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Cognitive Control and the Ageing Brain

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Introduction

The expected human lifespan is now longer than ever before, resulting in an expanding population of older (i.e., >65 years of age) adults. As this population continues to grow, it becomes imperative to understand the changes that occur in fundamental cognitive control abilities and its underpinnings in alterations of the ageing brain. Cognitive control refers to high-level executive functions of the brain such as attention, working memory, and task management (e.g., task switching, multitasking). Cognitive control abilities enable most activities of daily living, such as safely and effectively navigating our environment, and the consequence of cognitive control decline can severely alter the quality of life. This chapter will focus exclusively on research conducted on healthy older adults with an emphasis on neuroimaging research incorporating functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). To better understand cognitive control and the aging brain, the chapter is organised by functions: selective attention, inhibitory control, working memory, multitasking, task switching, and finally what we can do to enhance cognitive control abilities in older adults.

It is thought that by 90 years of age, brain weight has decreased by 11–14% of the maximum achieved weight in early adulthood (Dekaban, 1978; Jernigan et al., 2001). Compared to younger adults, older adults exhibit lower grey and white matter volumes, particularly in the prefrontal cortex (PFC) and parietal cortex (Gordon et al., 2008; Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010). Given the prominent role of the PFC in cognitive control (Cole et al., 2013; Corbetta & Shulman, 2002), many theories of cognitive ageing consider alterations of the PFC as a primary culprit for age-related declines in cognitive control (Dempster, 1992; Hasher, Lustig, & Zacks, 2007; Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Lustig, 2005; West, 1996). In response to these anatomical declines, compensatory neural activity may serve to maximise inefficient neural resources, especially in the PFC, in order to uphold behavioural performance. Moreover, once age-related peripheral sensory changes (e.g., visual acuity and hearing loss) are accounted for, perceptual declines in older adults remain (Strouse, Ashmead, Ohde, & Grantham, 1998; Zanto, Toy, & Gazzaley, 2010). Thus, diminished perceptual abilities may also require compensation by PFC-mediated cognitive control to retain performance abilities. Evidence now exists for age-related compensation of both perceptual

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decline and inefficient/reduced neural resources, placing greater demands on the cognitive control abilities of older adults. However, compensatory mechanisms are not always engaged, or they may be engaged but fail to sufficiently compensate, in which case age-related deficits become noticeable in multiple cognitive control domains, such as inhibitory control, working memory, task switching, and multitasking. Fortunately, the brain remains plastic throughout the lifespan, and many age-related declines in cognitive control may be reversed through physical exercise and cognitive training.

Selective Attention and Inhibitory Control

Selective attention refers to goal-directed focus on task-relevant information and the ignoring (or inhibition) of irrelevant information. A common approach to studying selective attention and inhibitory control is via the use of target detection paradigms. Target detection often requires participants to detect a target with or without the presence of simultaneous distracting non-targets and involves either open searching or the presentation of cues to orient attention toward relevant, and away from irrelevant, spatial locations, features, or objects. Note that we here employ the term *inhibitory control* to refer to the attentional suppression of the processing of task-irrelevant stimuli, which is distinct from inhibitory control in the domain of action, or *response inhibition* (see Chapter 6 by Verbruggen & Logan in this volume).

When presented with a visual cue that predicts the subsequent location of a target stimulus, younger and older adults exhibit comparable benefits in target detection abilities compared to uncued target detection (Gottlob & Madden, 1998; Hartley, Kieley, & Slabach, 1990; Nissen & Corkin, 1985). Similarly, in the auditory domain, comparable cue-based facilitation of target detection is observed between younger and older adults (Singh, Pichora-Fuller, & Schneider, 2008). Although this suggests that selectively orienting attention to a location is preserved in ageing, older adults utilise different brain regions to accomplish the same levels of performance. Notably, older adults exhibit declines in attentional modulation of sensory cortical activity, but exhibit increased prefrontal cortical (PFC) activity during spatial (Geerlings, Saliasi, Maurits, Renken, & Lorist, 2014; Li, Gratton, Fabiani, & Knight, 2013; Madden & Hoffman, 1997; Madden et al., 2007) and feature (Alperin, Mott, Rentz, Holcomb, & Daffner, 2014; Cashdollar et al., 2013; O'connell et al., 2012; Zhuravleva et al., 2014) target detection. Whereas optimal visual target detection performance in younger adults is associated with increased activity in the visual cortex, older adults who exhibit increased PFC activity show improved target detection performance (Allen & Payne, 2012; Madden et al., 2007; Madden, Turkington, Provenzale, Hawk, & Hoffman, 1997). The relationship between increased PFC activity and improved behaviour suggests that this PFC recruitment serves as a compensatory mechanism to offset sensory and/or perceptual deficits in ageing. The differential networks utilised by older adults support a posterior-to-anterior shift in ageing (PASA) model (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008), which proposes that age-related sensory cortical (posterior) declines may be compensated by the recruitment of PFC (anterior) regions to retain performance abilities.

Despite the ability of older adults to utilise compensatory mechanisms under certain conditions, there are many scenarios in which age-related performance in cognitive control abilities in the selective attention domain declines. For example, when target stimuli share features or spatial locations as distracting stimuli, older adults are slower and less accurate in detecting targets in both visual (Hommel, Li, & Li, 2004; Madden & Whiting, 2004; McDowd & Shaw, 2000) and auditory (Duquesnoy, 1983; Singh et al., 2008) domains. Age-related performance declines in target detection occur concomitantly with impaired

(attenuated and/or slowed) neural signatures of expectation, attentional orienting, and selection in the PFC and occipital regions (Kenemans, Smulders, & Kok, 1995; Lorenzo-Lopez et al., 2011; Lorenzo-Lopez, Amenedo, & Cadaveira, 2008; Quigley, Andersen, Schulze, Grunwald, & Muller, 2010; Quigley & Muller, 2014; Zanto et al., 2011). Thus, age-related declines in target detection are associated with alterations in multiple brain regions that span diverse cognitive processes, including expectation, attentional orientation, and selection. Moreover, older adults do not appear to successfully engage compensatory mechanisms when distractors are similar to targets.

When distractors share similar qualities as a target stimulus, this may be considered to be a more difficult task than target detection with more distinct distractors. As such, task difficulty may account for why compensatory mechanisms in ageing are not consistently engaged to uphold performance abilities comparable to younger adults. Indeed, the cognitive reserve hypothesis (Stern, 2002), the compensation-related utilisation of neural circuit hypothesis (CRUNCH; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Lustig, 2005), and the scaffolding theory of ageing and cognition (STAC; Park & Reuter-Lorenz, 2009) all suggest that compensatory mechanisms may be successfully engaged only until a capacity limit is reached. Therefore, it is proposed that older adults utilise and benefit from compensatory mechanisms during tasks with low demands, but exhibit performance declines as task demands increase. In support of this view, compared to younger adults, older adults exhibit a disproportionate decline in performance with increased task difficulty during target detection (Prakash et al., 2009) and discrimination (Wang, Fu, Greenwood, Luo, & Parasuraman, 2012). In accordance with performance declines during high task demands, older adults exhibit slowed neural processing associated with attentional selection (Wang et al., 2012). Whereas younger adults recruit additional PFC and parietal regions under high task demands, older adults do not exhibit such recruitment (Prakash et al., 2009). Because older adults display similar network activity during low task demands as younger adults during high task demands (Prakash et al., 2009), this provides evidence that older adults utilise all available resources during a low-demand task, which prevents the recruitment of additional compensatory mechanisms during high-demand tasks. Moreover, these age-related declines due to increased task difficulty have been associated with reduced grey matter volume (Muller-Oehring, Schulte, Rohlfing, Pfefferbaum, & Sullivan, 2013) and declines in white matter integrity (Bennett, Motes, Rao, & Rypma, 2012) within the PFC and parietal cortical regions that are associated with attentional control. Together, these results support theories and hypotheses that suggest the use of compensatory mechanisms in ageing is limited by cognitive resources, which may become unavailable with increased task demands.

The observed age-related slowing of both neural processes and target detection performance, as described above, reinforces theories that suggest age-related declines in cognitive control stem from slowed processing speed (Salthouse, 1996; Salthouse & Madden, 2007). Indeed, age-related declines in white matter integrity and grey matter volume are known to contribute to decreased processing speed (Rabbitt, Lunn, et al., 2007; Rabbitt, Mogapi, et al., 2007; Turken et al., 2008) and provide an anatomical basis for widespread cognitive control declines in ageing. The consequence of such generalised slowing of neural processing is the increased computational time required for a particular process, making less information available for higher-level functions in a set amount of time. Therefore, older adults require more time to orient attention to a target (Amenedo, Lorenzo-Lopez, & Pazo-Alvarez, 2012), away from a target (Cona, Bisiacchi, Amodio, & Schiff, 2013), and away from distractors (Cashdollar et al., 2013).

Alternatively, the disproportionate negative impact of distractors in ageing also supports theories attributing age-related declines in cognitive control to deficient inhibitory abilities that arise from anatomical and functional decline of the PFC (Dempster, 1992; Hasher et al.,

2007; Hasher & Zacks, 1988; West, 1996). Deficient target detection performance has been observed in ageing concomitantly with a selective decline in suppressing neural activity to irrelevant stimuli. This age-related suppression deficit has been observed in the PFC, parietal, and sensory regions during both visual (Alperin et al., 2013; Daffner, Alperin, Mott, & Holcomb, 2014; Haring et al., 2013) and auditory target detection tasks (Passow et al., 2014). Similar results have been observed with target discrimination tasks such that older adults exhibit declines in performance as well as increased distractor processing in sensory cortical regions (de Fockert, Ramchurn, van Velzen, Bergstrom, & Bunce, 2009; Wais & Gazzaley, 2014a). A common target discrimination task, the Stroop task, requires partici-pants to report the colour of a word and not the word itself. During this task, older adults exhibit diminished ability in inhibiting the irrelevant word and increased interference-related activity as well as increased interference-related extent of activity in the PFC and parietal regions (Langenecker, Nielson, & Rao, 2004; Nielson et al., 2004; Nielson, Langenecker, & Garavan, 2002), providing additional evidence for an age-related decline in suppressing irrel-evant information. These age-related deficits in inhibitory control during target discrimination have been associated with declines in white matter integrity in the anterior corpus callosum (Sullivan, Adalsteinsson, & Pfefferbaum, 2006) as well as within the parietal and occipital regions (Kennedy & Raz, 2009). Importantly, the relationship between age-based declines in inhibitory control and decreased white matter integrity may not be fully attributed to general slowing with age (Wolf et al., 2014). Thus, anatomical declines associated with ageing contribute to inhibitory deficits and slowed processing speed, both of which contribute to deficient cognitive control in ageing.

Overall, research on selective attention and inhibitory control in ageing has shown sce-narios in which older and younger adults exhibit comparable task performance, but differential neural activity profiles. Compared to younger adults, older adults often exhibit decreased posterior (sensory-related) activity concomitantly with increased PFC activity, which serves to compensate for deficient sensory and/or perceptual processes in ageing. However, older adults' use of compensatory neural regions is limited by the amount of cognitive resources, which may become unavailable during increased task demands. The consequence of unavail-able or failed compensatory mechanisms reveals age-related slowing of cognitive processing as well as a selective decline in inhibitory control, both of which contribute to deficient task performance. Importantly, the inability to utilise compensatory mechanisms as well as age-related declines in processing speed and inhibition are related to lower grey matter volume and decreased white matter integrity within the PFC and parietal cortex.

Working Memory

Change detection tasks are often used to assess working memory capacity and its underlying neural mechanisms. Generally, the goal of a change detection task is to determine whether previously presented stimuli that are held for a brief time mentally have changed in some way, such as a shift in features, spatial location, or orientation. Thus, change detection tasks may be referred to as a delayed match to sample task, location matching, N-back, or a same/different task. Given the amount of overlap between selective attention and working memory (Cowan, 1995; Gazzaley & Nobre, 2012), similar age-related declines in working memory may be observed (see also Chapter 3 by Meier & Kane in this volume). Indeed, in line with the target detection paradigms discussed above, older adults may recruit additional PFC and parietal regions to compensate for visual processing declines and retain performance abilities during change detection (Burianova, Lee, Grady, & Moscovitch, 2013; Lee, Grady, Habak, Wilson, & Moscovitch, 2011; Macpherson et al., 2014; Rypma & D'Esposito, 2000) and

verbal working memory (Grossman et al., 2002) tasks, which provide additional support for the PASA model (Davis et al., 2008).

However, older adults may also exhibit increased PFC and parietal activity during change detection tasks concomitantly with performance declines (Ansado et al., 2013; Ansado, Monchi, Ennabil, Faure, & Joanette, 2012; Grady, Yu, & Alain, 2008; Piefke, Onur, & Fink, 2012). This neural recruitment in ageing without a performance benefit is considered failed compensation (Grady, 2012) and may arise when task demands exceed available cognitive resources (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Lustig, 2005; Stern, 2002). Indeed, age-related performance declines in change detection (i.e., working memory) abilities are most pronounced under increased task difficulty (Ansado et al., 2012, 2013; Piefke et al., 2012; Prakash, Heo, Voss, Patterson, & Kramer, 2012; Sander, Werkle-Bergner, & Lindenberger, 2012). Interestingly, high-performing older adults exhibit more 'youth-like' neural activity modulation in the PFC and parietal cortex with increased task difficulty, suggesting that increased cognitive reserve in high-performing older adults may serve to uphold task performance in lieu of compensatory recruitment of regions (Nagel et al., 2009), at least until a resource ceiling is reached (Toepper et al., 2014).

Much research and theory, as described above, indicate that many age-related performance declines in working memory and inhibitory control stem from a lack of cognitive resources to compensate for sensory and/or perceptual deficits. However, age-related recruitment of PFC regions may not always be used to compensate for sensory and/or perceptual declines, but rather, compensate for reduced PFC resources and/or inefficient PFC processing. Evidence for this exists in the well-documented hemispheric asymmetry reduction in older adults (HAROLD) model (Cabeza, 2002), where younger adults exhibit unilateral PFC activity to achieve task goals and older adults recruit contralateral (i.e., bilateral) PFC activity to achieve the same goals. Notably, this reduced asymmetry in ageing has been linked to an age-related compensation for inefficient use of PFC resources such that low-performing older adults exhibit unilateral PFC activity similar to younger adults, whereas high-performing older adults utilise bilateral PFC regions (Cabeza, Anderson, Locantore, & McIntosh, 2002). This reduced asymmetry in ageing has been observed during working memory (Dixit et al., 2000; Piefke et al., 2012; Reuter-Lorenz et al., 2000) and inhibitory control processes (Langenecker et al., 2004; Nielson et al., 2002), and as such, may reflect a general compensatory response for cognitive control declines in ageing.

In order to better understand cognitive control changes in ageing, it is important to distinguish whether age-related declines stem from deficient higher-order processes or an inability to fully compensate for lower-level (i.e., sensory/perceptual) deficits. When age-related sensory and perceptual differences are equated and general age-related slowing has been accounted for, older adults still exhibit deficient working memory performance along with decreases in attentional modulation of visual cortical activity (Zanto et al., 2010). Changes in attentional modulation of the visual cortex have been attributed to declines in functional interactions with the PFC (Zanto, Chadick, Satris, & Gazzaley, 2013; Zanto, Rubens, Thangavel, & Gazzaley, 2011), supporting models that posit age-based declines in working memory stem from deficient communication between the PFC and the sensory cortex (Gazzaley, 2012). This deficit in working memory in ageing extends to a related cognitive control ability, mental imagery, which is marked by an age-related decline in the selectivity of representations in the visual cortex during imagery and a corresponding reduction in selectivity of functional connectivity between the PFC and the visual cortex (Kalkstein, Checksfield, Bollinger, & Gazzaley, 2011).

Older adults also exhibit a disproportionate decline in working memory performance in the presence of distractors during the encoding period, which is manifest through a selective decline in inhibiting sensory cortical activity to irrelevant stimuli (Clapp & Gazzaley, 2012;

Deiber et al., 2010; Gazzaley et al., 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005). Importantly, this deficit in suppressing irrelevant sensory information not only predicts working memory decline due to distraction, but is also related to decreased activity in the PFC as well as decreased functional connectivity between the sensory cortex and the PFC (Campbell, Grady, Ng, & Hasher, 2012; Chadick, Zanto, & Gazzaley, 2014). Because age-related declines in sensory and/or perceptual processes would equally affect processing of attended and ignored stimuli, it is unlikely that such changes would underlie a selective age-related decline in suppressing irrelevant information. Thus, deficient top-down communication between the PFC and the sensory cortex appears to be independent of sensory and/or perceptual decline and plays a role in decreased working memory and inhibitory control in ageing.

Suppression deficits in ageing during working memory encoding are observed as alterations in both amplitude and latency of neural activity to irrelevant information (Clapp & Gazzaley, 2012; Deiber et al., 2010; Gazzaley et al., 2008). Therefore, these findings help reconcile models that suggest age-related declines in cognition result from deficient inhibition (Hasher et al., 2007; Hasher & Zacks, 1988) or slowed processing speed (Salthouse, 1996; Salthouse & Madden, 2007). In line with other models of cognitive ageing that emphasise declines in PFC structure, age-related declines in working memory and top-down suppression signals between the PFC and the visual cortex have been associated with decreased grey matter volume and white matter integrity within the PFC (Chadick et al., 2014). Thus, age-related declines in the PFC structure leads to deficient top-down modulation of sensory cortical activity, which in turn results in lowered working memory performance.

It is interesting to note that age-related declines in top-down modulation of sensory cortical activity occur not only during attentional orientation and selection processes (i.e., 100–500 ms post stimulus onset; Deiber et al., 2010; Gazzaley et al., 2008), but also occur in anticipation of stimulus onset to impact both working memory and perceptual performance, suggesting the presence of an expectation deficit associated with ageing (Bollinger, Rubens, Masangkay, & Gazzaley, 2011; Sander et al., 2012; Zanto et al., 2011). Accordingly, predictive information does not help older adults suppress neural activity to expected irrelevant distractions, nor does it help improve working memory performance (Clapp & Gazzaley, 2012; Zanto, Hennigan, Ostberg, Clapp, & Gazzaley, 2010). Similarly, older adults, unlike younger adults, do not benefit from retrospective cues that would otherwise enhance working memory abilities by orienting attention away from irrelevant working memory representations (Rizio & Dennis, 2014). This age-related decline in suppressing working memory representations result from an inability to recruit the PFC and parietal regions that are selectively involved in suppressing irrelevant working memory representations (Rizio & Dennis, 2014). Together, the failure to ignore impending distractions or release irrelevant information from working memory may overload limited memory stores and hinder the ability to remember relevant information (Gazzaley et al., 2005; Schmitz, Cheng, & De Rosa, 2010). It is noteworthy that the negative impact of reduced inhibitory control in ageing extends beyond the brief time periods involved in working memory, and also results in deficient long-term memory retrieval (Wais, Martin, & Gazzaley, 2012), which is associated with impaired communication between the PFC, sensory cortex, and medial temporal lobe (Wais & Gazzaley, 2014a).

Overall, research on working memory in ageing has shown remarkable overlap with findings from inhibitory control research. Although there is less evidence for age-equivalent working memory performance compared to inhibitory control during target detection, when it does occur, older adults often exhibit increased PFC activity. This increased activity serves to compensate for deficient sensory/perceptual processes, reduced PFC resources, and/or inefficient PFC processes in ageing. However, the age-related recruitment of compensatory

neural regions is limited by the amount of cognitive resources available, which decline across the lifespan in response to anatomical changes, especially in the PFC. Therefore, older adults have less resources available for compensation during increased task demands. The consequences of unavailable or failed compensatory mechanisms reveal age-related declines in PFC modulation of sensory cortical activity, which would normally serve working memory performance by enhancing representations of relevant stimuli and suppressing irrelevant stimuli. These declines in top-down modulation of sensory processes are also associated with anatomical changes in the PFC, notably, decreased grey matter volume and white matter integrity.

Multitasking and Task Switching

Multitasking refers to an aspect of cognitive control that is characterised by dividing attention between multiple skills, tasks, or cognitive sets, whereas task switching refers to a type of multitasking that involves shifting between multiple skills, tasks, or cognitive sets (see Chapter 2 by Monsell in this volume). In line with research from the single-task paradigms discussed above, older adults may recruit the PFC and parietal regions as a compensatory mechanism to support multitasking performance abilities (Fernandes, Pacurar, Moscovitch, & Grady, 2006; Hartley, Jonides, & Sylvester, 2011; Wild-Wall, Hahn, & Falkenstein, 2011), especially during task switching (DiGirolamo et al., 2001; Goffaux, Phillips, Sinai, & Pushkar, 2008; Smith et al., 2001). Yet, age-related performance declines in multitasking become pronounced with increased task difficulty (McDowd & Craik, 1988). There is evidence that these age-related declines may stem from generalised slowing because older adults respond slower to a second task when the onset between tasks decreases (Allen, Smith, Vires-Collins, & Sperry, 1998; Glass et al., 2000). However, when generalised slowing is accounted for, age-based multitasking performance declines persist (Verhaeghen, Steitz, Sliwinski, & Cerella, 2003), which may reflect deficient task switching processes (Glass et al., 2000; Hartley & Little, 1999) that arise from reduced PFC engagement (Anguera et al., 2013) as well as reduced functional connectivity within the PFC and parietal cortex networks (Madden et al., 2010). Moreover, when older adults are required to disengage a secondary task and re-engage a primary task, they fail to dynamically allocate attention and switch between functional brain networks involving the PFC and the sensory cortex (Clapp, Rubens, Sabharwal, & Gazzaley, 2011). Thus, multitasking declines in ageing support models of cognitive ageing that attribute cognitive deficits to slowed processing speed (Salthouse & Madden, 2007; Salthouse, 1996) and deficient attentional orienting/task switching through diminished communication abilities between the PFC and the sensory cortex (Gazzaley, 2012).

Enhancing Cognitive Control in Ageing

Although many aspects of cognitive control decline with age, there is mounting evidence that the brain remains plastic throughout our lifespan, and cognitive control abilities may be maintained or recovered (see also Chapter 28 by Spencer-Smith & Klingberg in this volume). One of the most well-documented means of retaining or regaining cognitive control in ageing is through physical exercise. Physical exercise, notably cardiorespiratory and resistance training (Kelly et al., 2014), has been associated with increased grey and white matter volume, particularly in the PFC (Colcombe et al., 2006). As such, physical exercise improves cognitive function in ageing, and most prominently, cognitive control functions (Colcombe & Kramer, 2003). This includes improved inhibitory control (Dustman et al., 1984), working memory (Fabre, Chamari, Mucci, Massé-Biron, & Préfaut, 2002; but also see

Smith et al., 2010), and multitasking/task switching ability (Hawkins, Kramer, & Capaldi, 1992), which may arise from increased activity in the PFC and parietal cortex in older adults who exercise (Colcombe et al., 2004). It is interesting to note that physical exercise appears to benefit the brain regions and corresponding cognitive functions that are most affected in ageing.

In addition to physical exercise, cognitive exercise (also referred to as cognitive training or exergaming) may also help counteract age-related declines in various cognitive control abilities (for reviews, see Brehmer, Kalpouzos, Wenger, & Lövdén, 2014; Lampit, Hallock, & Valenzuela, 2014; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009). As discussed throughout this chapter, perceptual declines in ageing may contribute to cognitive performance declines, as limited cognitive resources may be usurped to compensate for perceptual deficits. Fortunately, perceptual training in older adults can improve perceptual abilities such that after training, older adults get better at discriminating two stimuli with similar features (Berry et al., 2010). The consequence of improved perceptual performance in older adults results in a transfer of benefit to improved visual working memory performance due to more efficient sensory processing in the visual cortex (Berry et al., 2010).

Aside from perceptual declines in ageing, another prominent source of age-related declines in cognitive control has been attributed to slow processing speed. Targeting this decline, cognitive speed of processing training in older adults not only speeds cognitive processing, but translates to improved everyday abilities such as driving performance (Ball, Edwards, & Ross, 2007), which has been attributed to speeded multitasking abilities (Edwards, Ruva, O'Brien, Haley, & Lister, 2013). Interestingly, auditory cognitive training that emphasises speed of processing enables faster and less variable neural responses within older adults' brainstem, and these benefits extend to improved working memory performance (Anderson, White-Schwoch, Parbery-Clark, & Kraus, 2013).

Cognitive training appears to be potentially beneficial for whatever cognitive domain is targeted, and in older adults, declines in inhibitory control are often in need of improvement. It was recently shown that distraction training in aged humans and aged rats shows improved inhibitory control concomitantly with sharpened sensory receptive fields (in aged rats) and decreased PFC activity to distractors (in aged humans ; Mishra, de Villers-Sidani, Merzenich, & Gazzaley, 2014). Interestingly, distraction training also resulted in a transfer of benefit to working memory and sustained attention abilities (Mishra et al., 2014). Similarly, age-related declines in multitasking performance have also been targeted by cognitive training in older adults, which demonstrated that improved performance occurs concomitantly with PFC activity profiles that become more similar to younger adults (Anguera et al., 2013; Erickson et al., 2007). Moreover, multitasking training has been shown to yield a transfer of benefit to working memory and attention abilities (Anguera et al., 2013; Basak, Boot, Voss, & Kramer, 2008).

Although more research will be needed to fully understand the how long cognitive training benefits may last after training has ceased, research thus far has reported post-training benefits that last from at least 6 months (Anderson, White-Schwoch, Choi, & Kraus, 2014; Anguera et al., 2013) to 2 years (Ball et al., 2007). Furthermore, it is unclear in which scenarios cognitive training will enhance untrained domains, as a transfer of benefit is not always observed, or is minimal (Gross et al., 2012; Verhaeghen, Marcoen, & Goossens, 1992). Finally, additional research will be required to understand any synergistic effects that may be gained by combining both physical and cognitive exercise. It may be that the combination of both physical and cognitive exercise will result in optimal cognitive control gains such that physical exercise increases the potential for neurogenesis/synaptogenesis, while cognitive exercise guides it to induce more targeted changes (Bamidis et al., 2014; Fissler, Küster, Schlee, & Kolassa, 2013).

Summary

Whereas behavioural performance measures do not always identify age-related declines in cognitive control abilities, neuroimaging data often uncover differential neural activity profiles between younger and older adults when engaged in demanding tasks. Owing to decreased grey and white matter volume in ageing, older adults may recruit additional neural regions, typically in the PFC, to support performance by compensating for declines in perception or inefficient/reduced cognitive resources. Because cognitive resources are limited, compensatory mechanisms are not always available under increased task demands. Thus, cognitively demanding tasks are among the most likely to uncover age-related declines in cognitive control. Fortunately, the brain remains plastic throughout the lifespan, and many age-related declines in cognitive control may be reversed through physical exercise and/or cognitive training.

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