RUNNING HEAD: Cerebellar Aging Meta-Analysis

Shaky Scaffolding: Age Differences In Cerebellar Activation Revealed Through Activation Likelihood Estimation Meta-Analysis

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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. But, 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, cerebellar activation is decreased. Conversely, we see an increase in activation in older adults 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

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 (OA), have broad impacts on quality of life across social and cognitive domains (Parikh, Troyer, Maione, & Murphy, 2016). Motor systems 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 are commonly seen in cases where young adults (YA) 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 (e.g., Bernard & Seidler, 2013b; Miller et al., 2013; Raz et al., 2005) 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). 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, 2013; Bernard et al., 2013; Miller 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). 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

cerebello-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). Further, cerebellar function may provide important scaffolding for behavior in OA (Filip, Gallea, Lehéricy, Lungu, & Bareš, 2019). 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 cerebellar activation in OA relative to YA would be expected. 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.

Method

Literature Search and Inclusion Criteria

The analyses reported on here were not formally preregistered. 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/. Papers were identified through PubMed (http://www.ncbi.nlm.nih.gov/pubmed) search using the search term: "cerebell* AND imaging" with the limits "Humans" and "English." Additionally, we included the limit "Adult 65+" to target the OA literature. This resulted in 3,913 articles. 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, Chen, Ho, & Desmond, 2012; Stoodley & Schmahmann, 2009). As such, we did not include an additional YA only search. 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.

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. 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., 2012; 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 and foci on which to complete our analyses. 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 an additional search using the terms "aging AND brain imaging" with the same limits as above, which returned 5,982 results as of August 6, 2018. Finally, 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, we included all the studies and foci from prior meta-analyses investigating cerebellar functional activation (E et al., 2012; Stoodley & Schmahmann, 2009) in overlapping task categories. Additional motor foci were extracted from the studies included by Stoodley & Schmahmann (2009), while those for language, working memory, and cognitive function (categorized as executive function) were taken from E and colleagues (2012). Notably, E and colleagues (2012) also had significant overlap with Stoodley & Schmahmann (2009) as they included all of the papers from the prior analysis, as well as new additions to the literature. Long-term memory was not included in these prior investigations. 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. Studies from E and colleagues (2012) categorized as executive function were put into this category. Table 1 includes a complete listing of the studies included in our meta-analysis organized by task domain. 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. 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 & Schamhmann (2009) and E and colleagues (2012), we had 143 studies, including data from 1,488 YA and 3,001 OA individuals, concatenated across all task domains.

[Table 1 about here]

ALE Meta-Analysis

All analyses were completed using BrainMap GingerALE 2.3.6 (http://brainmap.org; Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Eickhoff et al., 2009; Turkeltaub et al., 2012), using the most recent algorithm (Turkeltaub et al., 2012), designed to minimize the impact of individual experiments. 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 11.37mm, 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 an uncorrected $p<.001$ as the cluster-forming threshold, followed by FDR $p<.05$ for cluster-level inference with 5,000 threshold permutations. This statistical approach is consistent with recommendations from Eickhoff and colleagues (2012). 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. Behavioral domains where there were too few studies for group contrast analyses are noted specifically below. The resulting foci from all analyses were localized using the 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).

Results

Within Group Activation Overlap Patterns

Because several meta-analyses have already been conducted investigating cerebellar activation across task domains in YA (Bernard & Seidler, 2013a; E et al., 2012; 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 2 and presented visually in Figure 1. In YA, the motor and working memory analyses replicated prior meta-analyses investigating patterns of cerebellar functional activation (Stoodley & Schmahmann, 2009; E et al., 2012; Bernard & Seidler, 2013a), though notably, there was substantial overlap in the foci used for the analyses. Activation across language tasks was more limited than in past investigations, with one cluster in Crus I, while other cognitive tasks, primarily executive function, did not show any significant overlap in YA, counter to prior work (Stoodley & Schmahmann, 2009; E et al., 2012; for further discussion please see Supplementary Material). Finally, we extended prior meta-analyses with the inclusion of long-term memory. In YA, our results demonstrate activation overlap across tasks in the right posterior cerebellum.

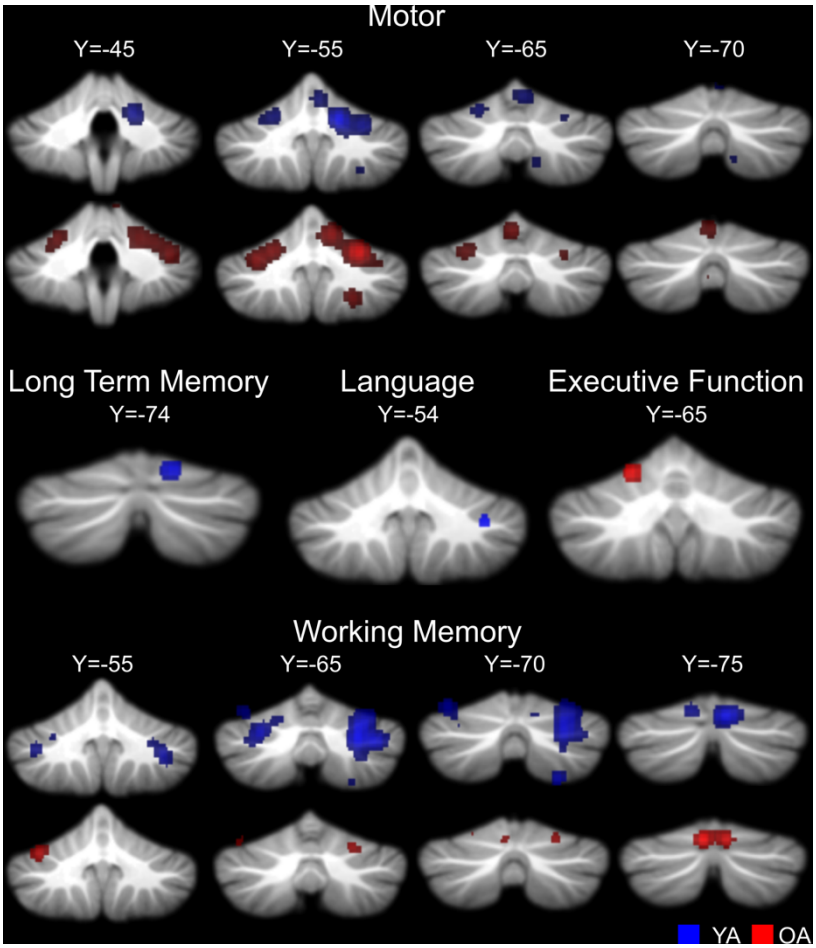

Figure 1. Activation overlap in the cerebellum across studies for each task domain in YA (blue) and OA (red). Areas of overlap are overlaid onto the SUIT cerebellum template. Notably, there were no significant areas of overlap across studies in OA for long-term memory and language tasks, while there was no significant overlap in YA across studies looking at executive function/attention.

Table 2. Activation by group and task. *Peak outside of SUIT Atlas space, the closest region to the reported peak is listed.

Cluster	Cluster Size (mm^3)	Extent & Weighted Center (x, y, z)	Local Extrema (x, y, z)	Location	ALE Value ($x10^{-3}$)
		Motor YA			
1	6288	From (0,-70,-34) to (34,-38,-8) Centered at (17.3,-55.3,-23.3)	16, -54, -24	Lobule V	47.55
			30, -58, -28	Lobule VI	27.83
			6, -62, -14	Lobule V	21.94
2	1600	From (-30,-68, -28) to (-16,-52,-16) Centered at (-22,-60.1,-21.8)	-20, -60, -20	Lobule VI	25.34
4	168	From (10,-70,-52) to (14,-64,-48) Centered at (11.8,-67.2,-50.2)	12, -68, -50	Lobule VIIIa	14.96
5	120	From (24,-58,-54) to (30,-54,-52) Centered at (27.7,-56.1,-52.9)	28, -56, -52	Lobule VIIIa	13.21
6	8	Centered at (32,-52,-54)	32, -52, -54	Lobule VIIIa	11.79

OA					
1	7640	From (4,-68,-38) to (42,-42,-4) Centered at (23.8,-52.7,-23)	28, -54, -24	Lobule VI	58.64
			12, -54, -14	Lobule V	33.50
			38, -50, -32	Lobule VI	30.67
2	4520	From (-38,-66,-36) to (-14,-44,-18) Centered at (-26.6,-55.9,-25.9)	-30, -52, -30	Lobule VI	29.28
			-22, -60, -24	Lobule VI	29.11
			-30, -62, -26	Lobule VI	28.75
			-24, -52, -24	Lobule VI	28.47
3	928	From (18,-64,-56) to (28,-52,-46) Centered at (23.4,-57.6,-50.4)	24, -56, -50	Lobule VIIIb	22.83
4	920	From (-6,-74,-20) to (2,-60,-10) Centered at (-1.5,-67.4,-14.9)	-2 ,-66, -14	Lobule V	24.60
5	152	From (-48,-62,-28) to (-44,-58,-22) Centered at (-46,-59.6,-25.5)	-46, -60, -26	Crus I	15.78
Language					
YA					
1	112	From (34,-56,-38) to (38,-52,-34) Centered at (36,-54.7,-36.7)	36, -54, -36	Crus I	18.04
OA					
N/A					
Long-Term Memory					
YA					
1	664	From (-16,-86,-20) to (-8,-78,-12) Centered at (-11.8,-82.4,-16.4)	16, -86, -20	Lobule VI/Crus I	18.65
2	440	From (10,-78,-24) to (18,-70,-18) Centered at (14.5,-73.6,-20.7)	14, -74, -20	Lobule VI	17.06
3	240	From (18,-88,-40) to (24,-82,-36) Centered at (21,-85.6,-38.3)	20, -86, -38	Crus II	13.19
OA					
N/A					
Working Memory					
YA					
1	7240	From (22,-74,-48) to (46,-50,-16) Centered at (31.8,-64.1,-31.6)	28, -66, -34	Crus I	37.51
			36, -64, -34	Crus I	31.58
			36, -54, -42	Crus II	26.50
2	2648	From (-42,-70,-42) to (-14,-56,-22) Centered at (-30.1,-62.1,-32.2)	-28, -62, -30	Lobule VI	35.32
			-38, -60, -38	Crus I	25.66
			-18, -64, -24	Lobule VI	17.72
3	2592	From (-14,-86,-34) to (16,-70,-12) Centered at (4,-77.8,-24.4)	8, -76, -24	Lobule VI	34.34
			-10, -76, -22	Lobule VI	21.00
			-2, -82, -14	Vermis VI*	18.12
4	672	From (-40,-74,-26) to (-32,-64,-16) Centered at (-36,-69.4,-20.4)	-36, -70, -20	Crus I*	23.71
5	376	From (22,-74,-62) to (28,-66,-56) Centered at (24.8,-70,-58.8)	26, -70, -60	Lobule VIIb	25.18
OA					
1	1184	from (-8,-80,-28) to (12,-70,-20) centered at (.2,-75.2,-23.4)	-4, -76, -24	Vermis VI	34.85
			8, -76, -24	Lobule VI	28.89
2	736	from (-40,-62,-30) to (-32,-50,-22) centered at (-35.7,-56.2,-25.1)	-36, -58, -26	Lobule VI	24.12

3	280	from (22,-72,-26) to (28,-64,-20) centered at (24.4,-67.5,-23.4)	24, -68, -24	Lobule VI	20.31
4	48	from (-40,-66,-22) to (-38,-64,-18) centered at (-38.7, -65.3, -19.6)	-38, -66, -18	Crus I*	15.67
5	8	at (-22,-72,-20)	-22, -70, -20	Lobule VI	15.53
Other Cognitive Tasks (Executive Function/Attention)					
YA					
N/A					
OA					
1	448	From (-6,-78,-28) to (4,-72,-22) Centered at (-.6,-74.9,-24.6)	0, -74, -24	Vermis VI	21.51
2	432	From (-22,-66,-20) to (-14,-58,-14) Centered at (-18.1,-61.3,-16.7)	-18, -62, -16	Lobule VI	22.66
3	96	From (-38,-72,-28) to (-34,-68,-24) Centered at (-35.5,-69.6,-26.3)	-36, -70, -26	Crus I	15.33
4	88	From (22,-66,-38) to (26,-62,-34) Centered at (24,-64,-36.7)	24, -64, -36	Dentate	16.14
5	88	From (0,-68,-4) to (2,-64,0) Centered at (1.1,-65.6,-2.5)	2, -66, -2	Lobule V*	15.94

In OA, across studies motor task activation largely paralleled YA in the regions that were active. That is, activation was localized largely to the anterior cerebellum in lobules V and VI, along with the secondary motor representation in lobule VIIIb. However, there was some activation overlap in Crus I as well. Working memory activation was primarily observed in Lobule VI and also included Crus I and Vermis VI, much like in YA. Unlike in YA, the OA sample did not show any significant overlap across studies for language tasks, or for long-term memory. The latter is particularly interesting given that there were more foci included in the analysis of long-term memory in OA as compared to the YA group (see Table 1). When looking at other cognitive tasks which were primarily those that tapped into executive functions, broadly defined, OA demonstrated significant overlap across studies in Lobule VI (both left hemisphere and vermis), Crus I, dentate nucleus, and Lobule V.

Age Differences in Cerebellar Activation Overlap

Group differences in activation across studies for motor and working memory tasks were computed (Figure 2, Table 3). Due 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, long-term memory, and the other cognitive task domains independently. With that said, it is worth noting that in the cases of language and long-term memory, YA showed significant overlap in cerebellar activation across studies, whereas OA did not, suggesting perhaps relative under-activation of the cerebellum in advanced age. At minimum, this suggests that activation patterns across studies of these domains in OA are less consistent than in YA.

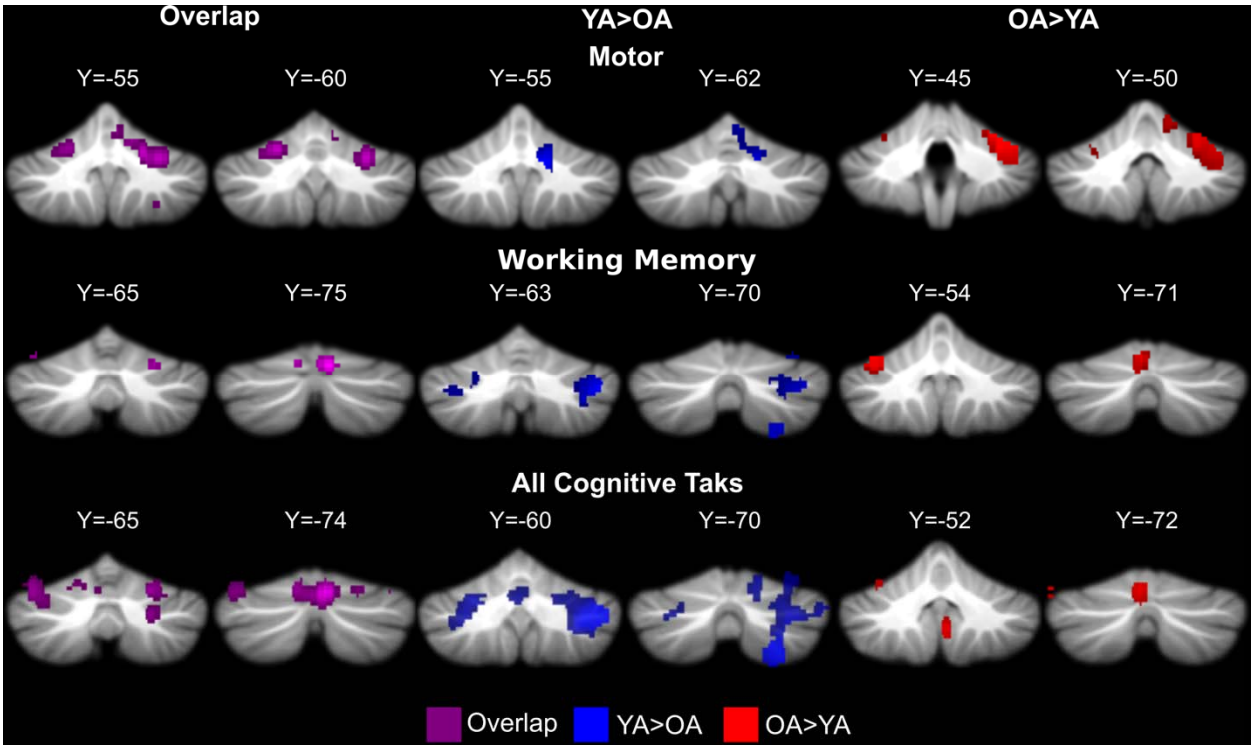

Figure 2. Overlap between age groups as well as age differences across studies in cerebellar activation. Because for several cognitive task domains there were not enough foci to compare the two age groups, or because there was no significant overlap within an age group, all of the cognitive task domains were combined and investigated together as well. Purple: overlap between age groups across tasks. Blue: YA>OA. Red: OA>YA.

Table 3. Group comparisons by task. *Peak outside of SUIT Atlas space, the closest region to the reported peak is listed.

Cluster	Cluster Size (mm^3)	Extent & Weighted Center (x, y, z)	Local Extrema (x, y, z)	Location	ALE Value ($x10^{-3}$)
Motor					
Group Overlap					
1	3184	From (4,-66,-32) to (34,-44,-10) Centered at (21.6,-54.7,-24.2)	20, -52, -24	Lobule V	33.39
			30, -58, -28	Lobule VI	27.83
			6, -56, -12	Lobule V	17.52
2	1272	From (-30,-66,-28) to (-16,-52,-18) Centered at (-22.6,-59.1,-22.6)	-20, -60, -22	Lobule VI	25.27
3	136	From (0,-68,-16) to (2,-62,-10) Centered at (1.3,-65.4,-13.2)	2, -64, -14	Lobule V	16.38
4	80	From (24,-58,-54) to (28,-54,-52) Centered at (26.8,-56.8,-52.8)	28, -56, -52	Lobule VIIIa	13.21
YA>OA					
1	1864	From (4, -68,-34) to (20,-48,-8) Centered at (13.4,-56.8,-23.8)	13.5, -55.5, -29.5	Dentate	3719.0
			6, -62, -8	Lobule V	2167.4
			8, -66, -10	Lobule V	2079.2
			10, -64, -18	Lobule V	2094.6
OA>YA					

1	2296	From (22,-56,-38) to (42,-44,-16) Centered at (32.6,-49.4,-27)	38, -44, -30	Lobule VI	3540.1
			34, -44, -30	Lobule VI	3290.5
			32.7, -46, -24.7	Lobule VI	3238.9
2	368	From (10,-56,-16) to (18,-48,-8) Centered at (12.9,-51.4,-11.7)	14, -50, -10	Lobule V	2349.4
3	144	From (-30,-60,-32) to (-26,-46,-22) Centered at (-27.5,-50.8,-27.3)	-30, -48, -24	Lobule VI	1944.8
			-26, -52, -30	Lobule VI	1817.1
			-26, -60, -32	Lobule VI	1704.9
4	120	From (-48,-62,-28) to (-44,-58,-22) Centered at -46,-59.7,-25.3)	-46, -62, -26	Crus I	1900.2
Working Memory					
Group Overlap					
1	432	From (2,-80,-28) to (12,-72,-20) Centered at (7,-75.7,-23.4)	8, -76, -24	Lobule VI	28.89
2	208	From (24,-70,-26) to (28,-64,-20) Centered at (25.2,-66.8,-23.7)	26, -66, -24	Lobule VI	19.43
3	152	From (-8,-80,-26) to (-4,-74,-20) Centered at (-6.3,-77.6,-23.5)	-8, -76, -22	Lobule VI	19.20
4	32	From (-40,-66,-20) to (-38,-64,-18) Centered at (-38.5,-65.5,-19)	-38, -66, -18	Crus I*	15.67
5	8	At (-34,-60,-28)	-34 ,-60, -28	Lobule VI	13.91
YA>OA					
1	2456	From (22,-74,-46) to (46,-50,-30) Centered at (36.2,-63.5,-36.5)	43.3, -62, -36	Crus I	3431.6
			36, -57, -36	Crus I	2967.7
			24,-72,-36	Crus I	2006.5
2	376	From (22,-74,-62) to (28,-66,-56) Centered at (24.8,-70,-58.8)	26, -74, -58	Lobule VIIb	2911.2
			22, -74, -58	Lobule VIIb	2758.9
			22, -70, -56	Lobule VIIb	2483.8
3	328	From (-40,-66,-42) to (-30,-60,-34) Centered at (-35.4,-62.8,-38.3)	-34,-64,-40	Crus I	2047.6
4	288	From (-26,-66,-36) to (-22,-58,-28) Centered at (-24.1,-61.1,-31)	-22, -60, -32	Lobule VI*	2149.4
			-26, -62, -36	Lobule VI*	1838.4
5	192	From (4,-86,-34) to (10,-80,-30) Centered at (6.7,-83.6,-32.3)	8, -86, -34	Crus II	2369.7
6	128	From (32,-72,-22) to (38,-68,-1) Centered at (34.3,-70.5,-20.1)	38, -72, -20	Crus I*	1943.1
OA>YA					
1	768	From (-40,-62,-30) to (-32,-50,-20) Centered at (-35.8,-55.4,-24.7)	-36, -56, -22	Lobule VI	3155.9
			-34, -52, -26	Lobule VI	3035.7
2	512	From (-6,-76,-28) to (2,-70,-18) Centered at (-2.6,-73.1,-22.5)	-2, -70, -22	Vermis VI	2988.9
All Cognitive Tasks Combined Group Overlap					
1	2496	From (-44,-76,-36) to (-30,-52,-16) Centered at (-37.3,-64.8,-26)	-36, -58, -28	Lobule VI	26.23
			-38, -70, -24	Crus I	25.57
2	2320	From (-10,-82,-32) to (12,-68,-18) Centered at (1.3,-75.8,-24.2)	4, -76, -24	Vermis VI	40.95
3	1664	From (20,-76,-40) to (40,-56,-18) Centered at (26.7,-64.9,-26.1)	24, -64, -36	Dentate	24.91
			26, -66, -22	Lobule VI	24.16

			36, -58, -20	Lobule VI*	19.44
4	176	From (-22,-68,-22) to (-12,-62,-18) Centered at (-15.8,-65.5,-20.5)	-16, -66, -20	Lobule VI	18.33
			-20, -64, -22	Lobule VI	17.16
5	104	From (-6,-68,-24) to (0,-66,-20) Centered at (-3.4,-67.4,-22.5)	-2, -68, -24	Vermis VI	17.06
6	8	At (24,-84,-38)	24, -84, -38	Crus II	15.67
7	8	At (38,-74,-24)	38, -74, -24	Crus I	15.48
8	8	At (10,-56,-24)	10, -56, -24	Interposed Nuclei	15.25
9	8	At (38,-76,-22)	38, -76 ,-22	Crus I	15.69
YA>OA					
1	9840	From (18,-78,-62) to (52,-48,-14) Centered at (34.4,-63.7,-38.4)	36.3, -63.1, -43.6	Crus II	3890.6
			40, -66, -45	Crus II	3719.0
			24, -58, -28	Lobule VI	2697.1
			34, -70, -18	Lobule VI*	2369.7
2	4560	From (-16,-88,-34) to (20,-66,-10) Centered at (-1.2,-79.8,-20.7)	-8.8, -83.1, -15.9	Crus I	3719.0
			16, -74, -16	Lobule VI	2820.1
			14, -78, -30	Crus I	2442.1
			4, -82, -30	Crus II	2373.9
3	2224	From (-40,-70,-44) to (-18,-54,-24) Centered at (-28.2,-62.2,-33.4)	-24, -58, -30	Lobule VI	3011.4
			-30, -64, -42	Crus II	2696.8
			-30, -60, -36	Crus I	2612.0
4	480	From (-6,-64,-30) to (6,-58,-22) Centered at (.1,-61.2,-26.1)	2, -62, -26	Vermis VI	2442.1
5	112	From (16,-90,-38) to (20,-84,-32) Centered at (18.6,-88.9,-33.9)	18, -90, -36	Crus II	1810.6
OA>YA					
1	312	From (-6,-76,-30) to (0,-70,-18) Centered at (-2.4,-72.6,-23.6)	-2, -74, -20	Vermis VI	2333.9
2	280	From (2,-54,-50) to (6,-50,-40) Centered at (4,-51.6,-45.4)	2, -52, -48	Lobule IX	2186.2
			2, -54, -44	Lobule IX	2183.5
3	208	From (-50,-72,-28) to (-46,-64,-22) Centered at (-48.1,-67,-25.1)	-50, -66, -26	Crus I	2462.4
4	104	From (-34,-56,-24) to (-32,-52,-20) Centered at (-33.2,-53.7,-21.4)	-32, -54, -20	Lobule VI*	1975.6

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 V and VI, as well as in the secondary motor representation in Lobule VIIIa. YA showed greater activation overlap across studies in the dentate nucleus and Lobule V, an area heavily involved in motor processing (Stoodley & Schmahmann, 2009), while OA showed greater activation overlap in Lobule VI and Crus I. Interestingly, some of this increased activation overlap in OA was bilateral and included the left hemisphere.

Working memory tasks also resulted in a great deal of activation overlap across studies for YA and OA. Not surprisingly, this was localized to bilateral Lobule VI and left Crus I. Greater overlap across studies in YA was seen almost exclusively in the right hemisphere in Crus I, Crus II, and Lobules VI, and VIIb. The lateralization is likely due in large part to the verbal nature of these tasks, though there were clusters in left Lobule VI and Crus I. Greater activation overlap in OA was

seen in left Lobule VI as well as vermis Lobule VI, though these areas of increased activation in OA are relatively minimal compared to what was seen for YA relative to OA, both in terms of number of clusters, and total volume of the overlap.

Finally, because we were unable to look at long-term memory, language, and other tasks tapping into executive functions independently, we combined all cognitive tasks to compare overlap between YA and OA. 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 prefrontal cortex (Bernard et al., 2012; Chen & Desmond, 2005; Krienen & Buckner, 2009; Salmi, Pallesen, & Neuvonen, 2010; Stoodley & Schmahmann, 2009), there was substantial overlap between the age groups in hemispheric Crus I and Lobule VI, though Vermis VI was also implicated along with the deep cerebellar nuclei. In YA, greater activation overlap was seen most consistently in Crus I and II, and while a majority of this was in the right hemisphere, there were left hemisphere foci as well. In OA, 3 out of the 4 foci with greater activation overlap were in the left hemisphere. These included Crus I and Lobule VI. Interestingly, Lobule IX was also implicated. Most notably, the overall volume of the areas of increased overlap was substantially smaller in the OA group (904 mm^3) as compared to the YA (17,216 mm^3).

Discussion

Here, using ALE meta-analysis, we directly compared cerebellar activation patterns 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. However, there is also substantial activation overlap between the 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. Most notably, there is evidence to suggest under-recruitment of the cerebellum in several 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 patterns differ for motor tasks. OA are under-recruiting the primary motor regions of the cerebellum, but are recruiting more 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.

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 activation across studies investigating working memory or other cognitive tasks. Indeed, though YA showed significant overlap in cerebellar activation across several domains, there was no reliable activation in OA. 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 as evidenced by the activation patterns across studies seen here.

Somewhat surprisingly, we found a distinct pattern of activation differences for motor tasks. OA showed significantly more activation in Lobule VI compared to YA, and this bilateral activation extended to Crus I. These regions have connectivity patterns with prefrontal cortical and premotor regions (e.g., Bernard et al., 2012; Krienen & Buckner, 2009) and show activation during cognitive task performance (Stoodley & Schmahmann, 2009). This over-activation 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). 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 indicate that in

OA cerebellar resources are under-recruited during cognitive tasks, 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. Additionally, we did not conduct a complete search of the entire YA imaging literature. 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 & Schmahamann, 2009; E et al., 2012).

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* cerebellar activation than YA, in contrast to what is seen in the prefrontal cortex (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, OA are unable to use this critical region and scaffolding for performance, resulting in behavioral declines. Conversely, we see increased activation 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.

Author Contributions

J.A.B. developed the study concept and study design. T.M., A.D.N., Y.L., J.R.M.G., H.K.B., and H.K.H completed the literature and pulled all of the data for analysis. J.A.B. completed the data analysis and the initial preparation of the manuscript. All authors provided critical additions and revisions to the manuscript. All authors approved the final version of the manuscript for submission.

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Tables

Table 1. Included studies by task type. 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. Further, additional YA data came from studies included in prior meta-analyses. #Studies included only as part of Stoodley & Schmahmann, 2009. *Studies included as part of Stoodley & Schmahmann, 2009 and E et al., 2014. **Studies only included in E et al., 2014. "—" denotes studies where group 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.

Study	Imaging Modality	N, YA	N, OA	Task	# YA Foci	# OA Foci
Other Cognitive Tasks/Executive Function						
Gianaros, Jennings, Sheu, Derbyshire, Matthews (2007). *Hypertension,* 49, 134-140.	3T fMRI	--	46	Stroop task	--	1
Hubert, Beaunieux, Chételat, Platel, Landeau, Viader, Desgranges, Eustache (2009). *Hum Brain Map*, 30, 1374-1386.	PET	--	12	Tower of Toronto task	--	6
Luis, Arrondo, Vidorreta, Martínez, Loayza, Fernández-Seara, Pastor (2015). *PLoS ONE,* 10, e0131536.	3T fMRI	--	20	N-back task combined across spatial and visual domains	--	2
Moffat, Elkins, Resnick (2006). *Neurobiol Aging,* 27, 965-972.	1.5T fMRI	30	21	Spatial navigation	1	1
Belville, Mellah, de Boysson, Demonet, Bier (2014). *PLoS*	3T fMRI	--	42	Dual-tasking using alphabetic equations	--	1

ONE, 9, e102710.						
Beauchamp, Dagher, Aston, Doyon (2003). *NeuroImage*, 20, 1649-1660.	PET	12	12	Tower of London task	3	3
Harrington, Castillo, Greenberg, Song, Lessig, Lee, Rao (2011). *PLoS ONE*, 6, e17461.	3T fMRI	--	19	Time perception	--	14
Drezga, Grimmer, Peller, Wermke, Siebner, Rauschecker, Schwaiger, Kurz (2005). *PLoS Med*, 2, e288.	PET	--	10	Spatial navigation of 3D environments	--	4
Grönholm, Rinne, Vorobyev, Laine (2005). *Cog Brain Res*, 25, 359-371.	PET	--	10	Object naming	--	10
Ramanoël, Kaufmann, Cousin, Dojat, Peyrin (2015). *PLoS ONE*, 10, e0134554.	3T fMRI	12	12	Spatial scene processing	0	1
Madden, Langley, Denny, Turkington, Provenzale, Hawk, Coleman (2002). *Brain Cogn*, 49, 297-321.	PET	12	12	Visual search	2	7
Geerligs, Maurits, Renken, Lorist (2014). *Hum Brain Mapp*, 35, 319-330.	3T fMRI	12	30	Visual oddball task	2	0
Gilbert, Bird, Brindley, Frith, Burgess (2008). *Neuropsychologia*, 46, 2281-2291.**	3T fMRI	18	--	Random generation task	3	--
Rao, Bobholz, Hammeke, Rosen, Woodley, Cunningham, Cox, Stein, Binder (1997). *NeuroReport*, 8, 1987-1993.*	1.5T fMRI	11	--	Conceptual reasoning	3	--
Dagher, Owen, Boecker, Brooks (1999). *Brain*, 122, 1973-1987.**	PET	6	--	Tower of London task	2	--
Jahanshahi, Dirnberger, Fuller, Frith (2000). *NeuroImage*, 12, 713-725.*	PET	6	--	Random number generation relative to counting	2	--
Liddle, Kiehl, Smith (2001). *Hum Brain Mapp*, 12, 100-109.*	1.5T fMRI	16	--	Go no-go task	15	--
Ernst, Bolla, Mouratidis, Contoreggi, Matochik, Kurian, Cadet, Kimes, London (2002). *Neuropsychopharmacol,* 26, 682-691.*	PET	20	--	Risk decision making	10	--
Kondo, Morishita, Osaka, Osaka, Fukuyama, Shibasaki (2004). *NeuroImage*, 21, 2-14.**	1.5T fMRI	10	--	Arithmetic and memory	6	--
Harrington, Boyd, Mayer, Sheltraw, Lee, Huang, Rao (2004). *Cog Brain Res*, 21, 193-205.*	1.5T fMRI	24	--	Interval timing decision making	4	--

Dreher & Grafman (2002). *Eur J Neurosci*, 16, 1609-1619.**	1.5T fMRI	18	--	Task switching during letter discrimination	4	--
Schall, Johnston, Lagopoulos, Jüptner, Jentzen, Thienel, Dittman-Balçar, Bender, Ward (2003). *NeuroImage*, 20, 1154-1161.**	PET/1.5T fMRI	6	--	Tower of London task	2	--
Daniels, Witt, Wolff, Jansen, Deuschl (2003). *Neurosci Lett*, 345, 25-28.*	1.5T fMRI	8	--	Random number generation at 1 Hz	2	--
Blackwood, ffytche, Simmons, Bentall, Murray, Howard (2004). *Cog Brain Res*, 20, 46-53.*	1.5T fMRI	8	--	Decision making under certain and uncertain conditions	2	--
Language						
Rizio, Moyer, Diaz (2017). *Brain Behav*, 7, e00660.	3T fMRI	20	20	Language interference naming	0	2
Provost, Brambati, Chapleau, Wilson (2016). *Cortex,* 84, 90-100.	3T fMRI	16	16	Word reading	0	1
Martins, Simard, Monchi (2014). *PLoS ONE*, 9, e99710.	3T fMRI	14	14	Lexical version of the Wisconsin card sorting task	6	3
Whatmough, Verret, Fung, Chertkow (2004). *J Cogn Neurosci*, 16, 1211-1226.	PET	--	15	Semantic judgments of word pairs	--	4
Olichney, Taylor, Hillert, Chan, Salmon, Gatherwright, Iragui, Kutas (2010). *Neurobiol Aging*, 31, 1975-1990.	1.5T fMRI	--	17	Word memory and repetition	--	3
Daselaar, Veltman, Rombouts, Raaijmakers, Jonker (2003). *Neurobiol Aging*, 24, 1005-1011.	1.5T fMRI	26	39	Semantic characterization after shallow or deep encoding	1	1
Madden, Langley, Denny, Turkington, Provenzale, Hawk, Coleman (2002). *Brain Cogn*, 49, 297-321.	PET	12	12	Lexical decision task	3	2
Seki, Okada, Koeda, Sadato (2004). *Cog Brain Res*, 20, 261-272.*	3T fMRI	19	--	Vowel exchange compared to reading words and non-words	2	--
Rauschecker, Pringle, Watkins (2008). *Hum Brain Mapp,* 29, 1231-1242.**	3T fMRI	14	--	Listening and cover repetition of non-words	4	--
Daselaar, Veltman, Rombouts, Raaijmakers, Jonker (2005). *Neuriobiol Learn Mem*, 83, 251-262.	1.5T fMRI	25	38	Word-stem completion	1	0
Ojemann, Buckner, Akbudak, Snyder, Ollinger, McKinstry, Rosen, Petersen, Raichle, Conturo (1998). *Hum Brain*	PET/1.5T fMRI	7	--	Word-stem completion	7	--

Mapp, 6, 203-215.*						
Schlosser, Hutchinson, Joseffer, Rusinek, Saarimaki, Stevenson, Dewey, Brodie (1998). *J Neurol Neurosurg Psychiatry*, 64, 492-498.*	1.5T fMRI	6	--	Verbal fluency task	6	--
Lurito, Kareken, Lowe, Chen, Mathews (2000). *Hum Brain Mapp*, 10, 99-106.*	1.5T fMRI	5	--	Word generation compared to viewing non-letter symbols	3	--
Seger, Desmond, Glover, Gabrieli (2000). *Neuropsychol*, 14, 361-369.*	1.5T fMRI	7	--	Verb generation task	16	--
Gurd, Amunts, Weiss, Zafiris, Zilles, Marshall, Fink (2002). *Brain*, 125, 1024-1038.*	1.5T fMRI	11	--	Semantic fluency relative to overlearned sequence fluency (days of the week)	1	--
Noppeney & Price (2002). *NeuroImage*, 15, 927-935.*	PET	12	--	Semantic decision task	2	--
McDermott, Petersen, Watson, Ojemann (2003). *Neuropsychologia*, 41, 293-303.*	1.5T fMRI	20	--	Word lists of semantic compared to phonological	3	--
Xiang, Lin, Ma, Zhang, Bower, Weng, Gao (2003). *Hum Brain Map*, 18, 208-214.*	1.5T fMRI	6	--	Semantic discrimination	1	--
Tieleman, Seurinck, Deblaere, Vandemaele, Vingerhoets, Achten (2005), *NeuroImage*, 26, 565-572.*	1.5T fMRI	22	--	Semantic compared to perceptual categorization	3	--
Frings, Dimitrova, Schorn, Elles, Hein-Kropp, Gizewski, Diener, Timmann (2006). *Neurosci Letters*, 409, 19-23.*	1.5T fMRI	16	--	Verb generation task	3	--
Callan, Tsytsarev, Hanakawa, Callan, Katsuhara, Fukuyama, Turner (2006), *NeuroImage*, 31, 1327-1342.**	3T fMRI	16	--	Listening to and covert production of singing relative to speech	2	--
Sweet, Paskavitz, Haley, Gunstad, Mulligan, Nyalakanti, Cohen (2008). *Neuropsychologia*, 46, 1114-1123.**	1.5T fMRI	34	--	Phonological similarity during verbal working memory	1	--
Durisko & Fiez (2010). *Cortex,* 46, 896-906.**	3T fMRI	19		Delayed serial recall task with letters	2	
Motor						
Wurster, Graf, Ackermann, Groth, Kassubek, Riecker (2015). *Brain Struct Func*, 220, 1637-1648.	3T fMRI	--	10	Finger tapping	--	2
Blumen, Holtzer, Brown, Gazes, Verghese (2015). *Hum Brain Mapp*, 35, 4090, 4104.	3T fMRI	--	33	Imagined walking and walking while talking	--	1
Allali, van der Meulen,	3T fMRI	14	14	Motor imagery	1	3

Beauchet, Rieger, Vuilleumier, Assal (2014). *J Gerontol A Biol Sci Med Sci*, 69, 1389-1398.						
Wittenberg, Lovelace, Foster, Maldjian (2014). *Brain Imaging Behav*, 8, 335-345.	1.5T fMRI	12	12	Ecologically valid motor self-care tasks (e.g., buttoning & zipping) and finger tapping	11	6
Crémers, D'Ostilio, Stamatakis, Delvaux, Garraux (2012). *Movement Disorders*, 27, 1498-1505.	3T fMRI	--	15	Imagined gait relative to imagined standing	--	3
Vidoni, Thomas, Honea, Koskutova, Burns (2012). *J Neurol Phys Ther*, 36, 8-16.	3T fMRI	--	10	Power grip	--	3
Zwergal, Linn, Xiong, Brandt, Strupp, Jahn (2012). *Neurobiol Aging*, 33, 1073-1084.	3T fMRI	20	20	Imagined movement, standing and walking	0	5
Askim, Indredavik, Haberg (2010). *Arch Phys Med Rehabil*, 91, 1529-1536.	1.5T fMRI	--	15	Finger tapping – paced and self-paced	--	3
Allen & Humphreys (2009). *Current Biol*, 19, 1044-1049.	3T fMRI	--	7	Somatomotor tactile stimulation	--	1
Eckert, Peschel, Heinze, Rotte (2006). *J Neurol*, 253, 199-207.	1.5T fMRI	--	9	Opening and closing fist	--	1
Heuninckx, Wenderoth, Debaere, Peeters, Swinnn (2005). *J Neurosci*, 25, 6787-6796.	3T fMRI	12	12	Coordinated hand and foot movements	8	31
Rowe, Stephan, Friston, Frackowiak, Lees, Passingham (2002). *Brain,* 125, 267-289.	Not Specified	--	12	Motor sequence learning	--	3
Kalpouzos, Garzón, Sitnikov, Heiland, Salami, Persson, Bäckman (2017). *Cereb Cortex*, 27, 3427-3436.	3T fMRI	22	15	Motor imagery	1	2
King, Saucier, Albouy, Fogel, Rumpf, Klann, Buccino, Binkofski, Classen, Karni, Doyon (2017). *Cereb Cortex*, 27, 1588-1601.	3T fMRI	--	26	Motor sequence learning, initial training only included here	--	3
Wang, Qiu, Liu, Yan, Yang, Zhang, Zhang, Sang, Zheng (2014). *Neuroraiol*, 56, 339=348.	3T fMRI	19	20	Motor execution and imagery	6	8
Heuninckx, Wenderoth, Swinnen (2010). *Neurobiol Aging,* 31, 301-314.	3T fMRI	12	12	Externally and internally guided movements	6	8
Riecker, Gröschel, Ackermann, Steinbrink, Witte, Kastrup (2006). *NeuroImage*, 32, 1345-1354.	1.5T fMRI	10	10	Motor tapping	1	1

Zapparoli, Invernizzi, Gandola, Verardi, Berlingeri, Sberna, De Santis, Zerbi, Banfi, Bottini, Paulesu (2012). *Exp Brain Res,* 224, 519-540.	1.5T fMRI	24	24	Finger to thumb opposition	1	0
Jäncke, Loose, Lutz, Specht, Shah (2000). *Cog Brain Res*, 10, 51-66.#	1.5T fMRI	8	--	Finger tapping	3	--
Lutz, Specht, Shah, Jäncke (2000). *NeuroReport*, 11, 1301-1306.#	1.5T fMRI	10	--	Finger tapping	4	--
Riecker, Wildgruber, Mathiak, Grodd, Ackermann (2003). *NeuroImage*, 18, 2003, 731-739.#	1.5T fMRI	8	--	Finger tapping	12	--
Hanakwa, Dimyan, Hallett (2008). *Cereb Cortex*< 18, 2775-2788.#	3T fMRI	13	--	Finger Tapping	2	--
Brunne, Skouen, Ersland, Grüner (2014). *Neuroreb Neral Repair*, 28, 874-884.	3T fMRI	20	--	Observation and execution of bimanual movements	4	--
Taniwaki, Okayama, Yoshiura, Togao, Nakamura, Yamsaki, Ogata, Shigeto, Shyagi, Kira, & Tobimatsu (2007). *NeuroImage*, 36, 1263-1276.	1.5T fMRI	12	12	Externally triggered or self-initiated finger movements	6	4
Taniwaki, Yoshiura, Ogata, Togao, Yamashita, Kida, Miura, Kira, Tobimatsu (2013). *Brain Res,* 1512, 45-59.	1.5T fMRI	--	12	Externally triggered or self-initiated finger movements	--	4
Daselaar, Rombouts, Veltman, Raaijmakers, Jonker (2003). *Neurobiol Aging*, 24, 1013-1019.	1.5T fMRI	26	40	Motor sequence learning	1	3
Onozuka, Fujita, Watanabe, Hirano, Niwa, Nishiyama, Saito (2003). *J Dent Res*, 82, 657-660.	1.5T fMRI	10	10	Chewing	1	1
Catalan, Honda, Weeks, Cohen, Hallett (1998). *Brain*, 121, 253-264.	PET	13	--	Motor sequence learning	1	--
Rijntjes, Buechel, Kiebel, Weiller (1999). *NeuroReport*, 10, 3653-3658.#	2T fMRI	9	--	Finger flexion and extensions	3	--
Hankawa, Immisch, Toma, Dimyan, van Gelderen, Hallett (2003). *J Neurophysiol*, 89, 989-1002.#	1.5T fMRI	10	--	Finger tapping	3	--
Working Memory						
Luis, Arrondo, Vidorreta, Martínez, Loayza, Fernández-Seara, Pastor (2015). *PLoS ONE*, 10, e0131536.	3T fMRI	--	20	N-back task	--	1
Boller, Mellah, Ducharme-	3T fMRI	--	40	N-back task	--	3

Laliberté, Belleville (2017). *Brain Imaging Behav*, 11, 304-317.						
Heinzel, Lorenz, Pelz, Heinz, Walter, Kathmann, Rapp, Stelzel (2016). *NeuroImage*, 134, 236-249.	3T fMRI	--	32	N-back task and Sternberg task, baseline assessment only	--	11
Charroud, Steffener, Le Bars, Deverdun, Bonafe, Abdennour, Portet, Molino, Stern, Ritchie, Menjot de Champfleur, Akbaraly (2015). *Neurobiol Learn Mem*, 1250, 211-223.	3T fMRI	--	337	Delayed-item recognition task	--	10
Luis, Arrondo, Vidorreta, Martínex, Loayza, Fernández-Seara, Pastor (2015). *PLoS ONE*, 10, e0131536.	3T fMRI	--	20	Verbal working memory load manipulation	--	4
Migo, Mitterschiffthaler, O'Daly, Dawson, Dourish, Craig, Simmons, Wilcock, McCulloch, Jackson, Kopelman, Williams, Morris (2015). *Aging, Neuropsychol, Cog,* 22, 106-127.	3T fMRI	--	11	N-back task	--	2
Griebe, Amann, Hirsch, Achtnichts, Hennerici, Gass, Szabo (2014). *PLoS ONE*, 9, e103359.	1.5T fMRI	--	14	N-back task	--	3
Emery, Heaven, Paxton, Braver (2008). *NeuroImage*, 42, 1577-1586.	1.5T fMRI	10	11	Letter-number sequencing	0	3
Jennings, van der Veen, Melzer (2006). *Brain Res*, 1092, 177-189.	PET	--	89	N-back task	--	3
Lensinger, Born, Meindl, Bokde, Britsch, Lopez-Bayo, Teipel, Möller, Hampel, Reiser (2007). *Dement Geriatr Cogn Disord*, 24, 235-246.	1.5T fMRI	15	19	Location matching task	5	6
Lamar, Yousem, Resnick (2004). *NeuroImage*, 21, 1368-1376.	1.5T fMRI	16	16	Delayed match to sample	2	1
Schneider-Garces, Gordon, Brumback-Peltz, Shin, Lee, Sutton, Maclin, Gratton, Fabiani (2010). *J Cogn Neurosci*, 22, 655-659.	3T fMRI	12	30	Sternberg task	1	0
Vellage, Becke, Strumpf, Baier, Schönfeld, Hopf, Müller (2016). *Brain Behav*, 6, e00544.	3T fMRI	40	38	Spatial working memory filtering task	2	0
Valera, Faraone, Beiderman, Poldrack, Seidman (2005). *Biol Psychiatry*, 57, 439-447.*	1.5T fMRI	20	--	N-back task	1	--
Hayter, Langdon, Ramnani (2007), *NeuroImage*, 36, 943-	3T fMRI	15	--	Paced auditory serial addition task	6	--

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Scheuerecker, Ufer, Zipse, Frodl, Koutsouleris, Zetzsche, Wiesmann, Albrecht, Brückmann, Schmitt, Möller, Meisenzahl (2008). *J Psychiat Res*, 42, 469-476.**	1.5T fMRI	23	--	N-back task	5	--
Hautzel, Mottaghy, Specht, Müller, Krause (2009). *NeuroImage*, 47, 2073-2082.**	1.5T fMRI	17	--	N-back task	19	--
Marvel and Desmond (2010). *Cortex*, 46, 880-895.**	3T fMRI	16	--	Sternberg task	2	--
Oren, Ash, Tarrasch, Hendler, Giladi, Shapira-Lichter (2017). *Neurobiol Aging*, 53, 93-102.	3T fMRI	24	28	N-back task	2	0
Grady, McIntosh, Bookstein, Horwitz, Rapoport, Haxby (1998). *NeuroImage*, 8, 409-425.	PET	13	16	Working memory of facial stimuli	1	0
Fiez, Raife, Balota, Schwarz, Raichle, Petersen (1996). *J Neurosci*, 16, 808-822.**	PET	12	--	Working memory during PET??	5	--
Schumacher, Lauber, Awh, Jonides, Smith, Koeppe (1996). *NeuroImage*, 3, 79-88.**	PET	8	--	Visual and auditory working memory	8	--
Jonides, Schumacher, Smith, Koeppe, Awh, Reuter-Lorenz, Marshuetz, Willis (1998). *J Neurosci*, 18, 5026-5034.**	PET	12	--	Storage and fixation, modeled after Fiez et al., 1996	3	--
LaBar, Gitelman, Parrish, Marsel Mesulam (1999). *NeuroImage*, 10, 695-704.*	1.5T fMRI	11	--	N-back task	1	--
Thomas, King, Franzen, Welsh, Berkowitz, Noll, Birmaher, Casey (1999). *NeuroImage*, 10, 327-338.**	1.5T fMRI	6	--	N-back task	1	--
Honey, Bullmore, Sharma (2000). *NeuroImage*, 12, 495-503.*	1.5T fMRI	20	--	N-back task	1	--
Gruber (2001). *Cereb Cortex*, 11, 1047-1055.*	3T fMRI	11	--	Letter memory relative to letter case judgment with or without articulatory suppression	1	--
Cairo, Liddle, Woodward, Ngan (2004). *Cog Brain Res*, 21, 377-387.*	1.5T fMRI	18	--	Sternberg task	13	--
Kirschen, Chen ,Schraedley-Desmond, Desmond (2005). *NeuroImage*, 24, 462-472.*	3T fMRI	17	--	Verbal working memory with increasing load	6	--
Chen and Desmond (2005b). *Neuropsychologia*, 43, 1227-1237.*	3T fMRI	15	--	Sternberg task	9	--
Chen and Desmond (2005a).	3T fMRI	15	--	Verbal working	9	--

NeuroImage, 24, 332-338.**				memory with high and low loads		
Tomasi, Caparelli, Chang, Ernst (2005). *NeuroImage*, 27, 377-386.*	4T fMRI	30	--	N-back task	3	--
Woodward, Cairo, Ruff, Takane, Hunter, Ngan (2006). *Neuroscience*, 139, 317-325.**	1.5T fMRI	18	--	Verbal working memory with varying loads	5	--
Geier, Garver, Luna (2007). *NeuroImage*, 35, 904-915.**	3T fMRI	18	--	Occulomotor delayed response task (spatial working memory)	3	--
Tomasi, Chang, Caparelli, Ernst (2007). *Brain Res*, 1132, 158-165.**	4T fMRI	22	--	N-back task	3	--
Yeh, Kuo, Liu (2007). *Brain Res*, 1130, 146-157.**	1.5T fMRI	10	--	Change detection spatial working memory task	1	--
O'Hare, Lu, Houston, Bookheimer, Sowell (2008). *NeuroImage*, 42, 1678-1685.**	3T fMRI	8	--	Verbal working memory with varying loads	4	--
Koelsch, Schulze, Sammler, Fritz, Müller, Gruber (2009). *Hum Brain Mapp*, 30, 859-873.**	3T fMRI	12	--	Tonal and verbal working memory	1	--
Durisko and Fiez (2010). *Cortex,* 46, 896-906.**	3T fMRI	19	--	Delayed serial recall task	7	--
Schulze, Zysset, Mueller, Friederici, Koelsch (2011). *Hum Brain Mapp*, 32, 771-783.**	3T fMRI	17	--	Verbal and tonal working memory	5	--
Kirschen, Chen, Desmond (2010). *Behav Neurol*, 23, 51-63.**	3T fMRI	16	--	Load dependent verbal working memory with visual and aural stimuli	10	--
Long-Term Memory						
Vidal-Piñeir, Martin-Trias, Arenaza-Urquijo, Sala-Llonch, Clemente, Mena-Sánchez, Bargalló, Falcón, Pascual-Leone, Bartrés-Faz (2014). *Brain Stim*, 7, 287-296.	3T fMRI	--	24	Memory for deep and shallow encoding	--	3
Beason-Held, Golski, Kraut, Esposito, Resnick (2005). *Neurobiol Aging*, 26, 237-250.	PET	--	11	Verbal and figural encoding and recognition	--	10
Peira, Ziaei, Persson (2016). *NeuroImage*, 125, 745-755.	3T fMRI	15	15	Prospective memory	0	2
Cohen, Rissman, Suthana, Castel, Knowlton (2016). *NeuroImage*, 125, 1046-1062.	3T fMRI	--	23	Memory for words with high and low value	--	3
Gong, Fu, Wang, Franz, Long (2014). *Int'l J Aging Hum Dev*, 79, 23-54.	3T fMRI	--	12	Emotional autobiographical memory retrieval	--	8
Miotto, Balardin, Savege, Martin, Batistuzzo, Amaro,	3T fMRI	--	17	Memory for semantically related and	--	1

Nitrini (2014). *Arq Neuropsiquiatr*, 72, 663-670.				unrelated words		
Brassen, Büchel, Weber-Fahr, Lehmbek, Sommer, Braus (2009). *Neurobiol Aging*, 30, 1147-1156.	3T fMRI	14	14	Correct retrieval during verbal episodic memory	0	1
Bartrés-Faz, Serra-Grabulosa, Sun, Solé-Padullés, Rami, Molineuvo, Bosch, Mercader, Bargalló, Falcón, vendrell, Junqué, D'Esposito (2008). *Neurobiol Aging*, 29, 1644-1653.	1.5T fMRI	--	20	Encoding of face-name pairs	--	1
Maguire and Frith (2003). *Brain*, 126, 1511-1523.	2T fMRI	12	12	Autobiographical memory	4	4
Gronholm, Rinne, Vorobyev, Laine (2005). *Cog Brain Res*, 25, 359-371.	PET	--	10	Memory for learned objects	--	6
Milton, Butler, Benattayallah, Zeman (2012). *Neuropsychologia*, 50, 3528-3541.	1.5T fMRI	--	17	Long-term autobiographical memory	--	6
Lam, Wächter, Globas, Karnath, Luft (2013). *Hum Brain Mapp*, 34, 176-185.	3T fMRI	--	10	Weather prediction task	--	2
Antonova. Parslow, Brammer, Dawson, Jackson, Morris (2009). *Memory*, 17, 125-143.	1.5T fMRI	10	10	Long-term memory of spatial information	4	4
Dannhauser, Shergill, Stevens, Lee, Seal, Walker, Walker (2008). *Cortex, 44, 869-880.*	1.5T fMRI	--	10	Verbal episodic memory	--	1
Bowman and Dennis (2015). *Brain Res*, 1612, 2-15.	3T fMRI	17	22	Remember/know judgments of long-term memory	0	1
Kircher, Weis, Leube, Freymann, Erb, Jessen, Grodd, Heun, Krach (2008). *Eur Arch Psychiatry Clin Neurosci*, 258, 363-372.	1.5T fMRI	--	29	Subsequent memory effect	--	1
Daselaar, Veltman, Rombouts, Raaijmakers, Jonker (2003). *Brain*, 126, 43-56.	1.5T fMRI	17	19	Correct rejection or recognition at retrieval	3	2
Haist, Gore, Mao (2001). *Nature Neurosci,* 4, 1139-1145.	1.5T fMRI	--	8	Remote memory for famous faces	--	2
Iidaka, Sadato, Yamada, Murata, Omori, Yonekura (2001). *Cog Brain Res*, 11, 1-11.	1.5T fMRI	7	7	Pictorial information, abstract object encoding	0	1
Madden, Turkington, Provenzale, Denny, Hawk, Gottlob, Coleman (1999). *Hum Brain Map*, 7, 115-135.	PET	12	12	Recognition memory task	1	2
Gao, Cheung, Chan, Chu, Mak, Lee (2014). *PLoS ONE*, 9,	3T fMRI	13	13	Prospective memory	1	0

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Grady, McIntosh, Horwitz, Maisog, Ungerleider, Mentis, Pietrini, Schapiro, Haxby (1995). *Science*, 269, 218-221.	PET	10	10	Recognition compared to matching in long-term memory	3	0