 | 24 | Finger to thumb opposition | 1 | 0 | YA: 27.0 OA: 60.0 |
| Jäncke, Loose, Lutz, Specht, Shah (2000). <i>Cog Brain Res</i> , 10, 51–66. | 1.5T fMRI | 8 | – | Finger tapping | 3 | – | YA: 20–32 OA: N/A |
| Lutz, Specht, Shah, Jäncke (2000). <i>NeuroReport</i> , 11, 1,301–1,306. | 1.5T fMRI | 10 | – | Finger tapping | 4 | – | YA: 24.1 (21–29) OA: N/A |
| Riecker, Wildgruber, Mathiak, Grodd, Ackermann (2003). <i>NeuroImage</i> , 18, 2003, 731–739. | 1.5T fMRI | 8 | – | Finger tapping | 12 | – | YA: 23.75 (19–32) OA: N/A |
| Hanakwa, Dimyan, Hallett (2008). <i>Cereb Cortex</i> , 18, 2,775–2,788. | 3T fMRI | 13 | – | Finger tapping | 2 | – | YA: 30.0 (21–48) OA: N/A |
| Brunne, Skouen, Erslund, Grüner (2014). <i>Neurorehab Neral Repair</i> , 28, 874–884. | 3T fMRI | – | 18 | Observation and execution of bimanual movements | – | 4 | YA: N/A OA: 60.6 |
| Taniwaki, Okayama, Yoshiura, Togao, Nakamura, Yamsaki, Ogata, Shigeto, Shyagi, Kira, & Tobimatsu (2007). <i>NeuroImage</i> , 36, 1,263–1,276. | 1.5T fMRI | 12 | 12 | Externally triggered or self-initiated finger movements | 6 | 4 | YA: 24.9 (23–29) OA: 62.9 (53–72) |
| Taniwaki, Yoshiura, Ogata, Togao, Yamashita, Kida, Miura, Kira, Tobimatsu (2013). <i>Brain Res</i> , 1,512, 45–59. | 1.5T fMRI | – | 12 | Externally triggered or self-initiated finger movements | – | 4 | YA: N/A OA: 62.0 (54–72) |
| Daselaar, Rombouts, Veltman, Raaijmakers, Jonker (2003). <i>Neurobiol Aging</i> , 24, 1,013–1,019. | 1.5T fMRI | 26 | 40 | Motor sequence learning | 1 | 3 | YA: 32.4 (30–35) OA: 66.4 (63–71) |
| Onozuka, Fujita, Watanabe, Hirano, Niwa, Nishiyama, Saito (2003). <i>J Dent Res</i> , 82, 657–660. | 1.5T fMRI | 10 | 10 | Chewing | 1 | 1 | YA: 19–26 OA: 65–73 |
| Rijntjes, Buechel, Kiebel, Weiller (1999). <i>NeuroReport</i> , 10, 3,653–3,658. | 2T fMRI | 9 | – | Finger flexion and extensions | 3 | – | YA: 32.0 OA: N/A |
| Hankawa, Immisch, Toma, Dimyan, van Gelderen, Hallett (2003). <i>J Neurophysiol</i> , 89, 989–1,002. | 1.5T fMRI | 10 | – | Finger tapping | 3 | – | YA: 32.0 OA: N/A |
| Loibl, Beutling, Kaza, Lotze (2011). <i>Behav Brain Res</i> , 223, 280–286. | 1.5T fMRI | 18 | 17 | Passive wrist movement, fist clenching, precision grip | 21 | 17 | YA: 25.39 (23–30) OA: 66.65 (57–72) |
| Linortner, Fazekas, Schmidt, Ropele, Pendl, Petrovic, Loitfelder, Neuper, Enzinger (2012). <i>Neurobiol Aging</i> , 197, e1-191-e9-17. | 3T fMRI | – | 17 | Ankle and finger movements | – | 2 | YA: N/A OA: 63.59 (48–84) |

TABLE 3 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|---|-----------|-----------|--------------------------------------|
| Linortner, Fazekas, Schmidt, Ropele, Pendl, Petrovic, Loitfelder, Neuper, Enzinger (2012). <i>Neurobiol Aging</i> , 197, e1-191-e9-17. | 3T fMRI | — | 13 | Ankle and finger movements | — | 3 | YA: N/A OA: 73.31 (48–84) |
| Kim, Lee, Lee, Song, Yoo, Lee, Kim, Chang (2010). <i>Neurological Res</i> , 32, 995–1,001. | 3T fMRI | 20 | 26 | Weighted and unweighted elbow flexion/extension | 0 | 3 | YA: 23.0 OA: 65.5 |
| Rieckman, Fischer, Bäckman (2010). <i>NeuroImage</i> , 50, 1,303–1,312. | 1.5T fMRI | 14 | 13 | Serial reaction time task | 2 | 1 | YA: 24.71 OA: 68.08 |
| Huang, Lee, Hsiao, Kuan, Wai, Ko, Wan, Hsu, Liu (2010). <i>J Neurosci Methods</i> , 189, 257–266. | 1.5T fMRI | 16 | — | Hand flexion | 1 | — | YA: 22.0 (18–25) OA: N/A |
| Bo, Peltier, Noll, Seidler (2011). <i>Neurosci Letters</i> , 504, 68–72. | 3T fMRI | 14 | 14 | Motor sequence learning with symbolic and spatial presentation of stimuli | 1 | 0 | YA: 21.4 OA: 72.7 |
| Dennis, Cabeza (2011). <i>Neurobiol Aging</i> , 2,318.17-2,318.e30. | 4T fMRI | 12 | 12 | Serial reaction time task | 1 | 0 | YA: 22.2 (18–30) OA: 67.4 (60–79) |

Note: Notably, while many of the included studies had both YA and OA, in some instances OA data came from clinical studies wherein the OA served as a control group. Furthermore, additional YA data came from studies included in prior meta-analyses. “—” denotes studies where a particular age group was not included and as such no coordinates are possible. Cases where there were no cerebellar coordinates are indicated by a 0 in the appropriate foci column. The study by Linortner and colleagues (2012) is listed twice. Because two distinct and unique samples of older adults were included, the foci were entered separately into the analyses. Huang and colleagues (2010) looked at older adults in a separate experiment investigating working memory (see Table 4), and the motor task was only conducted in the young adult sample. However, the data are included here as based on our search terms; this study met our criteria. N/A: not applicable.

*Studies included as part of Stoodley and Schmahmann (2009).

TABLE 4 Included studies of working memory

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|---|------------------|-------|-------|--|-----------|-----------|------------------------------|
| Working memory | | | | | | | |
| Luis, Arrondo, Vidorreta, Martínez, Loayza, Fernández-Seara, Pastor (2015). <i>PLoS ONE</i> , 10, e0131536. | 3T fMRI | — | 20 | N-back task | — | 1 | YA: N/A OA: 62.2 (58–66) |
| Boller, Mellah, Ducharme-Laliberté, Belleville (2017). <i>Brain Imaging Behav</i> , 11, 304–317. | 3T fMRI | — | 40 | N-back task | — | 3 | YA: N/A OA: 68.59 (60–84) |
| Heinzel, Lorenz, Pelz, Heinz, Walter, Kathmann, Rapp, Stelzel (2016). <i>NeuroImage</i> , 134, 236–249. | 3T fMRI | — | 32 | N-back task and Sternberg task, baseline assessment only | — | 11 | YA: N/A OA: 66.07 (60–75) |
| Charroud, Steffener, Le Bars, Deverdun, Bonafe, Abdennour, Portet, Molino, Stern, Ritchie, Menjot de Champfleury, Akbaraly (2015). <i>Neurobiol Learn Mem</i> , 1,250, 211–223. | 3T fMRI | — | 337 | Delayed-item recognition task | — | 10 | YA: N/A OA: 82.1 |
| Luis, Arrondo, Vidorreta, Martínex, Loayza, Fernández-Seara, Pastor (2015). <i>PLoS ONE</i> , 10, e0131536. | 3T fMRI | — | 20 | Verbal working memory load manipulation | — | 4 | YA: N/A OA: 62.2 (58–66) |
| Migo, Mitterschiffthaler, O'Daly, Dawson, Dourish, Craig, Simmons, Wilcock, McCulloch, Jackson, Kopelman, Williams, Morris (2015). <i>Aging, Neuropsychol, Cog</i> , 22, 106–127. | 3T fMRI | — | 11 | N-back task | — | 2 | YA: N/A OA: 70.27 (60–80) |

(Continues)

TABLE 4 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|---|------------------|-------|-------|---|-----------|-----------|--------------------------------------|
| Griebe, Amann, Hirsch, Achtnichts, Hennerici, Gass, Szabo (2014). <i>PLoS ONE</i> , 9, e103359. | 1.5T fMRI | — | 14 | N-back task | — | 3 | YA: N/A OA: 67.0 (55–79) |
| Emery, Heaven, Paxton, Braver (2008). <i>NeuroImage</i> , 42, 1,577–1,586. | 1.5T fMRI | 10 | 11 | Letter-number sequencing | 0 | 3 | YA: 21.9 (18–27) OA: 71.2 (65–82) |
| Jennings, van der Veen, Melzer (2006). <i>Brain Res</i> , 1,092, 177–189. | PET | — | 89 | N-back task | — | 3 | YA: N/A OA: 61.0 (50–70) |
| Lensing, Born, Meindl, Bokde, Britsch, Lopez-Bayo, Teipel, Möller, Hampel, Reiser (2007). <i>Dement Geriatr Cogn Disord</i> , 24, 235–246. | 1.5T fMRI | 15 | 19 | Location matching task | 5 | 6 | YA: 28.0 OA: 71.0 |
| Lamar, Yousem, Resnick (2004). <i>NeuroImage</i> , 21, 1,368–1,376. | 1.5T fMRI | 16 | 16 | Delayed match to sample | 2 | 1 | YA: 27.9 (20–40) OA: 69.1 (60–80) |
| Schneider-Garces, Gordon, Brumback-Peltz, Shin, Lee, Sutton, Maclin, Gratton, Fabiani (2010). <i>J Cogn Neurosci</i> , 22, 655–659. | 3T fMRI | 12 | 30 | Sternberg task | 1 | 0 | YA: 23.8 (18–27) OA: 70.9 (65–80) |
| Vellage, Becke, Strumpf, Baier, Schönfeld, Hopf, Müller (2016). <i>Brain Behav</i> , 6, e00544. | 3T fMRI | 40 | 38 | Spatial working memory filtering task | 2 | 0 | YA: 25.7 (21–32) OA: 65.8 (58–74) |
| Valera, Faraone, Beiderman, Poldrack, Seidman (2005). <i>Biol Psychiatry</i> , 57, 439–447.* | 1.5T fMRI | 20 | — | N-back task | 1 | — | YA: 33.0 (18–55) OA: N/A |
| Hayter, Langdon, Ramnani (2007). <i>NeuroImage</i> , 36, 943–954.** | 3T fMRI | 15 | — | Paced auditory serial addition task | 6 | — | YA: 18–29 OA: N/A |
| Scheuerecker, Ufer, Zipse, Frodl, Koutsouleris, Zetzsche, Wiesmann, Albrecht, Brückmann, Schmitt, Möller, Meisenzahl (2008). <i>J Psychiat Res</i> , 42, 469–476.** | 1.5T fMRI | 23 | — | N-back task | 5 | — | YA: 32.6 OA: N/A |
| Hautzel, Mottaghy, Specht, Müller, Krause (2009). <i>NeuroImage</i> , 47, 2073–2082.** | 1.5T fMRI | 17 | — | N-back task | 19 | — | YA: 25.7 OA: N/A |
| Marvel and Desmond (2010). <i>Cortex</i> , 46, 880–895.** | 3T fMRI | 16 | — | Sternberg task | 2 | — | YA: 23.69 (19–28) OA: N/A |
| Oren, Ash, Tarrasch, Hendler, Giladi, Shapira-Lichter (2017). <i>Neurobiol Aging</i> , 53, 93–102. | 3T fMRI | 24 | 28 | N-back task | 2 | 0 | YA: 29.0 (22.35) OA: 71.8 (65–79) |
| Grady, McIntosh, Bookstein, Horwitz, Rapoport, Haxby (1998). <i>NeuroImage</i> , 8, 409–425. | PET | 13 | 16 | Working memory of facial stimuli | 1 | 0 | YA: 25.0 OA: 66.0 |
| Fiez, Raife, Balota, Schwarz, Raichle, Petersen (1996). <i>J Neurosci</i> , 16, 808–822.** | PET | 12 | — | Working memory during PET?? | 5 | — | YA: 24.0 OA: N/A |
| Schumacher, Lauber, Awh, Jonides, Smith, Koeppel (1996). <i>NeuroImage</i> , 3, 79–88.** | PET | 8 | — | Visual and auditory working memory | 8 | — | YA: Not reported OA: N/A |
| Jonides, Schumacher, Smith, Koeppel, Awh, Reuter-Lorenz, Marshuetz, Willis (1998). <i>J Neurosci</i> , 18, 5,026–5,034.** | PET | 12 | — | Storage and fixation, modeled after Fiez et al., 1996 | 3 | — | YA: Not reported OA: N/A |
| LaBar, Gitelman, Parrish, Marsel Mesulam (1999). <i>NeuroImage</i> , 10, 695–704.* | 1.5T fMRI | 11 | — | N-back task | 1 | — | YA: 32.6 OA: N/A |

TABLE 4 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|---|------------------|-------|-------|---|-----------|-----------|--------------------------------------|
| Thomas, King, Franzen, Welsh, Berkowitz, Noll, Birmaher, Casey (1999). <i>NeuroImage</i> , 10, 327–338.** | 1.5T fMRI | 6 | — | N-back task | 1 | — | YA: 22.0 (19–26) OA: N/A |
| Honey, Bullmore, Sharma (2000). <i>NeuroImage</i> , 12, 495–503.* | 1.5T fMRI | 20 | — | N-back task | 1 | — | YA: 39.3 (19–64) OA: N/A |
| Gruber (2001). <i>Cereb Cortex</i> , 11, 1,047–1,055.* | 3T fMRI | 11 | — | Letter memory relative to letter case judgment with or without articulatory suppression | 1 | — | YA: 23.6 OA: N/A |
| Cairo, Liddle, Woodward, Ngan (2004). <i>Cog Brain Res</i> , 21, 377–387.* | 1.5T fMRI | 18 | — | Sternberg task | 13 | — | YA: 27.5 (18–35) OA: N/A |
| Kirschen, Chen, Schraedley-Desmond, Desmond (2005). <i>NeuroImage</i> , 24, 462–472.* | 3T fMRI | 17 | — | Verbal working memory with increasing load | 6 | — | YA: 25.0 OA: N/A |
| Chen and Desmond (2005b). <i>Neuropsychologia</i> , 43, 1,227–1,237.* | 3T fMRI | 15 | — | Sternberg task | 9 | — | YA: 22.53 (18–28) OA: N/A |
| Chen and Desmond (2005a). <i>NeuroImage</i> , 24, 332–338.** | 3T fMRI | 15 | — | Verbal working memory with high and low loads | 9 | — | YA: 28.6 OA: N/A |
| Tomasi, Caparelli, Chang, Ernst (2005). <i>NeuroImage</i> , 27, 377–386.* | 4T fMRI | 30 | — | N-back task | 3 | — | YA: 31.0 OA: N/A |
| Woodward, Cairo, Ruff, Takane, Hunter, Ngan (2006). <i>Neuroscience</i> , 139, 317–325.** | 1.5T fMRI | 18 | — | Verbal working memory with varying loads | 5 | — | YA: 27.5 (18–35) OA: N/A |
| Geier, Garver, Luna (2007). <i>NeuroImage</i> , 35, 904–915.** | 3T fMRI | 18 | — | Occulomotor delayed response task (spatial working memory) | 3 | — | YA: 18–30 OA: N/A |
| Tomasi, Chang, Caparelli, Ernst (2007). <i>Brain Res</i> , 1,132, 158–165.** | 4T fMRI | 22 | — | N-back task | 3 | — | YA: 30.0 OA: N/A |
| Yeh, Kuo, Liu (2007). <i>Brain Res</i> , 1,130, 146–157.** | 1.5T fMRI | 10 | — | Change detection spatial working memory task | 1 | — | YA: 23.5 (21–25) OA: N/A |
| O'Hare, Lu, Houston, Bookheimer, Sowell (2008). <i>NeuroImage</i> , 42, 1,678–1,685.** | 3T fMRI | 8 | — | Verbal working memory with varying loads | 4 | — | YA: 24.0 (20–28) OA: N/A |
| Koelsch, Schulze, Sammler, Fritz, Müller, Gruber (2009). <i>Hum Brain Mapp</i> , 30, 859–873.** | 3T fMRI | 12 | — | Tonal and verbal working memory | 1 | — | YA: 26.7 (25–30) OA: N/A |
| Durisko and Fiez (2010). <i>Cortex</i> , 46, 896–906.** | 3T fMRI | 19 | — | Delayed serial recall task | 7 | — | YA: 23.0 (19–33) OA: N/A |
| Schulze, Zysset, Mueller, Friederici, Koelsch (2011). <i>Hum Brain Mapp</i> , 32, 771–783.** | 3T fMRI | 17 | — | Verbal and tonal working memory | 5 | — | YA: 25.47 (21–29) OA: N/A |
| Kirschen, Chen, Desmond (2010). <i>Behav Neurol</i> , 23, 51–63.** | 3T fMRI | 16 | — | Load dependent verbal working memory with visual and aural stimuli | 10 | — | YA: 21.7 OA: N/A |
| Piefke, Onur, Fink (2012). <i>Neurobiol Aging</i> , 33, 1,284–1,297. | 1.5T fMRI | 15 | 14 | N-back and delayed match to sample tasks | 2 | 2 | YA: 23.6 OA: 65.1 |
| Huang, Lee, Hsiao, Kuan, Wai, Ko, Wan, Hsu, Liu (2010). <i>J Neurosci Methods</i> , 189, 257–266. | 1.5T fMRI | — | 12 | N-back task | — | 1 | YA: N/A OA: 65.0 (60–74) |
| Dreher, Koch, Kohn, Apud, Weinberger, Berman (2012). <i>Biol Psychiatry</i> , 71, 890–897. | PET | 19 | 17 | Spatial n-back task | 2 | 0 | YA: 27.5 (20–36) OA: 67.5 (54–79) |

Note: Notably, while many of the included studies had both YA and OA, in some instances, OA data came from clinical studies wherein the OA served as a control group. Furthermore, additional YA data came from studies included in prior meta-analyses. “—” denotes studies where a particular age group was not included and as such no coordinates are possible. Cases where there were no cerebellar coordinates are indicated by a 0 in the appropriate foci column. N/A: not applicable.

*Studies included as part of Stoodley and Schmahmann (2009) and E et al. (2014).

**Studies only included in E et al. (2014).

TABLE 5 Included studies of long-term memory

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|--|------------------|-------|-------|---|-----------|-----------|--|
| Long-term memory | | | | | | | |
| Vidal-Piñeir, Martin-Trias, Arenaza-Urquijo, Sala-Llonch, Clemente, Mena-Sánchez, Bargalló, Falcón, Pascual-Leone, Bartrés-Faz (2014). <i>Brain Stim</i> , 7, 287–296. | 3T fMRI | – | 24 | Memory for deep and shallow encoding | – | 3 | YA: N/A OA: 71.75 (61–80) |
| Beason-Held, Golski, Kraut, Esposito, Resnick (2005). <i>Neurobiol Aging</i> , 26, 237–250. | PET | – | 11 | Verbal and figural encoding and recognition | – | 10 | YA: N/A OA: 71.1 (63–82) |
| Peira, Ziaei, Persson (2016). <i>NeuroImage</i> , 125, 745–755. | 3T fMRI | 15 | 15 | Prospective memory | 0 | 2 | YA: 22.4 (20–26) OA: 68.1 (64–74) |
| Cohen, Rissman, Suthana, Castel, Knowlton (2016). <i>NeuroImage</i> , 125, 1,046–1,062. | 3T fMRI | – | 23 | Memory for words with high and low value | – | 3 | YA: N/A OA: 68.7 (60–80) |
| Gong, Fu, Wang, Franz, Long (2014). <i>Int'l J Aging Hum Dev</i> , 79, 23–54. | 3T fMRI | – | 12 | Emotional autobiographical memory retrieval | – | 8 | YA: N/A OA: 66.3 (60–74) |
| Miotto, Balardin, Savege, Martin, Batistuzzo, Amaro, Nitrini (2014). <i>Arq Neuropsiquiatr</i> , 72, 663–670. | 3T fMRI | – | 17 | Memory for semantically related and unrelated words | – | 1 | YA: N/A OA: 68.12 |
| Brassen, Büchel, Weber-Fahr, Lehmbeck, Sommer, Braus (2009). <i>Neurobiol Aging</i> , 30, 1,147–1,156. | 3T fMRI | 14 | 14 | Correct retrieval during verbal episodic memory | 0 | 1 | YA: 25.6 (21–33) OA: 64.9 (60–71) |
| Bartrés-Faz, Serra-Grabulosa, Sun, Solé-Padullés, Rami, Molineuvo, Bosch, Mercader, Bargalló, Falcón, vendrell, Junqué, D'Esposito (2008). <i>Neurobiol Aging</i> , 29, 1,644–1,653. | 1.5T fMRI | – | 20 | Encoding of face-name pairs | – | 1 | YA: N/A OA: 66.0 |
| Maguire and Frith (2003). <i>Brain</i> , 126, 1,511–1,523. | 2T fMRI | 12 | 12 | Autobiographical memory | 4 | 4 | YA: 32.42 (23–39) OA: |
| Gronholm, Rinne, Vorobyev, Laine (2005). <i>Cog Brain Res</i> , 25, 359–371. | PET | – | 10 | Memory for learned objects | – | 6 | YA: N/A OA: 74.75 (67.80) |
| Milton, Butler, Benattayallah, Zeman (2012). <i>Neuropsychologia</i> , 50, 3,528–3,541. | 1.5T fMRI | – | 17 | Long-term autobiographical memory | – | 6 | YA: N/A OA: >50 |
| Lam, Wächter, Globas, Karnath, Luft (2013). <i>Hum Brain Mapp</i> , 34, 176–185. | 3T fMRI | – | 10 | Weather prediction task | – | 2 | YA: N/A OA: 64.6 (43–85) |
| Antonova, Parslow, Brammer, Dawson, Jackson, Morris (2009). <i>Memory</i> , 17, 125–143. | 1.5T fMRI | 10 | 10 | Long-term memory of spatial information | 4 | 4 | YA: 23.6 (20–26) OA: 72.14 (64–79) |
| Dannhauser, Shergill, Stevens, Lee, Seal, Walker, Walker (2008). <i>Cortex</i> , 44, 869–880. | 1.5T fMRI | – | 10 | Verbal episodic memory | – | 1 | YA: N/A OA: 68 (50–84) |
| Bowman and Dennis (2015). <i>Brain Res</i> , 1,612, 2–15. | 3T fMRI | 17 | 22 | Remember/know judgments of long-term memory | 0 | 1 | YA: 21.28 (18–25) OA: 74.18 (67–83) |
| Kircher, Weis, Leube, Freymann, Erb, Jessen, Grodd, Heun, Krach (2008). <i>Eur Arch Psychiatry Clin Neurosci</i> , 258, 363–372. | 1.5T fMRI | – | 29 | Subsequent memory effect | – | 1 | YA: N/A OA: 67.7 (60–81) |
| Daselaar, Veltman, Rombouts, Raaijmakers, Jonker (2003). <i>Brain</i> , 126, 43–56. | 1.5T fMRI | 17 | 19 | Correct rejection or recognition at retrieval | 3 | 2 | YA: 32.7 (30–35) OA: 66.4 (63–71) |
| Haist, Gore, Mao (2001). <i>Nature Neurosci</i> , 4, 1,139–1,145. | 1.5T fMRI | – | 8 | Remote memory for famous faces | – | 2 | YA: N/A OA: 64.6 (60–70) |

TABLE 5 (Continued)

| Study | Imaging modality | N, YA | N, OA | Task | # YA foci | # OA foci | Age: Mean (range) |
|---|------------------|-------|-------|--|-----------|-----------|---------------------------------------|
| Iidaka, Sadato, Yamada, Murata, Omori, Yonekura (2001). <i>Cog Brain Res</i> , 11, 1–11. | 1.5T fMRI | 7 | 7 | Pictorial information, abstract object encoding | 0 | 1 | YA: 25.7 OA: 66.2 |
| Madden, Turkington, Provenzale, Denny, Hawk, Gottlob, Coleman (1999). <i>Hum Brain Map</i> , 7, 115–135. | PET | 12 | 12 | Recognition memory task | 1 | 2 | YA: 23.17 (20–29) OA: 71.0 (62–79) |
| Gao, Cheung, Chan, Chu, Mak, Lee (2014). <i>PLoS ONE</i> , 9, e90307. | 3T fMRI | 13 | 13 | Prospective memory | 1 | 0 | YA: 27.1 OA: 76.2 |
| Grady, McIntosh, Horwitz, Maisog, Ungerleider, Mentis, Pietrini, Schapiro, Haxby (1995). <i>Science</i> , 269, 218–221. | PET | 10 | 10 | Recognition compared to matching in long-term memory | 3 | 0 | YA: 25.2 OA: 69.4 |
| Zamboni, de Jager, Drazich, Douaud, Jenkinson, Smith, Tracey, Wilcock (2013). <i>Neurobiol Aging</i> , 34, 961–972. | 3T fMRI | — | 28 | Paired associates task | — | 1 | YA: N/A OA: 74.4 (64–91) |
| Braskie, Small, Bookheimer (2009). <i>Hum Brain Map</i> , 30, 3,981–3,992. | 3T fMRI | — | 32 | Long term memory of word lists at retrieval | — | 2 | YA: N/A OA: 60.0 (42–77) |
| Düzel, Scütze, Yonelinas, Heinze (2011). <i>Hippocampus</i> , 21, 803–814. | 1.5T fMRI | 24 | 56 | Incidental encoding task, activation at recollection | 4 | 0 | YA: 23.0 OA: 65.0 |

Note: Notably, while many of the included studies had both YA and OA, in some instances OA data came from clinical studies wherein the OA served as a control group. “—” denotes studies where a particular age group was not included and as such no coordinates are possible. Cases where there were no cerebellar coordinates are indicated by a 0 in the appropriate foci column. N/A: not applicable.

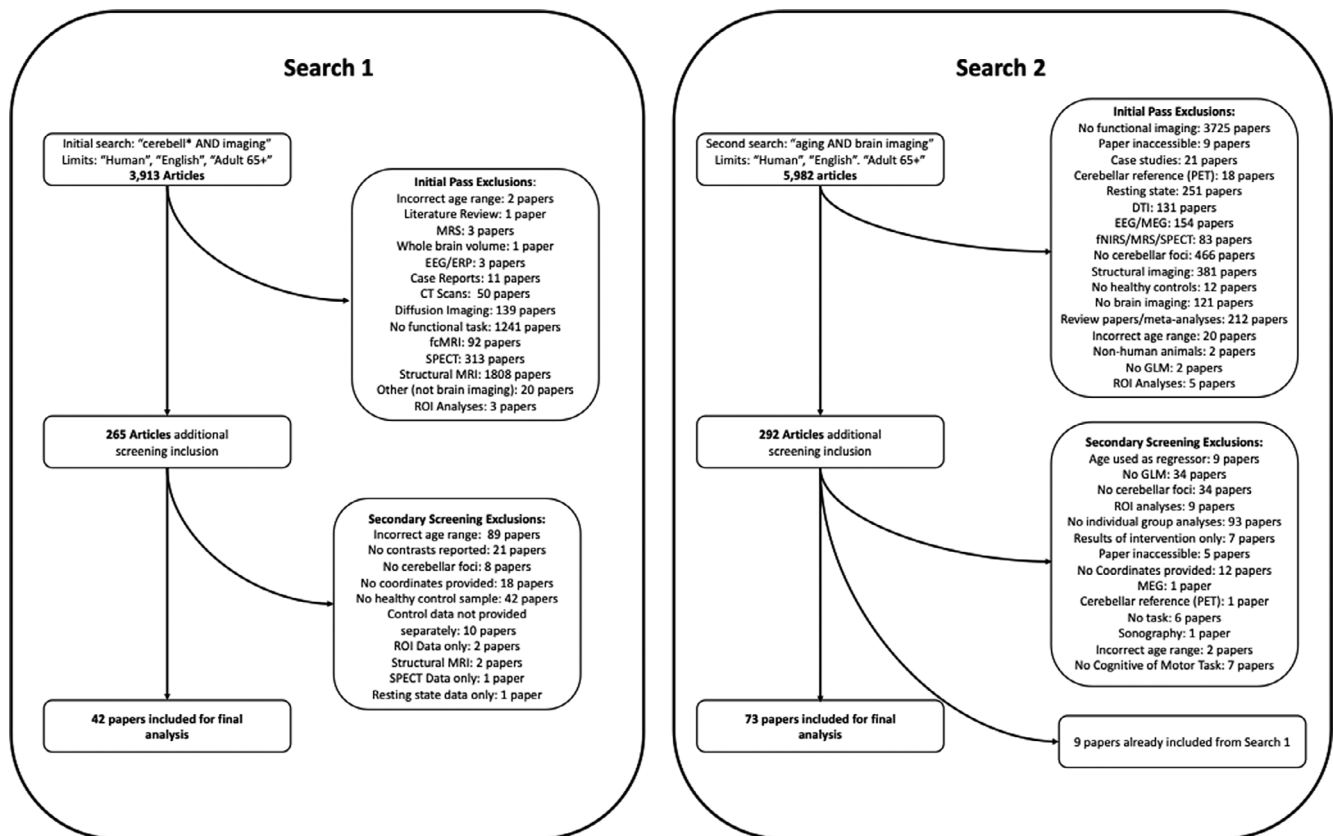


FIGURE 1 Flowchart describing the two search processes. In both cases, an initial overview of papers was conducted to eliminate initial obvious exclusions. Secondary screening was conducted while foci were pulled from papers for analysis, though additional exclusions occurred at this stage as well. A full list of included papers can be found in Tables 1–5, organized by task domain. Hundred and fifteen studies were included based off our two literature searches. However, additional studies from prior meta-analyses of cerebellar function were also added to our sample, bringing the total number of included studies to 175

2.2 | Activation likelihood estimation meta-analysis

All analyses were completed using BrainMap GingerALE 3.0.2 (<http://brainmap.org>; Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Eickhoff et al., 2009; Turkeltaub et al., 2012). Activation likelihood estimation (ALE) allows us to combine across studies, sites, scanning modalities, and study designs to investigate overlap in activation patterns, and the algorithm includes a metrics to account for variability in subjects and testing sites (Eickhoff et al., 2012). Unlike behavioral meta-analyses, because the algorithm looks at activation foci, and models these to account for uncertainty, the variability in design and analysis approaches can be reasonably accounted for. Foci were first organized for analysis by task domain; however, we also performed additional analyses concatenating across all cognitive task domains. As there are two standard atlas spaces used for normalization and presentation of activation (MNI or Talairach), it is critical to ensure that all foci are in the same atlas space prior to analysis for the purpose of comparison across studies. As such, all foci in Talairach space were converted to MNI space prior to analysis. For studies where data were normalized directly to Talairach space, and those that specified the use of the Lancaster transform (icbm2tal; Lancaster et al., 2007), we used this transform to move them to MNI space. This transform was also used for studies published after the icbm2tal transform became available, and for which no specific transform information was provided. For studies where the Brett transform (mni2tal) was used to bring data from MNI space to Talairach space, and for articles published prior to 2007 without any transform details, we used the inverse Brett transform to bring the data into MNI space. All transforms were completed using tools available in GingerALE.

Once in MNI space, all activation foci were organized into text files for analysis with GingerALE. The ALE algorithm computes ALE values for all of the voxels in the brain, producing an estimation of the likelihood that a particular voxel is active under particular task conditions (Eickhoff et al., 2009). During analysis, GingerALE uses a full-width half-maximum (FWHM) Gaussian blur on each set of foci, with the size based off of the sample size used to generate each set of foci (Eickhoff et al., 2009). Output of our analyses indicated that the FWHM blur ranged from 8.46 to 11.37 mm, across all analyses. In completing our analyses, we used the smaller more conservative mask option available in GingerALE, in conjunction with the non-additive ALE method (Turkeltaub et al., 2012). For within group analyses, all ALE maps were thresholded using a cluster-level family-wise error $p < .001$ with 5,000 threshold permutations and a p -value of $p < .001$. Group contrasts and conjunctions were evaluated using an uncorrected $p < .05$ with 10,000 p -value permutations, and a minimum cluster size of 50 mm^3 . This approach is consistent with our prior meta-analyses (Bernard & Mittal, 2015; Bernard et al., 2017), as well as other recent work (e.g., Stawarczyk & D'Argembeau, 2015), and allows us to look at contrasts, even though GingerALE is not very robust when small numbers of studies (fewer than 15 per group) are used for group contrasts. The resulting areas of convergence from all analyses were localized using the Spatially Unbiased Infratentorial Template (SUIT) atlas (Diedrichsen,

Balsters, Flavell, Cussans, & Ramnani, 2009). Foci located in the white matter in the area of the cerebellar nuclei were localized using an atlas of cerebellar nuclei (Dimitrova et al., 2002).

3 | RESULTS

3.1 | Within group activation convergence across studies

Because several meta-analyses have already been conducted investigating cerebellar activation across task domains in YA (Bernard & Seidler, 2013a; E et al., 2014; Stoodley & Schmahmann, 2009), we provide only a brief overview of the YA results. Details of the areas of activation overlap across studies for both age groups and each task domain are provided in Table 6 and presented visually in Figure 2. In YA, the motor and working memory analyses replicated prior meta-analyses investigating patterns of cerebellar functional activation (Stoodley & Schmahmann, 2009; E et al., 2014; Bernard & Seidler, 2013a), though notably, there was substantial overlap in the foci used for the analyses. Activation overlap across language tasks was also consistent with prior work with a large cluster extending across Crus I and Lobule VI, while that for other cognitive tasks, which primarily included executive function tasks, also paralleled prior work (Stoodley & Schmahmann, 2009; E et al., 2014). Notably, this area is also consistent with recent work mapping function in the cerebellum by King et al. (2019), where tasks similar to those categorized here showed activation in lateral posterior cerebellum. Finally, we extended prior meta-analyses with the inclusion of long-term memory. In YA, our results demonstrate activation overlap across tasks in Lobule VI and Crus I. The overlap in Crus I is consistent with Crus I activation seen with autobiographical recall by King et al. (2019).

In OA, across studies motor task activation largely paralleled YA in the regions where we observed activation overlap. That is, activation was localized largely to the anterior cerebellum in Lobules V and VI, along with the secondary motor representation in Lobules VIIIa and VIIIb. Working memory activation convergence was limited to Lobule VI and Vermis VI; however, unlike in YA, we did not see any convergence across studies in Crus I and II. With respect to long-term memory, convergence across studies in OA appears to be more extensive than in YA, extending from Lobule VI to Crus II and also including Lobule IX. When looking at other cognitive tasks which were primarily those that tapped into executive functions, broadly defined, OA demonstrated significant overlap across studies in Crus I, Vermis VI, and Lobule V. Finally, for language tasks, there was no significant convergence across studies in OA.

3.2 | Age differences in cerebellar activation overlap

Group differences in activation convergence across studies for all task domains, except for language, were computed (Figure 3, Table 7). Due

TABLE 6 Activation by group and task

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|-----------------|---------------------------------|--|--|--|--|---|
| Motor | | | | | | |
| YA | | | | | | |
| 1 | 22,784 | From (-40, -72, -58) to (36, -38, -4) centered at (6.5, -57, -26.4) | 16, -54, -24 -20, -60, -20 30, -58, -26 4, -56, -12 6, -66, -14 6, -66, -34 -34, -56, -30 12, -68, -50 8, -66, -42 -6, -66, -28 28, -56, -52 -26, -42, -32 -30, -72, -20 | Lobule V Lobule VI Lobule VI Lobules I-IV Lobule V Vermis VIIIa Lobule VI Lobule VIIIa Vermis VIIIa Vermis VI* Lobule VIIIa Lobule V Lobule VI | 53.22 30.81 28.10 20.31 16.94 16.56 15.60 15.32 13.55 13.25 13.21 10.74 8.35 | 10.30 7.34 6.94 5.69 5.07 5.01 4.84 4.79 4.43 4.36 4.35 3.82 3.35 |
| OA | | | | | | |
| 1 | 18,504 | From (-14, -86, -38) to (44, -36, 0) centered at (18.6, -55.4, -21.7) | 26, -54, -24 12, -54, -16 38, -50, -32 -2, -66, -14 -4, -76, -20 -8, -82, -18 26, -76, -24 | Lobule VI Lobule V Crus I Lobule V Vermis VI Lobule VI* Crus I | 62.19 36.45 30.67 24.67 15.63 14.69 14.16 | 10.54 7.54 6.76 5.89 4.42 4.25 4.15 |
| 2 | 8,840 | From (-50, -68, -36) to (-12, -40, -14) centered at (-27.4, -56, -25.8) | -26, -52, -26 -22, -58, -22 -28, -62, -26 -46, -60, -26 | Lobule VI Lobule VI Lobule VI Crus I | 40.63 36.27 35.51 15.93 | 8.07 7.52 7.42 4.48 |
| 3 | 1952 | From (16, -66, -56) to (30, -50, -44) centered at (23, -57.7, -50.1) | 24, -56, -50 | Lobule VIIIb | 22.8 | 5.62 |
| 4 | 1,360 | From (-8, -76, -46) to (14, -60, -30) centered at (3, -68.4, -39.3) | -2, -72, -42 10, -64, -40 6, -70, -32 | Vermis VIIIa Lobule VIIIa Vermis VIIb | 17.29 14.05 11.53 | 4.71 4.13 3.62 |
| Language | | | | | | |
| YA | | | | | | |
| 1 | 7,304 | From (20, -78, -46) to (52, -48, -14) centered at (36.6, -63.4, -30.7) | 36, -54, -36 34, -74, -18 44, -66, -32 46, -62, -40 28, -62, -26 22, -72, -26 | Crus I Crus I* Crus I Crus I Lobule VI Lobule VI | 18.04 17.07 14.31 12.58 12.43 9.69 | 5.49 5.32 4.77 4.41 4.37 3.82 |
| OA | | | | | | |
| N/A | | | | | | |

(Continues)

TABLE 6 (Continued)

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|-------------------------|---------------------------------|--|---|---|---|--|
| Long-term memory | | | | | | |
| YA | | | | | | |
| 1 | 1984 | From (-18, -88, -22) to (-6, -70, -10) centered at (-11.8, -81.1, -16) | -12, -82, -16 -14, -72, -12 | Lobule VI* Lobule VI* | 18.66 8.53 | 6.17 4.02 |
| 2 | 1,216 | From (8, -80, -26) to (20, -68, -16) centered at (14.4, -73.7, -20.5) | 14, -74, -20 | Lobule VI | 17.06 | 5.89 |
| 3 | 984 | From (16, -90, -42) to (26, -80, -34) centered at (21, -85.5, -38.1) | 20, -86, -38 | Crus II | 13.19 | 5.01 |
| OA | | | | | | |
| 1 | 5,640 | From (-2, -88, -44) to (48, -48, -16) centered at (21.6, -74.5, -31.2) | 24, -84, -38 4, -72, -32 10, -84, -38 38, -58, -20 30, -86, -28 32, -50, -20 36, -76, -24 46, -72, -20 | Crus II Vermis crus II Crus II Lobule VI* Crus I Lobule VI* Crus I Crus I* | 15.66 14.01 13.81 13.35 12.89 10.73 9.49 9.21 | 4.96 4.63 4.58 4.48 4.38 3.95 3.71 3.65 |
| 2 | 2,368 | From (-54, -82, -32) to (-28, -56, -20) centered at (-44, -68.7, -25.6) | -50, -60, -26 -40, -76, -24 -28, -80, -30 | Crus I Crus I Crus I | 17.83 14.56 7.50 | 5.34 4.74 3.15 |
| 3 | 1976 | From (-6, -58, -54) to (16, -48, -20) centered at (7.1, -52.4, -37.5) | 6, -52, -46 12, -54, -24 -4, -54, -42 | Lobule IX Lobules I-IV Lobule IX | 14.71 13.59 7.78 | 4.77 4.53 3.29 |
| Working memory | | | | | | |
| YA | | | | | | |
| 1 | 29,840 | From (-44, -88, -52) to (50, -46, -10) centered at (7.9, -66.3, -29.8) | 28, -66, -34 -28, -62, -30 38, -64, -36 8, -76, -24 -38, -58, -40 36, -54, -42 -36, -70, -20 -10, -76, -22 -2, -82, -14 -18, -64, -14 -16, -52, -20 14, -54, -36 -6, -48, -14 | Crus I Lobule VI Crus I Lobule VI Crus I Crus II Lobule VI* Lobule VI N/A Lobule VI Lobule V Lobule IX Lobules I-IV | 37.51 35.33 34.41 34.34 28.42 26.75 23.71 21.00 18.12 17.99 16.18 15.26 11.35 | 7.55 7.27 7.15 7.14 6.33 6.09 5.65 5.22 4.75 4.73 4.44 4.78 3.51 |
| OA | | | | | | |
| 1 | 3,744 | From (-46, -74, -36) to (-28, -46, -14) centered at (-36.4, -59.2, -24.5) | -36, -58, -26 -38, -66, -18 | Lobule VI N/A | 24.12 15.67 | 5.88 4.53 |
| 2 | 3,440 | From (-10, -82, -32) to (14, -64, -16) centered at (1.3, -74.9, -23.4) | -4, -76, -24 8, -76, -24 | Vermis VI Lobule VI | 34.86 31.01 | 7.37 6.86 |
| 3 | 3,216 | From (20, -80, -40) to (36, -52, -16) centered at (28.1, -64.8, -25.4) | 26, -66, -24 32, -58, -24 | Lobule VI Lobule VI | 22.95 17.42 | 5.72 4.84 |

TABLE 6 (Continued)

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|---|---------------------------------|---|---------------------|-------------------|--------------------------------|---------|
| Other cognitive tasks (executive function/attention) | | | | | | |
| YA | | | | | | |
| 1 | 2,752 | From (-44, -78, -52) to (8, -52, -22) centered at (-28.5, -65.4, -33.) | -28, -64, -36 | Crus I | 13.11 | 4.48 |
| | | | -36, -60, -32 | Dentate nucleus | 10.96 | 4.06 |
| | | | -12, -74, -32 | Crus I | 10.00 | 3.88 |
| | | | -42, -76, -24 | Crus I | 9.14 | 3.72 |
| | | | -40, -70, -26 | Crus I | 9.11 | 3.71 |
| 2 | 1,096 | From (10, -58, -30) to (32, -48, -22) centered at (24.1, -52, -26) | -24, -66, -50 | Lobule VIIIa | 8.71 | 3.64 |
| | | | 28, -52, -26 | Lobule VI | 13.63 | 4.60 |
| | | | 14, -50, -26 | Interposed nuclei | 9.89 | 3.86 |
| OA | | | | | | |
| 1 | 1832 | From (-46, -76, -42) to (-32, -60, -22) centered at (-37.1, -66.8, -30.6) | -36, -70, -26 | Crus I | 15.34 | 5.00 |
| | | | -38, -64, -36 | Crus I | 13.70 | 4.64 |
| 2 | 1824 | From (-8, -82, -30) to (6, -70, -18) centered at (-.9, -75.4, -24.6) | 0, -76, -24 | Vermis VI | 24.22 | 6.56 |
| 3 | 1,304 | From (-24, -68, -22) to (-12, -56, -12) centered at (-17.9, -61.6, -16.7) | -18, -62, -16 | Lobule V | 22.66 | 6.30 |

*Peak outside of SUIT Atlas space, the closest region to the reported peak is listed.

to the nature of the ALE algorithm, comparisons cannot be made when one group does not show any significant activation across tasks. As such, we were unable to analyze language. With that said, it is worth noting that in YA, there was significant convergence across language tasks but this was not the case at all in OA, suggesting less reliable activation across studies in advanced age, perhaps due to less activation overall.

With respect to motor tasks, it is first notable that there was significant overlap between the two age groups in regions of the anterior cerebellum, including Lobules I-IV, V, and VI. YA showed greater convergence across studies in the dentate nucleus and Lobule V, an area heavily involved in motor processing (Stoodley & Schmahmann, 2009). In addition, some convergence extended into Lobule VI. In OA, convergence across studies relative to YA was seen primarily in Lobule VI. Notably, while greater convergence across studies in YA was limited primarily to the right hemisphere, in OA this was bilateral.

Working memory tasks also resulted in a great deal of activation overlap across studies when looking at the conjunction of the two age groups. Not surprisingly, this was localized to bilateral Lobule VI and left Crus I. Greater convergence across studies in YA was seen in Crus I and II, the dentate nucleus, Lobule VIIIb, and Lobule VIIIa. Greater activation convergence in OA was much more limited and seen only left Lobule VI and Vermis VI. The spatial extent of the overlap unique to OA was just more than one quarter (28.7%) of that which was unique to YA. With respect to long-term memory, there was some shared convergence across studies in both age groups localized to Crus II. Greater convergence in YA as compared to OA was seen in

Lobule VI, Crus I, and Crus II. Similar lobules were observed when looking at areas where OA had greater convergence, but localization within these lobules was unique relative to YA, and again, the spatial extent of the convergence areas that were greater in YA was much larger. In this instance, the area in OA was only 21.9% of that seen in YA. In both of these memory domains, this suggests that across studies in YA, there is more consistent activation across larger aspects of the cerebellum as compared to OA, where convergence was more limited in its spatial extent.

When investigating other cognitive tasks, which primarily includes executive function tasks, convergence in activation across studies was seen in Crus I and Vermis VI. When looking at the two groups relative to one another greater convergence in YA was seen in VIIIb, and greater convergence in OA was seen in Lobule VI. However, in both cases these were relatively small areas. Because there was no significant convergence across language tasks in OA, we were unable to conduct a group comparison.

Finally, we combined all cognitive tasks to compare overlap between YA and OA. This allowed us to include language in a broader analysis of group differences in convergence across tasks. Consistent with the broader literature suggesting that the lateral posterior cerebellum is involved in cognitive task processing and has connections (both structural and functional) with the PFC (Bernard et al., 2012; Chen & Desmond, 2005; Krienen & Buckner, 2009; Salmi, Pallesen, & Neuvonen, 2010; Stoodley & Schmahmann, 2009), there was substantial convergence overlap between the age groups in hemispheric Crus I and Lobule VI, though Vermis VI was also implicated along with the

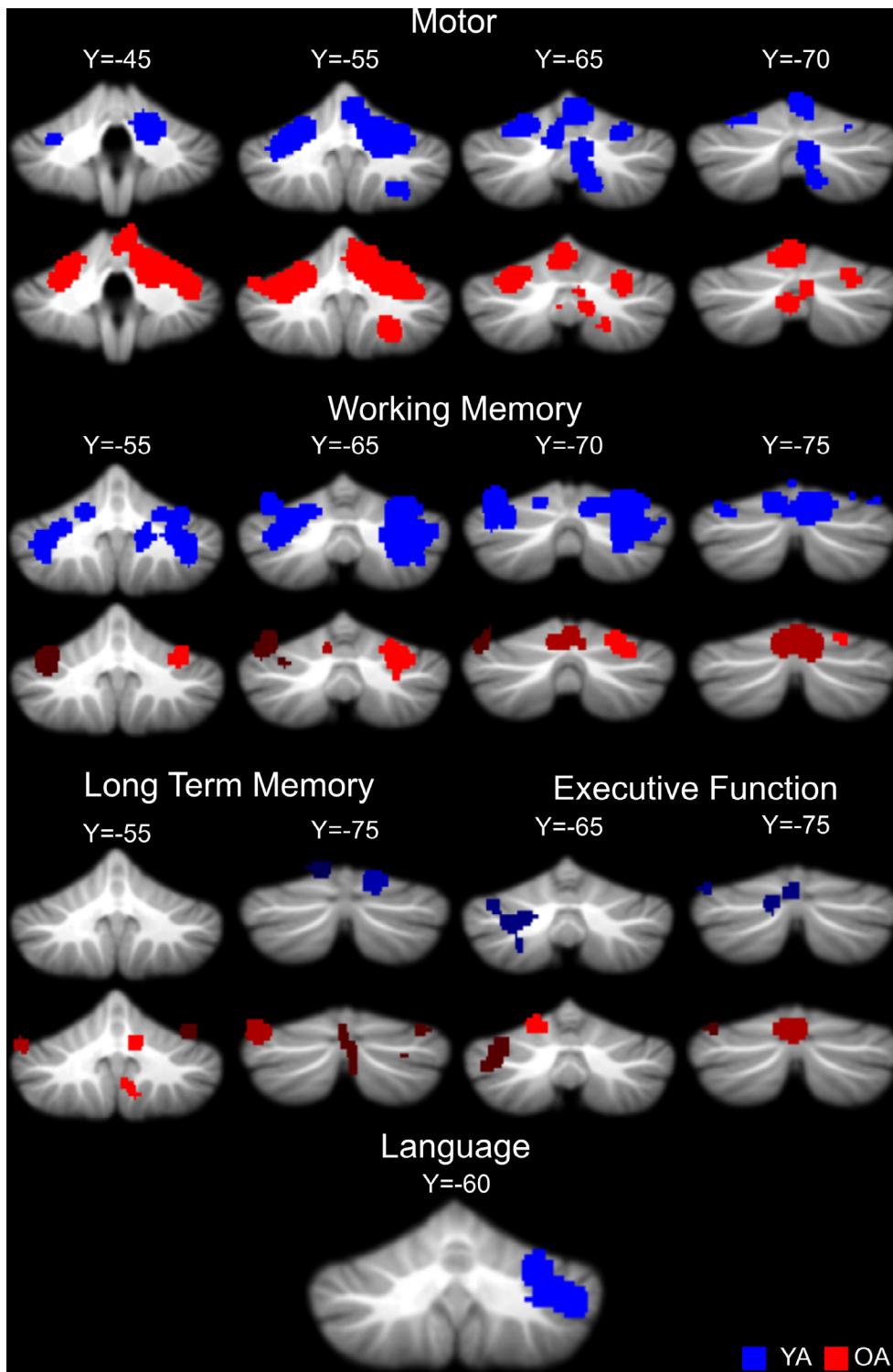


FIGURE 2 Activation overlap in the cerebellum across studies for each task domain in YA (blue) and OA (red). Areas of overlap are overlaid onto the SUIIT cerebellum template. Notably, there were no significant areas of overlap across studies in OA for language tasks. The color differentials, which are particularly noticeable for the red OA clusters, is to help distinguish clusters, and do not convey information with respect to ALE values

cerebellar dentate nucleus. In YA, greater convergence was seen in a wide swath of the posterior cerebellum. This included Lobule VI, Crus I, and Crus II, as well as Lobule VIIb and Lobule IX. In OA relative to YA, there was convergence in Lobule IX, Crus I, and Lobule VI, though there was also an area in Lobule V. Convergence in Lobules I–IV and V was unique to the OA sample. Most notably, the overall volume of the areas of increased overlap was substantially smaller in the OA group ($1,634 \text{ mm}^3$) as compared to the YA ($22,760 \text{ mm}^3$).

4 | DISCUSSION

Here, using ALE meta-analysis, we directly compared cerebellar activation convergence across task domains in OA and YA for the first time. Our results indicate that YA and OA recruit cerebellar resources differently during task performance, as evidenced by group differences in areas of activation convergence across studies. However, there is also substantial overlap in the convergence patterns when comparing the

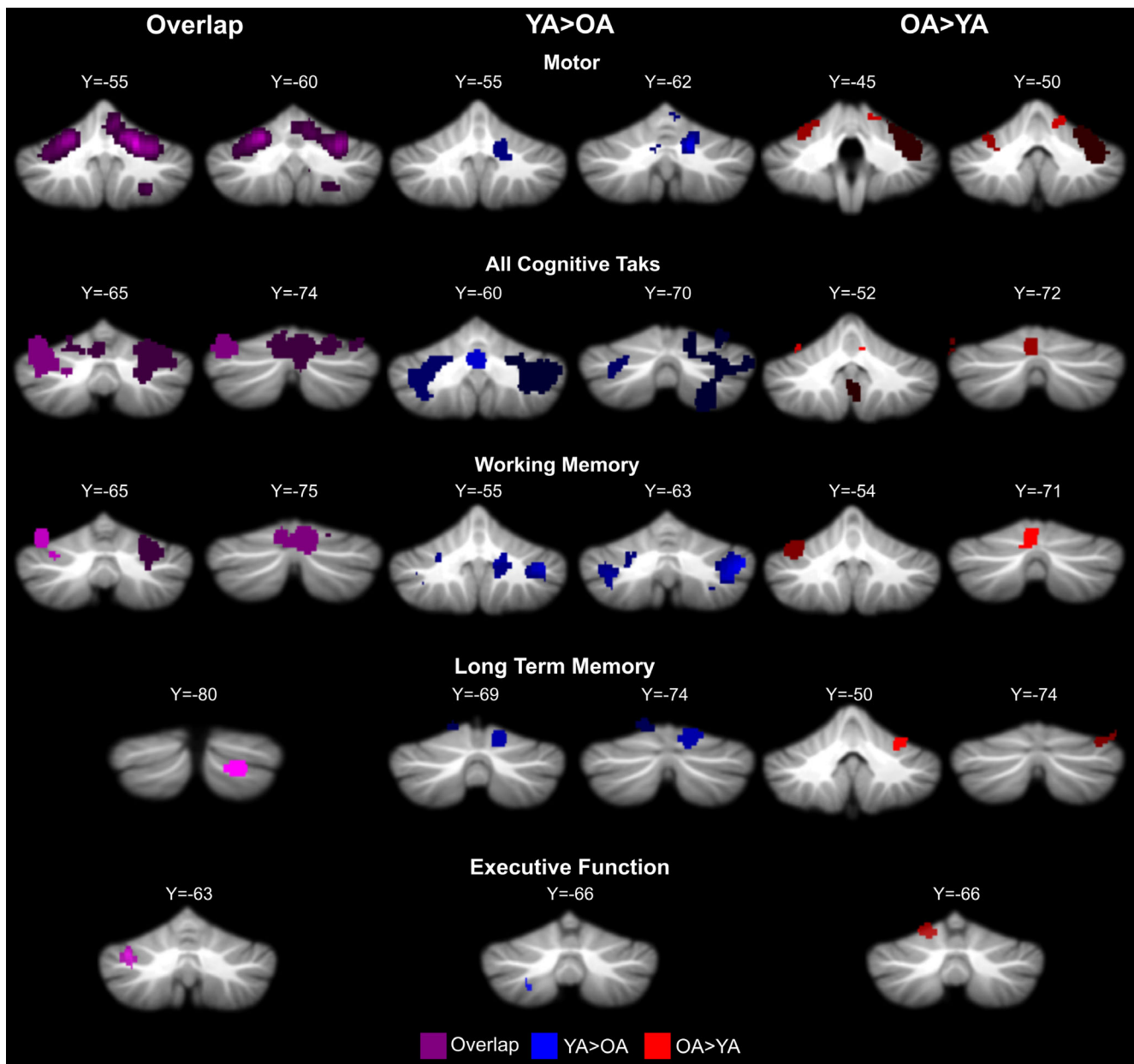


FIGURE 3 Overlap between age groups as well as age differences across studies in cerebellar activation. Because for several cognitive task domains there were not enough foci to compare the two age groups, or because there was no significant overlap within an age group, all of the cognitive task domains were combined and investigated together as well. The color differentials are to help distinguish clusters and do not convey information with respect to ALE values. Purple: overlap between age groups across tasks. Blue: YA > OA. Red: OA > YA

two age groups. These findings represent several important practical and theoretical advances in our understanding of cerebellar contributions to behavior in advanced age. First, this expands our understanding of the cerebellum in aging beyond the anatomical and connectivity domains to include functional activation patterns. Second, more broadly, this extends our understanding of the neural underpinnings of task performance in OA to include the cerebellum. Though as this investigation demonstrates, cerebellar activation has long been found in functional imaging studies of aging, but it has not been the focus of study. Concatenation across investigations in this manner provides a powerful tool to better understand cerebellar functional activation patterns in advanced

age. Most notably, there is evidence to suggest potential under-recruitment of the cerebellum in individual cognitive domains, and when all cognitive tasks are investigated together. This is consistent with our predictions based on degraded connectivity and volume in the cerebellum in OA (Bernard & Seidler, 2014). However, the activation convergence patterns differ for motor tasks. There is less convergence in OA in the primary motor regions of the cerebellum relative to YA, but across studies, there is greater convergence in secondary cerebellar motor regions. Together, these results suggest that with advanced age, cerebellar resources are not relied upon as effectively and efficiently in OA during task performance.

TABLE 7 Group comparisons by task

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|-------------------------------------|---------------------------------|--|---|---|---|------------------------------|
| Motor | | | | | | |
| Group overlap | | | | | | |
| 1 | 9,008 | From (-8, -72, -34) to (36, -38, -4) centered at (17.8, -54.5, -22.6) | 18, -52, -24 30, -58, -26 6, -54, -12 2, -66, -14 | Lobule V Lobule VI Lobules I-IV Lobule V | 44.23 28.10 19.32 14.87 | — |
| 2 | 4,192 | From (-40, -68, -36) to (-14, -44, -16) centered at (-25.1, -57, -25) | -20, -60, -22 -34, -56, -30 -26, -44, -30 | Lobule VI Lobule VI Lobule V | 30.70 15.56 9.04 | |
| 3 | 728 | From (16, -66, -56) to (30, -52, -48) centered at (24.3, -58, -52.1) | 28, -56, -30 16, -64, -48 | Lobule VI Lobule VIIa | 13.21 9.26 | |
| 4 | 600 | From (2, -72, -44) to (14, -60, -30) centered at (8, -66, -38.1) | 10, -64, -42 6, -68, -32 | Lobule VIIa Lobule VIIb | 12.98 11.11 | |
| YA > OA | | | | | | |
| 1 | 1,696 | From (8, -64, -36) to (20, -50, -20) centered at (14.7, -56.7, -28.7) | 13.3, -58, -30 | Dentate nucleus | — | 3.89 |
| 2 | 360 | From (4, -68, -22) to (12, -62, -8) centered at (8.6, -65.2, -14.2) | 6, -62, -8 12, -66, -18 8, -66, -10 12, -64, -22 | Lobule V Lobule VI Lobule V Lobule VI | | 2.08 2.05 2.01 1.92 |
| 3 | 88 | From (-8, -72, -34) to (36, -38, -4) centered at (17.8, -54.5, -22.6) | -4, -64, -30 | Vermis VIIa | | 1.86 |
| OA > YA | | | | | | |
| 1 | 3,048 | From (22, -56, -38) to (44, -42, -16) centered at (33.5, -48.4, -27.6) | 33.5, -44.5, -26.5 29, -46, -20 | Lobule VI Lobule VI | — | 3.54 3.23 |
| 2 | 880 | From (-12, -86, -24) to (2, -72, -14) centered at (-5.6, -79.3, -18.1) | -8, -86, -16 -8, -78, -16 | — Lobule VI | | 2.64 2.34 |
| 3 | 624 | From (-32, -52, -30) to (-18, -42, -14) centered at (-25.9, -47, -22.1) | -30, -46, -22 -24, -44, -18 | Lobule VI Lobule V | | 2.36 2.15 |
| 4 | 376 | From (10, -54, -16) to (20, -46, -10) centered at (14, -50.3, -13) | 14, -48, -12 | Lobule V | | 2.15 |
| 5 | 312 | From (-34, -68, -32) to (-26, -62, -24) centered at (-29.6, -65.1, -28.2) | -30, -64, -28 | Lobule VI | | 1.99 |
| All cognitive tasks combined | | | | | | |
| Group overlap | | | | | | |
| 1 | 14,616 | From (-24, -88, -42) to (44, -50, -14) centered at (15.7, -70.3, -26.3) | 6, -76, -24 -6, -80, -24 26, -66, -24 24, -64, -36 32, -56, -26 -20, -64, -22 -2, -68, -24 24, -84, -38 10, -84, -36 38, -76, -22 -14, -66, -22 -20, -66, -14 -40, -68, -24 | Vermis VI Lobule VI Lobule VI Lobule VI Lobule VI Lobule VI Vermis VI Crus II Crus II Crus I Lobule VI Lobule VI Crus I | 42.26 29.26 27.19 26.05 21.67 17.08 16.75 16.10 15.93 15.67 14.49 13.21 26.46 | — |
| 2 | 5,976 | | | | | |

TABLE 7 (Continued)

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|---------|---------------------------------|--|---------------------|--------------|--------------------------------|---------|
| | | From (-44, -78, -38) to (-20, -44, -14) centered at (-36.6, -63.9, -27.1) | -36, -58, -28 | Lobule VI | 26.24 | |
| | | | -22, -64, -36 | Dentate | 14.83 | |
| | | | -36, -46, -30 | Lobule VI | 13.62 | |
| 3 | 136 | From (12, -58, -28) to (18, -50, -24) centered at (14.8, -53.8, -26.1) | 16, -54, -26 | Lobule V | 12.81 | |
| 4 | 24 | From (-26, -54, -24) to (-26, -50, -24) centered at (-26, -52, -24) | -26, -52, -24 | Lobule VI | 11.65 | |
| YA > OA | | | | | | |
| 1 | 13,984 | From (10, -82, -62) to (54, -48, -14) centered at (33.1, -64.1, -38.6) | 34, -64.4, -46.5 | Lobule VIIb | — | 3.35 |
| | | | 51, -58.7, -34.2 | Crus I | | 3.72 |
| | | | 28, -54, -42 | Dentate | | 3.54 |
| | | | 22, -58, -28 | Lobule VI | | 2.88 |
| | | | 14, -76, -16 | Lobule VI | | 2.81 |
| | | | 16, -64, -26 | Lobule VI | | 2.53 |
| 2 | 4,552 | From (-44, -70, -52) to (-16, -48, -24) centered at (-30, -61.5, -36.8) | 34, -70, -16 | — | | 2.40 |
| | | | -28.6, -62.2, -50.3 | Lobule IX | | 3.89 |
| | | | -34, -64, -48 | Lobule VIIb | | 3.54 |
| | | | -23, -58, -29 | Lobule VI | | 3.43 |
| | | | -30, -60, -38 | Crus I | | 2.77 |
| 3 | 3,208 | From (-18, -88, -36) to (2, -74, -10) centered at (-9.5, -81.8, -18.5) | -16, -52, -26 | Lobule V | | 1.82 |
| | | | -7.7, -82.7, -15 | — | | 3.54 |
| | | | -6, -86, -14.4 | — | | 3.72 |
| | | | -10, -85, -20.5 | Crus I | | 3.43 |
| | | | -14, -78, -30 | Crus I | | 2.59 |
| 4 | 712 | From (-6, -64, -32) to (6, -56, -22) centered at (0.1, -60.5, -27.5) | -8, -78, -34 | Crus II | | 2.19 |
| | | | 0, -60, -28 | Vermis VI | | 2.62 |
| 5 | 144 | From (16, -92, -40) to (20, -88, -32) centered at (18.1, -89.8, -35) | 16, -92, -36 | Crus II | | 1.899 |
| 6 | 104 | From (-36, -78, -52) to (-30, -74, -46) centered at (-32.6, -76.6, -48.2) | -32, -78, -52 | Crus II | | 2.65 |
| 7 | 56 | From (6, -84, -24) to (10, -84, -20) centered at (7.4, -84, -21.9) | 6, -84, -20 | — | | 1.86 |
| OA > YA | | | | | | |
| 1 | 752 | From (-2, -56, -54) to (8, -48, -40) centered at (3.1, -51.2, -46.6) | 0, -50, -50 | Lobule IX | — | 2.25 |
| | | | 2, -48, -44 | Lobule IX | | 2.21 |
| 2 | 392 | From (-6, -76, -30) to (2, -70, -18) centered at (-2.1, -72.6, -24.1) | -2, -74, -22 | Vermis VI | | 2.33 |
| 3 | 320 | From (-16, -64, -18) to (-8, -58, -12) centered at (-12.1, -61.3, -14.5) | -12, -60, -12 | Lobule V | | 2.35 |
| 4 | 296 | From (-52, -74, -30) to (-46, -64, -20) centered at (-49, -67.7, -25) | -50, -68, -24 | Crus I | | 2.63 |
| 5 | 88 | From (-34, -56, -24) to (-32, -52, -18) centered at (-33.1, -53.6, -20.7) | -32, -54, -20 | Lobule VI | | 1.92 |
| 6 | 56 | From (4, -52, -22) to (8, -48, -20) centered at (6.3, -50.3, -20.8) | 6, -50, -20 | Lobules I-IV | | 1.98 |

(Continues)

TABLE 7 (Continued)

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|-------------------------|---------------------------------|--|--|--|---|--------------------------------------|
| Working memory | | | | | | |
| Group overlap | | | | | | |
| 1 | 2,880 | From (20, -76, -40) to (36, -54, -16) centered at (28.4, -64.7, -25.7) | 26, -66, -24 32, -58, -24 | Lobule VI Lobule VI | 22.10 12.42 | — |
| 2 | 2,200 | From (-10, -82, -32) to (14, -70, -18) centered at (3.8, -76.5, -24.1) | 8, -76, -24 -8, -76, -22 | Lobule VI Lobule VI | 31.01 19.20 | |
| 3 | 1,392 | From (-42, -74, -34) to (-28, -54, -14) centered at (-35.8, -63.8, -24.4) | -38, -66, -18 -34, -58, -30 | Lobule VI* Lobule VI | 15.67 14.78 | |
| 4 | 8 | At (-36, -54, -36) | -36, -54, -36 | Crus I | 8.51 | |
| YA > OA | | | | | | |
| 1 | 4,240 | From (22, -74, -50) to (50, -46, -28) centered at (38.1, -63.2, -37.2) | 46, -60, -35 48, -66, -36 38, -70, -40 26, -74, -36 22, -74, -34 28, -66, -50 32, -66, -50 38, -48, -44 | Crus I Crus I Crus I Crus I Crus I Lobule VIIb Lobule VIIb Crus II | — 2.41 2.17 2.16 2.04 1.77 | 3.89 3.72 3.19 |
| 2 | 1816 | From (-42, -70, -52) to (-18, -56, -26) centered at (-31.7, -62, -38.1) | -34, -66, -42 -30, -62, -50 -20, -62, -32 -22, -58, -32 -34, -64, -48 -24, -64, -36 | Crus II Lobule VIIa Dentate nucleus/ Lobule VI Dentate nucleus/ Lobule VI Lobule VIIb Lobule VI | 2.55 2.44 2.36 2.30 2.26 1.92 | 2.44 2.36 2.30 2.26 1.92 |
| 3 | 872 | From (10, -60, -42) to (22, -50, -26) centered at (15.3, -55.6, -34.2) | 14, -50, -34 12, -56, -42 | Dentate nucleus Lobule IX* | 2.99 2.16 | 2.99 2.16 |
| 4 | 160 | From (34, -76, -22) to (40, -72, -18) centered at (37.6, -74, -20.3) | 40, -76, -20 | Crus I* | 1.95 | 1.95 |
| 5 | 144 | From (2, -88, -38) to (6, -84, -30) centered at (4.2, -85.8, -34) | 2, -86, -32 6, -88, -36 | Crus II* Crus II | 1.93 1.81 | 1.93 1.81 |
| OA > YA | | | | | | |
| 1 | 1,328 | From (-42, -62, -30) to (-30, -48, -18) centered at (-36.1, -54.6, -23.9) | -36.7, -53.3, -20 | Lobule VI* | — | 3.35 |
| 2 | 752 | From (-8, -78, -28) to (4, -68, -18) centered at (-2.6, -71.7, -22.3) | -2, -70, -20 | Vermis VI | | 2.89 |
| Long term memory | | | | | | |
| Group overlap | | | | | | |
| 1 | 696 | From (16, -88, -42) to (26, -80, -34) centered at (21.4, -84.4, -38.7) | 22, -86, -38 | Crus II | 12.80 | — |
| YA > OA | | | | | | |
| 1 | 1928 | From (-18, -88, -22) to (-4, -70, -10) centered at (-11.6, -80.3, -15.8) | 12, -72, -14 -10.7, -76.7, -13.1 -12.3, -79.8, -16.7 -12, -84, -10 | Lobule VI Lobule VI* Lobule VI* — | — 2.93 2.93 | 2.99 2.93 2.93 2.89 |

TABLE 7 (Continued)

| Cluster | Cluster size (mm ³) | Extent & weighted center (x, y, z) | ALE peaks (x, y, z) | Location | ALE value (×10 ⁻³) | Z-value |
|---------------------------|---------------------------------|---|---------------------|------------------|--------------------------------|---------|
| 2 | 1,120 | From (8, -80, -26) to (20, -68, -16) centered at (14, -73.5, -20.2) | 12, -70, -16 | Lobule VI* | — | 2.95 |
| | | | 16, -80, -22 | Crus I | — | 2.48 |
| 3 | 168 | From (18, -, -90, -40) to (20, -84, -32) centered at (19.3, -88.2, -35.8) | 20, -88, -34 | Crus II | — | 1.83 |
| OA > YA | | | | | | |
| 1 | 456 | From (34, -78, -26) to (46, -60, -18) centered at (40.2, -70.8, -22.6) | 41.2, -70, -22.4 | Crus I | — | 1.89 |
| | | | 38.5, -76, -25 | Crus I | — | 1.77 |
| | | | 38, -62, -24 | Lobule VI | — | 1.77 |
| | | | 40, -66, -21 | Lobule VI/crus I | — | 1.75 |
| | | | 45.2, -73.6, -20 | Crus I* | — | 1.72 |
| 2 | 248 | From (26, -54, -26) to (34, -48, -20) centered at (29.7, -50.3, -22.3) | 28, -49.3, -24.7 | Lobule VI | — | 1.93 |
| | | | 32, -50.7, -22.7 | Lobule VI | — | 1.89 |
| Executive function | | | | | | |
| Group overlap | | | | | | |
| 1 | 600 | From (-40, -76, -38) to (-32, -60, -24) centered at (-36.8, -65.1, -30.5) | -36, -62, -32 | Crus I | 10.93 | — |
| | | | -40, -70, -26 | Crus I | 9.11 | — |
| | | | -40, -74, -24 | Crus I | 8.63 | — |
| YA > OA | | | | | | |
| 1 | 120 | From (-26, -68, -52) to (-24, -64, -44) centered at (-25.1, -66, -48.8) | -26, -68, -50 | Lobule VIIIb | — | 2.52 |
| OA > YA | | | | | | |
| 1 | 448 | From (-24, -68, -20) to (-12, -58, -12) centered at (-18, -64.3, -16.4) | -22, -66, -16 | Lobule VI | — | 2.27 |
| | | | -14, -68, -20 | Lobule VI | — | 1.9 |

*Peak outside of SUIT Atlas space, the closest region to the reported peak is listed.

Unlike in the cerebral cortex where an increase in bilateral activation and compensatory recruitment during cognitive task performance in OA has been reported (Cabeza, 2002; Cappell, Gmeindl, & Reuter-Lorenz, 2010; Reuter-Lorenz et al., 1999), here we demonstrate a relative *decrease* in convergence across studies investigating cognitive task domains. Though this does not directly indicate activation, it does imply that the organization of activation across studies is not consistent with cortical bilateral patterns of activation. We suggest that OA may not be consistently engaging bilateral regions of the cerebellum during cognitive task performance as they do in the cortex. Alternatively, it may also be the case that there is more variability in the cerebellar resources that are recruited in OA. This would also result in less convergence across studies, and with this methodology, we cannot fully dissociate these two possibilities. Though surprising in the context of the cortical literature, this is consistent with the hypothesis put forth in our recent review (Bernard & Seidler, 2014). Because connectivity is lower in OA relative to YA, information exchange between the cortex and cerebellum may be degraded. As such, OA may not be able to effectively recruit cerebellar resources for information processing (Bernard & Seidler, 2014). The results here are consistent with this idea, and we suggest that this difference in the recruitment of the cerebellum may be particularly important for behavior.

Specifically, cerebellar resources may be especially important scaffolding for performance in advanced age (e.g., Reuter-Lorenz & Park, 2014). Reliance upon more automatic processing in the cerebellum via internal models of behavior (Ramnani, 2014) would free up cortical resources and help maintain performance. However, those resources are not recruited consistently in OA as evidenced by the activation convergences patterns across studies seen here. Furthermore, it may in fact be the case that the inability to utilize these cerebellar resources contributes, at least in part, to the bilateral cortical activation patterns seen in OA.

Somewhat surprisingly, we found a distinct pattern of convergence differences for motor tasks. OA showed significantly more convergence in Lobule VI compared to YA, and these clusters extend into Crus I, as seen in Figure 3. This region has connectivity patterns with prefrontal cortical and premotor regions (e.g., Bernard et al., 2012; Krienen & Buckner, 2009) and also shows activation during cognitive task performance (Stoodley & Schmahmann, 2009), while Crus I has connectivity patterns associated with the lateral PFC (e.g., Bernard et al., 2012; Krienen & Buckner, 2009) and is engaged across a variety of cognitive task domains (Stoodley & Schmahmann, 2009; King et al., 2019). This convergence pattern is more consistent with activation patterns seen in the cortex in OA (e.g., Cabeza, 2002; Cappell

et al., 2010; Reuter-Lorenz et al., 1999). This is also consistent with work in OA demonstrating increased recruitment of frontal cortical regions during motor task performance (e.g., Heuninckx et al., 2008; reviewed in Seidler et al., 2010). It is likely that this pattern in the cerebellum is paralleling what has been reported in the cerebral cortex to an extent. Again, though not directly indexing activation, seeing a consistency in this pattern across studies suggests that perhaps OA are engaging these other cerebellar regions in a compensatory manner. Notably, recent work using a predictive motor timing task demonstrated increased activation in the lateral posterior cerebellum with increasing age (Filip et al., 2019). The authors suggest that this activation pattern may provide scaffolding for performance in OA (Filip et al., 2019), consistent with extant models of aging (e.g., Reuter-Lorenz and Park, 2014). However, given that we did not see this pattern for cognitive tasks, why such scaffolding is present for motor tasks raises interesting mechanistic and theoretical questions.

As described above, in our past work, we had hypothesized that lower connectivity between the cerebellum and cortex coupled with volumetric differences in OA relative to YA would result in decreased activation during task performance, indicative of an inability to rely upon cerebellar resources for performance (Bernard & Seidler, 2014). Data from studies administering cognitive tasks are consistent with this notion, while data from motor tasks better parallel cortical findings (e.g., Reuter-Lorenz & Cappell, 2008) and are consistent with recent work suggesting that the cerebellum provides scaffolding for motor performance in advanced age (Filip et al., 2019). Though seemingly contradictory, these findings may in fact be quite consistent with inputs to the cerebellum, particularly in the context of control theory (Ramnani, 2006). In this context, and as we previously proposed (Bernard & Seidler 2014), inputs and outputs between the cerebellum and cortex are degraded in advanced age, resulting in less efficient internal models, evidenced through decreased functional activation. However, a key part of these models is the function of the comparator, which compares the predicted behavior to its consequences (Ramnani, 2006). The inferior olive is suggested to be the comparator for both motor and cognitive processes; however, the *input* to this region differs. For cognitive processes, input to the inferior olive comes from cortico-olivo-cerebellar pathways, while those for motor come from the spino-olivo-cerebellar pathways (Ramnani, 2006). We speculate that the spinal pathways are relatively intact, particularly as compared to the cortical pathways, and as such, OA are better able to recruit cerebellar resources during motor task performance. Thus, in the context of control theory, while the cerebellum may be capable of providing compensatory activation, because of the input from the cortex for the updating of internal models, these resources cannot be brought online effectively. Together, our findings suggest that in OA cerebellar resources may be under-recruited during cognitive tasks as evidenced by the relative decrease in convergence across studies when compared with YAs, and we propose that compensatory scaffolding during motor performance is due to spino-olivo-cerebellar inputs.

While the meta-analytic approach employed here allows for insights into cerebellar activation patterns across studies, it is not

without limitations. Most notably, we were unable to account for behavioral performance and brain-behavior relationships. While an understanding of brain-behavior relationships is a key question moving forward, the inclusion of a behavioral meta-analysis here is beyond the scope of our work. Furthermore, there are numerous existing behavioral meta-analyses across domains demonstrating age differences in performance (e.g., Maldonado, Orr, Goen, & Bernard, 2020; Verhaeghen and Cerella, 2002; Wasylshyn et al., 2011), negating the need for an additional behavioral meta-analysis here. Furthermore, in some studies, it is possible that there were no cerebellar foci reported due to incomplete coverage of the structure. This also means that activation in some cerebellar regions, particularly the most inferior lobules of the cerebellum, may be more generally under reported. Due to cortically focused hypotheses and scanning limitations, parts of the cerebellum may not have been covered by the field of view. While the more anterior lobules related to motor function, and lateral posterior regions of Crus I and II typically have good coverage, without the original scan data we cannot know for sure. As such, this may have influenced our analyses. Notably, however, this would have a similar impact on YA and OA and should not impact the age differences reported here. Relatedly, some clusters appear in our figures as being outside of the cerebellum. This is likely due to normalization procedures that smoothed the initial data into inferior cortical regions, as processes were optimized for whole-brain analysis. This also is likely due in part to the estimation around the included foci based on sample size. Additionally, we did not conduct a complete search of the entire YA imaging literature, and our search only goes through August 2018. This would have resulted in large differences in statistical power between groups and potentially biased results in favor of the YA sample. As such, this is not a comprehensive investigation of cerebellar activation patterns in YA, but several meta-analyses on this topic have already been conducted (Stoodley & Schmahmann, 2009; E et al., 2014). Furthermore, it is notable that even with less power in the YA data sample, we nonetheless see less overlap across studies in OA during cognitive task performance. If anything, this sample was biased in favor of seeing more consistent activation overlap in OA given the size of the sample; however, for cognitive task processing, the opposite pattern was demonstrated, providing powerful evidence for differences in cerebellar engagement with age. With respect to the search cut-off, this has resulted in the most recent studies not being included here. However, with the timeline of analysis, review, and eventual publication, with this type of work, there will always be a delay. We encourage future meta-analyses following up on these results to incorporate newer literature, and additional novel analysis angles to further improve our understanding of the cerebellum in advanced age.

Somewhat relatedly, we did not include investigations that looked at age across adulthood using regression-modeling approaches. Given the way the analyses were set up, if a study did not include contrasts for a given age group, the study could not be included in the analysis here. Foci from studies taking an adult lifespan approach are often the result of correlations with age, and as such include individuals from across adulthood. There is no way to include these studies in the

group comparisons here, despite the wealth of knowledge this type of work provides. This would however be an interesting focus in future meta-analytic work, to follow-up on this examination of age differences.

One of the greatest benefits of meta-analyses is the ability to concatenate across large literatures. However, this also means concatenating across studies with different methodological approaches, and varying degrees of information related to the study samples. As such, we included both PET and fMRI studies, consistent with past meta-analyses of cerebellar function (Stoodley & Schmahmann, 2009; E et al., 2014), as well as different inclusion and exclusion criteria. Notably, however, the ALE algorithm accounts for uncertainty and variability across subjects and sites so as to be relatively robust to these methodological differences (Eikhoff et al., 2012). While this means we cannot carefully control for these individual factors, this work also provides a powerful indicator of activation patterns seen in different age groups, and the diversity in the samples is likely more representative of the broader population as a whole.

Together, this work represents the first comprehensive investigation into cerebellar activation patterns in OA. First, we demonstrated that during the performance of cognitive tasks, OA show less convergence in cerebellar foci across studies than YA, perhaps indicative of decreases in activation, in contrast to what is seen in the PFC (e.g., Reuter-Lorenz et al., 1999; Cabeza, 2002; Reuter-Lorenz & Cappell, 2008), consistent with our hypothesis and prior work (Bernard & Seidler, 2014). We suggest that cerebellar processing is critical for optimal and efficient behavior. In advanced age, these resources are not brought online, likely due to degraded communication with the cortex (Bernard & Seidler, 2014). As such, OAs are unable to use this critical region and scaffolding for performance, resulting in behavioral declines. Conversely, we see more extensive convergence across studies in OA during motor tasks. However, we propose that this is due to spinal afferents that bypass the cortex and allow for compensatory activation (Filip et al., 2019). Thus, on the basis of these findings, we suggest that cerebellar functional activation differences with advanced age result in dissociable behavioral impacts due to the source of inputs through the inferior olive. While the cerebellum may be able to engage in compensatory activation for motor tasks, this is not the case in the cognitive domain.

ACKNOWLEDGMENTS

J. A. B. was supported, in part, by a Brain and Behavior Research Foundation NARSAD Young Investigator Award as the Donald and Janet Boardman Family Investigator. She is also currently supported in part by National Institute on Aging (Grant R01AG064010-01).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All materials associated with the analysis in the form of text files of foci are freely available for download at <https://osf.io/gx5jw/>.

ETHICS STATEMENT

This investigation used published, anonymous data and as such was not subject to ethics review.

ORCID

Jessica A. Bernard  <https://orcid.org/0000-0001-7697-3675>

Hanna K. Hausman  <https://orcid.org/0000-0001-9694-9760>

T. Bryan Jackson  <https://orcid.org/0000-0002-6318-1916>

REFERENCES

- Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E., & Buckner, R. L. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron*, *56*(5), 924–935. <https://doi.org/10.1016/j.neuron.2007.10.038>
- Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2011). Failure to engage spatial working memory contributes to age-related declines in visuomotor learning. *Journal of Cognitive Neuroscience*, *23*(1), 11–25. <https://doi.org/10.1162/jocn.2010.21451>
- Balsters, J. H., Whelan, C. D., Robertson, I. H., & Ramnani, N. (2013). Cerebellum and cognition: Evidence for the encoding of higher order rules. *Cerebral Cortex*, *23*(6), 1433–1443. <https://doi.org/10.1093/cercor/bhs127>
- Bernard, J. A., & Mittal, V. A. (2015). Dysfunctional activation of the cerebellum in schizophrenia. *Clinical Psychological Science*, *3*(4), 545–566. <https://doi.org/10.1177/2167702614542463>
- Bernard, J. A., Russell, C. E., Newberry, R. E., Goen, J. R. M., & Mittal, V. A. (2017). Patients with schizophrenia show aberrant patterns of basal ganglia activation: Evidence from ALE meta-analysis. *NeuroImage: Clinical*, *14*, 450–463. <https://doi.org/10.1016/j.nicl.2017.01.034>
- Bernard, J. A., & Seidler, R. D. (2013a). Cerebellar contributions to visuomotor adaptation and motor sequence learning: An ALE meta-analysis. *Frontiers in Human Neuroscience*, *7*, 27. <https://doi.org/10.3389/fnhum.2013.00027>
- Bernard, J. A., & Seidler, R. D. (2013b). Relationships between regional cerebellar volume and sensorimotor and cognitive function in young and older adults. *Cerebellum*, *12*(5), 721–737. <https://doi.org/10.1007/s12311-013-0481-z>
- Bernard, J. A., & Seidler, R. D. (2014). Moving forward: Age effects on the cerebellum underlie cognitive and motor declines. *Neuroscience and Biobehavioral Reviews*, *42*, 193–207.
- Bernard, J. A., Seidler, R. D., Hassevoort, K. M., Benson, B. L., Welsh, R. C., Wiggins, J. L., ... Peltier, S. J. (2012). Resting state cortico-cerebellar functional connectivity networks: A comparison of anatomical and self-organizing map approaches. *Frontiers in Neuroanatomy*, *6*, 1–19. <https://doi.org/10.3389/fnana.2012.00031>
- Bernard, J. A., Peltier, S. J., Wiggins, J. L., Jaeggi, S. M., Buschkuhl, M., Fling, B. W., ... Seidler, R. D. (2013). Disrupted cortico-cerebellar connectivity in older adults. *NeuroImage*, *83*, 103–119. <https://doi.org/10.1016/j.neuroimage.2013.06.042>
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, *17*(1), 85–100. <https://doi.org/10.1037/0882-7974.17.1.85>
- Cappell, K. A., Gmeindl, L., & Reuter-Lorenz, P. A. (2010). Age differences in prefrontal recruitment during verbal working memory maintenance depend on memory load. *Cortex*, *46*(4), 462–473. <https://doi.org/10.1016/j.cortex.2009.11.009>
- Chen, S. H. A., & Desmond, J. E. (2005). Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks. *NeuroImage*, *24*(2), 332–338. <https://doi.org/10.1016/j.neuroimage.2004.08.032>
- Diedrichsen, J., Balsters, J. H., Flavell, J., Cussans, E., & Ramnani, N. (2009). A probabilistic MR atlas of the human cerebellum. *NeuroImage*, *46*(1), 39–46. <https://doi.org/10.1016/j.neuroimage.2009.01.045>

- Diedrichsen, J., King, M., Hernandez-Castillo, C., Sereno, M., & Ivry, R. B. (2019). Universal transform of multiple functionality? Understanding the contribution of the human cerebellum across task domains. *Neron*, 102(5), 918–928. <https://doi.org/10.1016/j.neuron.2019.04.021>
- Dimitrova, A., Weber, J., Redies, C., Kindsvater, K., Maschke, M., Kolb, F. P., & Forsting, M. (2002). MRI atlas of the human cerebellar nuclei. *NeuroImage*, 255, 240–255. <https://doi.org/10.1006/nimg.2002.1124>
- E, K.-H., Chen, S.-H. A., Ho, M.-H. R., & Desmond, J. E. (2014). A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. *Human Brain Mapping*, 35(2), 593–615. <https://doi.org/10.1002/hbm.22194>
- Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *NeuroImage*, 59(3), 2349–2361. <https://doi.org/10.1016/j.neuroimage.2011.09.017>
- Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping*, 30(9), 2907–2926. <https://doi.org/10.1002/hbm.20718>
- Filip, P., Gallea, C., Lehericy, S., Lungu, O., & Bareš, M. (2019). Neural scaffolding as the foundation for stable performance of aging cerebellum. *Cerebellum*, 18(3), 500–510. <https://doi.org/10.1007/s12311-019-01015-7>
- Han, S., An, Y., Carass, A., Prince, J. L., & Resnick, S. M. (2020). Longitudinal analysis of regional cerebellum volumes during normal aging. *NeuroImage*, 220(15), 117062. <https://doi.org/10.1016/j.neuroimage.2020.117062>
- Heuninckx, S., Wenderoth, N., Debaere, F., Peeters, R., & Swinnen, S. P. (2005). Neural basis of aging: The penetration of cognition into action control. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 25(29), 6787–6796. <https://doi.org/10.1523/JNEUROSCI.1263-05.2005>
- Heuninckx, S., Wenderoth, N., & Swinnen, S. P. (2008). Systems neuroplasticity in the aging brain: Recruiting additional neural resources for successful motor performance in elderly persons. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 28(1), 91–99. <https://doi.org/10.1523/JNEUROSCI.3300-07.2008>
- Huxhold, O., Li, S.-C., Schmiedek, F., & Lindenberger, U. (2006). Dual-tasking postural control: Aging and the effects of cognitive demand in conjunction with focus of attention. *Brain Research Bulletin*, 69(3), 294–305. <https://doi.org/10.1016/j.brainresbull.2006.01.002>
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., Pütz, B., ... Kawato, M. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature*, 403(6766), 192–195. <https://doi.org/10.1038/35003194>
- Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience*, 9(4), 304–313. <https://doi.org/10.1038/nrn2332>
- King, M., Hernandez-Castillo, C. R., Poldrack, R. A., Ivry, R. B., & Diedrichsen, J. (2019). Functional boundaries in the human cerebellum revealed by a multi-domain task battery. *Nature Neuroscience*, 22, 1371–1378. <https://doi.org/10.1038/s41593-019-0436-x>
- Koppelmans, V., Young, Y., & Sarah, H. (2017). Regional cerebellar volumetric correlates of manual motor and cognitive function. *Brain Structure & Function*, 222, 1929–1944. <https://doi.org/10.1007/s00429-016-1317-7>
- Krienen, F. M., & Buckner, R. L. (2009). Segregated Fronto-cerebellar circuits revealed by intrinsic functional connectivity. *Cerebral Cortex*, 19(10), 2485–2497. <https://doi.org/10.1093/cercor/bhp135>
- Lancaster, J. L., Tordesillas-Gutiérrez, D., Martínez, M., Salinas, F., Evans, A., Zilles, K., ... Fox, P. T. (2007). Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. *Human Brain Mapping*, 28(11), 1194–1205. <https://doi.org/10.1002/hbm.20345>
- Langan, J., Peltier, S. J., Bo, J., Fling, B. W., Welsh, R. C., & Seidler, R. D. (2010). Functional implications of age differences in motor system connectivity. *Frontiers in Systems Neuroscience*, 4, 17. <https://doi.org/10.3389/fnsys.2010.00017>
- Maldonado, T., Orr, J. M., Goen, J. R. M., & Bernard, J. A. (2020). Age differences in the subcomponents of executive functioning. *The Journals of Gerontology: Series B*, 75(6), e31–e55. <https://doi.org/10.1093/geronb/gbaa005>
- Middleton, F. A., & Strick, P. L. (2001). Cerebellar projections to the prefrontal cortex of the primate. *The Journal of Neuroscience*, 21(2), 700–712. <https://doi.org/10.1523/JNEUROSCI.21-02-00700.2001>
- Miller, T. D., Ferguson, K. J., Reid, L. M., Wardlaw, J. M., Starr, J. M., Seckl, J. R., ... MacLullich, A. M. J. (2013). Cerebellar vermis size and cognitive ability in community-dwelling elderly men. *Cerebellum*, 12(1), 68–73. <https://doi.org/10.1007/s12311-012-0397-z>
- Naccarato, M., Calautti, C., Jones, P. S., Day, D. J., Carpenter, T. a., & Baron, J.-C. (2006). Does healthy aging affect the hemispheric activation balance during paced index-to-thumb opposition task? An fMRI study. *NeuroImage*, 32(3), 1250–1256. <https://doi.org/10.1016/j.neuroimage.2006.05.003>
- Parikh, P. K., Troyer, A. K., Maione, A. M., & Murphy, K. J. (2016). The impact of memory change on daily life in Normal aging and mild cognitive impairment. *Gerontologist*, 56(5), 877–885. <https://doi.org/10.1093/geront/gnv030>
- Park, D. C., Polk, T. A., Mikels, J. A., Taylor, S. F., & Marshuetz, C. (2001). Cerebral aging: Integration of brain and behavioral models of cognitive function. *Dialogues in Clinical Neuroscience*, 3(3), 151–165.
- Park, D. C., & Reuter-Lorenz, P. A. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, 60, 173–196. <https://doi.org/10.1146/annurev.psych.59.103006.093656>
- Ramrani, N. (2006). The primate cortico-cerebellar system: Anatomy and function. *Nature Reviews Neuroscience*, 7(7), 511–522. <https://doi.org/10.1038/nrn1953>
- Ramrani, N. (2014). Automatic and controlled processing in the corticocerebellar system. *Progress in Brain Research*, 210, 255–285. <https://doi.org/10.1016/B978-0-444-63356-9.00010-8>
- Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., ... Acker, J. D. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, 15(11), 1676–1689. <https://doi.org/10.1093/cercor/bhi044>
- Reuter-Lorenz, P. A., & Park, D. C. (2014). How does it STAC up? Revisiting the scaffolding theory of aging and cognition. *Neuropsychology Review*, 24(3), 355–370. <https://doi.org/10.1007/s11065-014-9270-9>
- Reuter-Lorenz, P. A., Stanczak, L., & Miller, a. C. (1999). Neural recruitment and cognitive aging: Two hemispheres are better than one, especially as you age. *Psychological Science*, 10(6), 494–500. <https://doi.org/10.1111/1467-9280.00195>
- Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, 17(3), 177–182. <https://doi.org/10.1111/j.1467-8721.2008.00570.x>
- Salmi, J., Pallesen, K., & Neuvonen, T. (2010). Cognitive and motor loops of the human cerebro-cerebellar system. *Journal of Cognitive Neuroscience*, 22(11), 2663–2676.
- Seidler, R. D., Bernard, J. A., Burdett, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., ... Lipps, D. B. (2010). Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neuroscience and Biobehavioral Reviews*, 34(5), 721–733. <https://doi.org/10.1016/j.neubiorev.2009.10.005>
- Stawarczyk, D., & D'Argembeau, A. (2015). Neural correlates of personal goal processing during episodic future thinking and mind-wandering: An ALE meta-analysis. *Human Brain Mapping*, 2947(April), 2928–2947. <https://doi.org/10.1002/hbm.22818>

- Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: A meta-analysis of neuroimaging studies. *NeuroImage*, 44(2), 489–501. <https://doi.org/10.1016/j.neuroimage.2008.08.039>
- Stoodley, C. J., Valera, E. M., & Schmahmann, J. D. (2012). Functional topography of the cerebellum for motor and cognitive tasks: An fMRI study. *NeuroImage*, 59, 1560–1570. <https://doi.org/10.1016/j.neuroimage.2011.08.065>
- Strick, P. L., Dum, R. P., & Fiez, J. A. (2009). Cerebellum and nonmotor function. *Annual Review of Neuroscience*, 32, 412–434. <https://doi.org/10.1146/annurev.neuro.31.060407.125606>
- Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., & Fox, P. (2012). Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Human Brain Mapping*, 33(1), 1–13. <https://doi.org/10.1002/hbm.21186>
- Verhaeghen, P., & Cerella, J. (2002). Aging, executive control, and attention: A review of meta-analyses. *Neuroscience and Biobehavioral Reviews*, 26, 849–857. [https://doi.org/10.1016/s0149-7634\(02\)00071-4](https://doi.org/10.1016/s0149-7634(02)00071-4)
- Walhovd, K. B., Westlye, L. T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., ... Fjell, A. M. (2011). Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiology of Aging*, 32(5), 916–932. <https://doi.org/10.1016/j.neurobiolaging.2009.05.013>
- Wasylyshyn, C., Verhaeghen, P., & Sliwinski, M. J. (2011). Aging and task switching: A meta-analysis. *Psychology and Aging*, 26, 15–20. <https://doi.org/10.1037/a0020912>

How to cite this article: Bernard JA, Nguyen AD, Hausman HK, et al. Shaky scaffolding: Age differences in cerebellar activation revealed through activation likelihood estimation meta-analysis. *Hum Brain Mapp*. 2020;41: 5255–5281. <https://doi.org/10.1002/hbm.25191>