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Review

Moving forward: Age effects on the cerebellum underlie cognitive and motor declines

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ABSTRACT

Though the cortical contributions to age-related declines in motor and cognitive performance are well-known, the potential contributions of the cerebellum are less clear. The diverse functions of the cerebellum make it an important structure to investigate in aging. Here, we review the extant literature on this topic. To date, there is evidence to indicate that there are morphological age differences in the cerebellum that are linked to motor and cognitive behavior. Cerebellar morphology is often as good as – or even better – at predicting performance than the prefrontal cortex. We also touch on the few studies using functional neuroimaging and connectivity analyses that further implicate the cerebellum in age-related performance declines. Importantly, we provide a conceptual framework for the cerebellum influencing age differences in performance, centered on the notion of degraded internal models. The evidence indicating that cerebellar age differences associate with performance highlights the need for additional work in this domain to further elucidate the role of the cerebellum in age differences in movement control and cognitive function.

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1. Introduction

Daily life requires a wide variety of motor and cognitive behaviors. Take for example a trip to the grocery store to purchase ingredients for dinner. One needs to navigate the store, execute a series of reach and grasp movements to place ingredients into a grocery cart, and rely upon memory to ensure that all of the necessary ingredients have been purchased. With healthy aging, there are performance declines in both the motor and cognitive domains. As the population rapidly ages, understanding the factors that contribute to these age-related performance declines is critical for the development of appropriate targeted interventions and preventative measures. While much progress has been made to date with respect to our understanding of these performance declines, the majority of this work has focused on the cerebral cortex. However, accumulating evidence supports a role for the cerebellum in both motor and cognitive behaviors (e.g. Leiner et al., 1986, 1993; Stoodley and Schmahmann, 2009; Stoodley et al., 2012), and study of this structure may also provide important insights into aging. Here, we provide an overview of the cognitive and motor deficits in aging with respect to cortical structure and function. Importantly, we also provide a review of the extant literature on the role of the cerebellum in these functional age differences. While much of this work has focused on cross-sectional morphological comparisons, we will also briefly touch upon task-based functional magnetic resonance imaging (fMRI) studies and work using resting state functional connectivity MRI (fcMRI). In concert, this literature supports an important role for the cerebellum in the cognitive and motor performance declines associated with aging, perhaps due to degraded internal models of motor and cognitive behaviors. Lastly, we will discuss potential targets for both future basic science research and applied interventions focusing on the cerebellum in order to mitigate these declines.

1.1. Cognitive and motor function and aging

With advanced age, individuals begin to exhibit performance declines in a variety of domains, including working memory, processing speed, spatial processing, and long-term memory, though notably, crystallized knowledge, such as vocabulary, remains intact (Park et al., 2001). Neural functional changes have been associated with performance declines (cf. Reuter-Lorenz and Park, 2010; Seidler et al., 2010). It has been suggested that the brain relies upon neural scaffolding to try to maintain performance (Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2010). That is, additional prefrontal cortical resources are recruited to compensate for functional declines, and though this activation may not be as neurally efficient as that seen in young adults, the additional brain activation may allow older adults to maintain higher levels of performance (Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2010). Indeed, over-activation in healthy aging is thought to perhaps be compensatory in nature, given that in prefrontally-mediated cognitive tasks, activation of additional brain regions is often associated with better task performance for older adults (Reuter-Lorenz and Cappell, 2008).

Bilateral prefrontal cortical recruitment during cognitive task performance in older adults was first demonstrated by Reuter-Lorenz and colleagues (2000) during the performance of verbal and spatial working memory tasks. Subsequent to this finding, such activation patterns were conceptualized within the hemispheric asymmetry reduction in older adults (HAROLD) framework (Cabeza, 2002). Since these initial findings, this pattern has been repeatedly demonstrated numerous times, indicating that such bilateral patterns of activation are a robust difference between young and older adults during cognitive task performance (for reviews see Reuter-Lorenz and Cappell, 2008; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2010).

In addition to the known cognitive performance declines associated with advanced age, deficits are also seen in the motor domain (reviewed in Seidler et al., 2010). There are gait and balance declines associated with advanced age (Bohannon et al., 1984; Holviala et al., 2012; Laughton et al., 2003; Maki et al., 1990; Prince et al., 1997), and older adults show less learning on sensorimotor adaptation (Anguera et al., 2011) and motor sequence learning tasks (Bo et al., 2011a, 2009). Perhaps not surprisingly, much like during cognitive task performance, there are also differences in neural recruitment during the performance of motor tasks.

Using a simple button-pressing task, Mattay and colleagues demonstrated that there is greater activation in the motor cortex as well as in the cerebellum in older adults (Mattay et al., 2002). Similarly, during a finger-to-thumb opposition task Naccarato and colleagues (2006) also showed decreased laterality in motor cortical activation with advanced age. The extent of this bilateral activation was positively correlated with age (Naccarato et al., 2006). More recently, multi-voxel pattern analysis was employed to analyze a tapping task in young and older adults, with the results showing decreased distinctiveness in motor representations in the motor cortex and cerebellum in older adults (Carp et al., 2011). More bilateral motor cortical representations in older adults have also been demonstrated at rest in the absence of task performance using transcranial magnetic stimulation (Bernard and Seidler, 2012).

Along with more bilateral activation in motor cortical regions during motor task performance, older adults also recruit additional prefrontal cortical regions (Heuninckx et al., 2008, 2005). Indeed, motor performance (alternating hand and foot movements) was positively correlated with the degree of activation in the prefrontal cortex in older adults (Heuninckx et al., 2008). Finally, dual-task motor and cognitive paradigms have shown greater motor performance declines in older adults (Huxhold et al., 2006; Li et al., 2001; Lindenberger et al., 2000; Lövdén et al., 2008) indicating an increased reliance on cognitive resources during motor performance.

Taken together, the literature to date provides a great deal of evidence for age-related declines in cognitive and motor function. Notably however, the work investigating the neural underpinnings of these declines has focused largely on the cerebral cortex. A complete overview of this literature is beyond the scope of the current review; the reader is referred to other articles for additional information (Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Cappell, 2008; Seidler et al., 2010). While previous work focusing on age differences in the cerebral cortex has greatly advanced our knowledge and understanding of the aging mind and brain, an emerging literature points to the cerebellum as an important area of interest in aging. This is particularly pertinent given work implicating the cerebellum in both cognitive and motor tasks (e.g. Leiner et al., 1986, 1989, 1991, 1993; Chen and Desmond, 2005a, 2005b; Stoodley and Schmahmann, 2009). The majority of this work to date has focused on cerebellar morphology, but evidence from both fMRI and resting state fcMRI also point to a potential role for the cerebellum in age related cognitive and motor performance declines.

2. Cerebellar morphology in aging

As briefly noted above, the majority of the literature investigating the cerebellum in advanced age is focused on cerebellar structure. Within this literature, several methodological approaches have been used. These include stereological studies done on the post-mortem brain, neuroimaging methods quantifying the volume of hand-traced regions of interest, voxel-based