

Benefits of regular aerobic exercise for executive functioning in healthy populations

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Abstract Research suggests that regular aerobic exercise has the potential to improve executive functioning, even in healthy populations. The purpose of this review is to elucidate which components of executive functioning benefit from such exercise in healthy populations. In light of the developmental time course of executive functions, we consider separately children, young adults, and older adults. Data to date from studies of aging provide strong evidence of exercise-linked benefits related to task switching, selective attention, inhibition of prepotent responses, and working memory capacity; furthermore, cross-sectional fitness data suggest that working memory updating could potentially benefit as well. In young adults, working memory updating is the main executive function shown to benefit from regular exercise, but cross-sectional data further suggest that task-switching and posterror performance may also benefit. In children, working memory capacity has been shown to benefit, and cross-sectional data suggest potential benefits for selective attention and inhibitory control. Although more research investigating exercise-related benefits for specific components of executive functioning is clearly needed in young adults and children, when considered across the age groups, ample evidence indicates that regular engagement in aerobic exercise can provide a simple means for healthy people to optimize a range of executive functions.

Keywords Chronic physical activity · Executive functions · Cognitive control · Children · Young adults · Older adults

Mounting evidence indicates that regular engagement in exercise can confer a benefit for some of the executive functions known to develop late (throughout childhood and adolescence) and to deteriorate early in the course of healthy aging (see, e.g., Colcombe & Kramer, 2003; Tomporowski, Lambourne, & Okumura, 2011). *Executive functions* are strategic in nature and depend on higher-order cognitive processes that underpin planning, sustained attention, selective attention, resistance to interference, volitional inhibition, working memory, and mental flexibility (reviewed in Chan, Shum, Touloupoulou, & Chen, 2008). These functions are crucial for human survival and depend largely on the frontal lobes, with support from temporal and parietal cortices (reviewed in Miyake et al., 2000). While the majority of the data to date supporting exercise-related benefits in executive functioning within healthy populations have involved older adults, evidence is beginning to emerge that regular engagement in aerobic exercise might also be beneficial for such functioning in young adulthood, despite executive functioning peaking developmentally in that age group (Åberg et al., 2009; Hansen, Johnsen, Sollers, Stenvik, & Thayer, 2004; Kamijo & Takeda, 2010; Themanson & Hillman, 2006; Themanson, Pontifex, & Hillman, 2008). Given the increasingly sedentary disposition of Western society (World Health Organization, 2012a, 2012b) and the rapidly aging population (United Nations Population Division, 2009), it is in the interests of health providers and the public that the links between exercise and executive functioning across the lifespan be thoroughly examined.

The purpose of this review is to consider which components of executive functioning have been shown to improve with regular aerobic exercise in healthy populations. We focus on executive functions in particular because evidence suggests that they may be more sensitive to exercise than basic perceptual and motor functions, not just in populations

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whose executive functions are still developing or are in decline (see Colcombe & Kramer, 2003; Kramer et al., 1999; Tomporowski, et al., 2011), but also in populations at peak in terms of executive functioning (see Hillman, Erickson, & Kramer, 2008; Hillman, Kramer, Belopolsky, & Smith, 2006). In addition, we focus on aerobic exercise, rather than resistance or other types of training, because aerobic exercise is readily accessible, requires no specialist knowledge or equipment, and is more directly linked to cardiovascular fitness, which has also been linked to executive function capabilities. Finally, we focus on the longer-term effects associated with regular exercise, rather than on the transient effects that might be observed during or immediately after a period of activity, since it is chronic influences that could potentially provide insight toward a useful method for alleviating the current public health crisis associated with an increasingly inactive, aging society.

Although the influence of exercise on the brain and cognition has been the subject of several previous reviews and meta-analyses (e.g., Angevaren, Aufdemkampe, Verhaar, Aleman, & Vanhees, 2008; Chodzko-Zajko & Moore, 1994; Etnier & Chang, 2009; Etnier, Nowell, Landers, & Sibley, 2006; Etnier et al., 1997; Kramer, Erickson, & Colcombe, 2006; P. J. Smith et al., 2010; Voss, Nagamatsu, Liu-Ambrose, & Kramer, 2011), interpretation of the results with regard to general public health is clouded, due to three main factors. The first factor relates to an intermixing of studies involving clinical and nonclinical populations. Because nonclinical populations represent the greatest proportion of the overall population and, therefore, pose the most costly public health threat, it is important to separately consider the effects of regular exercise on executive functioning in these populations. The second factor relates to the intermixing of studies involving acute and chronic exercise. Transient benefits afforded by ongoing or recent exercise do not necessarily inform us about the longer-term effects of regular exercise. The third factor relates to the inclusion of studies focusing on either global measures of executive functioning or composite scores (derived from multiple tasks within comprehensive cognitive test batteries). Given that executive functioning reflects a range of distinct cognitive processes, assessing only the global construct may dilute some of the more specific cognitive benefits of exercise. As an additional point, it should be noted that many previous reviews did not differentiate between distinct exercise-related variables (in particular, aerobic fitness vs. engagement in aerobic exercise), even though it is well established that aerobic fitness depends in part on genetic factors (e.g., sex; Levine, 2008), thus fitness level does not necessarily reflect exercise engagement. In the present review, we specify the exercise-related variable linked to each type of executive function so that the reader can gain a clearer understanding of what is known so far.

The first part of this review summarizes evidence that provides the foundation critical for understanding how regular aerobic exercise might benefit executive functioning. After considering the benefits related to the structure and basic function of the brain, we go on to examine the specific cognitive processes sensitive to regular exercise, in an effort to understand whether the anatomical and physiological benefits translate into improvements in executive control processes, including task switching, selective attention, inhibitory control, and working memory. Establishing connections between regular exercise and these executive functions is important because their efficacy has been linked to daily activities such as driving (Anstey & Wood, 2011; Mäntylä, Karlsson, & Marklund, 2009), academic performance (reviewed recently in Best, Miller, & Naglieri, 2011), and gait (Yogev-Seligmann, Hausdorff, & Giladi, 2008).

Aerobic exercise and the brain

Support for the idea that higher levels of aerobic activity may be associated with superior brain structure has been gained through cross-sectional studies in older adults and children (for a recent review, see Voss, Nagamatsu, et al., 2011). For example, studies of aging utilizing magnetic resonance imaging (MRI) have shown that, as compared with unfit, highly fit older adults exhibit the following: less age-related atrophy in the prefrontal and temporal cortices (Colcombe et al., 2003); preserved neural tracts connecting the prefrontal cortex to other regions of the brain (Marks, Madden, Bucur, & Provenzale, 2007); superior white matter integrity in the corpus callosum (Johnson, Kim, Clasey, Bailey, & Gold, 2012); greater gray matter density in the frontal, temporal, and parietal cortices (Gordon et al., 2008); and greater hippocampal volumes (Erickson et al., 2009). Furthermore, researchers into aging have found that physically active older adults have both higher circulating neurotrophin levels and gray matter volumes in the prefrontal and cingulate cortex (Flöel et al., 2010). In line with these studies of aging, developmental research has linked fitness levels in children to the volumes of the dorsal striatum (Chaddock, Erickson, Prakash, VanPatter, et al., 2010) and the hippocampus (Chaddock, Erickson, Prakash, Kim, et al., 2010), both of which were also linked to cognitive performance (selective attention and memory, respectively). Although these aging and developmental studies employed cross-sectional designs and, thus, the reported effects may reflect some factor other than aerobic activity level (e.g., nutrition, education, or genetics, including intrinsic fitness), together the findings point to potential anatomical changes that could support exercise-related improvements in executive functioning in older adults and children.

To assess whether aerobic exercise actually improves the structural integrity of the aging human brain, which

potentially could allow for cognitive improvements, researchers have conducted several randomized controlled trials in which initially sedentary older participants were assigned to aerobic exercise (typically, brisk walking) or strength and flexibility training groups. On one such trial, older adults completed three 1-h sessions of exercise a week for 6 months (Colcombe et al., 2006). MRI brain scans conducted before and after the intervention indicated that, as compared with the participants in the strength and flexibility training group, those who had been aerobically exercising for 6 months showed significant increases in gray and white matter volumes in areas of the frontal and temporal lobes associated with aspects of executive control, which are known to deteriorate with advancing age. More recent randomized controlled trials of 12-month duration provide further support for the contention that aerobic exercise ameliorates age-related neurological decline. For example, Erickson et al. (2011) showed that 12 months of aerobic exercise led to significant increases in anterior hippocampal volume in older adults and that such increases were associated with improvements in spatial memory. In addition, Voss et al. (2010) showed that while both the aerobic and strength/flexibility exercise groups exhibited, at the end of the 12-month intervention, significant increases in functional connectivity (as measured by correlation of the low-frequency BOLD signal when the brain was under low, nonexecutive cognitive demand), only those in the aerobic exercise group exhibited improved connectivity between the left and right prefrontal cortices, two areas that are crucial to the effective functioning of the fronto-executive network.

A poverty of published intervention studies in young adults and children leaves the influences of aerobic exercise on the brain less clear in these age groups. In one randomized controlled trial, 30 sedentary young adults underwent MRI scans before and after either an aerobic exercise intervention involving 30 sessions of an aerobic dance class for 4.5 months or no intervention (Gondoh et al., 2009). While the pre- and postintervention brain scans revealed no change in gray matter volumes for those in the exercise group, the scans showed a *decrease* in the volume of the left insula for those in the control group. This pattern was interpreted as evidence for a neuroprotective effect of aerobic exercise in young adulthood. Another intervention study in relatively young adults (21–45 years) found that 3 months of aerobic exercise led to increased cerebral blood volume in the hippocampal dentate gyrus, which was shown in mice (juvenile to young adult) to be an indicator of exercise-induced neurogenesis in the dentate gyrus (although it should be noted that the rodent experiment entailed just 2 weeks of aerobic exercise; Pereira et al., 2007).

Further support for exercise-related benefits in brain blood supply comes from two recent studies showing associations with aerobic fitness. Ainslie et al. (2008) measured

resting blood flow velocity through the middle cerebral artery in 307 sedentary and aerobically trained men. Although this measure does not provide region-specific information regarding cerebral blood flow, it is considered a good indicator of global cerebral blood perfusion (reviewed in Ogoh & Ainslie, 2009) and, thus, may be informative with regard to the higher metabolic demand associated with executive functioning. Ainslie and colleagues found that, although resting cerebral blood flow velocity decreases with advancing age, aerobically trained men between 18 and 79 years of age had consistently higher velocities than their sedentary peers. Another study that assessed only relatively older adults (50–90 years) found associations between aerobic fitness and other measures of cerebrovascular function (arterial blood pressure and related changes in blood flow), which partially mediated a positive association between fitness and composite scores of executive functioning (Brown et al., 2010). Thus, superior cerebrovascular function may potentially assist toward better executive functioning in older adults who exercise regularly.

Aerobic exercise and executive functioning

Given the evidence supporting exercise-related benefits in brain structure and mechanical function, it is not surprising that benefits in cognitive function have also been reported, particularly in older adults. Using composite scores of executive functioning, researchers have shown that aerobic fitness is linked to efficacy of the overall cognitive construct in older adulthood (Brown et al., 2010; Netz, Dwolatzky, Zinker, Argov, & Agmon, 2010). Other studies have also reported positive links between aerobic fitness or exercise and older adults' performance on standard clinical tests of executive functioning, including the Wisconsin card sorting task (Albinet, Boucard, Bouquet, & Audiffren, 2010; Gordon et al., 2008), the REY Auditory Verbal Learning Test (Trials 7 and 10; see Kramer et al., 2001), the Trails B test, the Digit Symbol test, and the verbal fluency test (Trails B, Digit Symbol, verbal fluency, Barnes, Yaffe, Satariano, & Tager, 2003; Trails B, Digit Symbol, Blumenthal et al., 1991). In addition, academic achievement in children has been positively linked to both chronic engagement in physical activity (reviewed in Tomporowski et al., 2011) and aerobic fitness (Castelli, Hillman, Buck, & Erwin, 2007); and a recent study linked successful street crossing, particularly when distracted, to aerobic fitness (Chaddock, Neider, Lutz, Hillman, & Kramer, 2012b). Together, these data support the idea that regular exercise can aid performance with respect to the broad construct of executive functioning. However, the multifaceted nature of these tasks makes it difficult to discern which cognitive functions underlie the reported links. Below, we review the evidence to date from

exercise–cognition research using simple cognitive tests in an effort to determine which components of executive functioning benefit from regular exercise (see Table 1). Three specific components of executive functioning will be reviewed, since they have been tested most extensively in the exercise–cognition literature and they have also been linked to effective performance of daily activities: (1) task switching, (2) selective attention and inhibitory control, and (3) working memory.

Task switching

The typical task-switching paradigm involves responding to similar target stimuli, but on the basis of one of two different rules. For example, a participant might be instructed as follows: If the target digit is green, indicate whether the digit is greater or less than 5; if the target digit is red, indicate whether the digit is even or odd. On nonswitch trials, the response rule remains the same as on the previous trial; on switch trials, the response rule changes. The difference in reaction times between rule switch and nonswitch trials is referred to as the *switching cost*, because it reflects the degree of slowing arising from the need to mentally change task goals before responding. Such mental-set-shifting requires executive control, including volitional inhibition, working memory, and mental flexibility; thus, smaller switching costs can be interpreted as reflecting more efficient executive functioning (Banich, 2009; Monsell, 2003). Consistent with this interpretation, larger switching costs have been demonstrated in populations widely believed to have impaired executive function, including older adults (e.g., Cepeda, Kramer, & Gonzalez de Sather, 2001).

Exercise–cognition researchers who utilized task-switching paradigms have reported some promising results, particularly in older adults. While behavioral data from cross-sectional studies involving young and older adults indicate that the magnitude of switching costs does not depend on the amount of self-reported physical activity per week in either young or older adults (Hillman, Kramer, et al., 2006; Themanson, Hillman, & Curtin, 2006), event-related potential (ERP) data collapsed across young and older adults from the Hillman, Kramer, et al. study supported shorter P3 latencies during task switching in more active participants, and data from the Themanson et al. (2006) study supported a positive association between physical activity and error-related negativity (which is thought to reflect efficiency of error detection and ability to deal with the conflict arising during switch trials). Furthermore, a large randomized controlled trial on which sedentary older adults engaged in either aerobic exercise (brisk walking) or strength and flexibility training for 6 months indicated that aerobic exercisers showed a significantly greater reduction in the magnitude of the switching cost, as compared with

those in the strength and flexibility group, at the end of the intervention (see also Hawkins, Kramer, & Capaldi, 1992; Kramer et al., 2001). In summary, it seems that older adults can benefit from regular physical activity in terms of task-switching performance; however, it is not clear that young adults reap such benefits (regarding fitness, see Scisco, Leynes, & Kang, 2008). A more recent young adult study found that task-switching performance does depend on physical activity levels (Kamijo & Takeda, 2010). However, in this study, task switching was predictable because a switch occurred every two trials; thus the exercise-related benefits in performance may have reflected better preparatory processes or working memory, rather than switching capabilities specifically (note that the same argument can be made regarding Hawkins et al., 1992). Regarding children, a lack of published studies utilizing task-switching paradigms prevents comment, but given the lack of improvement in switching costs seen throughout childhood (Kray, Karbach, & Blaye, 2012), exercise-related benefits may be unlikely in healthy children.

Selective attention and inhibitory control

In this review, tasks that tap selective attention and inhibitory control capabilities are grouped together because their designs typically prevent separate assessment of the two constructs (e.g., Sanders & Lamers, 2002; Shiu & Komblum, 1996). In other words, successful performance of these tasks depends on both selective attention and inhibitory control, although it could be argued that some tasks rely more on one construct than on the other (Schulte et al., 2009). For example, tasks that involve suppression of stimuli with prepotent response links presumably rely more on motor inhibition than on selective attention (Eimer, Hommel, & Prinz, 1995), whereas tasks that involve suppression of stimuli with relatively arbitrary response links presumably rely more on selective attention than on motor inhibition (discussed in Machado, Devine, & Wyatt, 2009). In the present section, we review studies that investigated the relationships between regular exercise and performance on tasks that entail suppressing more prepotent responses (Stroop, go/no-go, stop signal, flanker arrows), as well as those that involve stimuli with more arbitrary response links (flanker letters, flanker colors).

The most common version of the Stroop (1935) task involves asking participants to indicate the color of the ink that a word appears in by either saying it aloud or pressing a specific button. The key condition in this task is when the ink color does not match the identity of the color word (e.g., “red”)—that is, when there is interference between the distracting word (“red”) and the target ink color (black). Performance during this interference condition is considered an effective measure of executive functioning because, in

Table 1 Aerobic exercise and executive functioning studies

Task	Study	Ages	N	Exercise type or measure	De-sign	Results	Behavioural	EEG	fMRI	p
TASK SWITCHING										
	Themanson et al., 2006	60–71	32	Self-reported PA (Yale Survey for Older Adults)	CS	Association between kilocalories/week and:	Switch cost Accuracy	Smaller ERN		*
	Hillman et al., 2006a	18–21	34	Self-reported PA (Yale Survey for Older Adults)	CS	Association between kilocalories/week and:	Switch cost Accuracy	Smaller ERN		*
	Kramer et al., 2001	~64 ~19	32 34	Self-reported PA (Yale Survey for Older Adults)	CS	Compared to sedentary, active adults showed: After training, aerobic exercise group showed:	Switch cost Accuracy	Faster P3		*
	Kamijo & Takeda, 2010	~21	40	Aerobic exercise (brisk walking) on 3 days/week for 6 months	RCT	Compared to sedentary, active adults showed:	Reduced switch cost			**
	Seisco et al., 2008	18–28	52	Self-reported PA (International Questionnaire)	CS	Compared to low fit (<30th percentile), high fit (>70th percentile) showed:	Smaller switch cost	No difference in ERP measures		n.s.
	Dustman et al., 1984	55–70	13	Aerobic exercise (brisk walking) 60 min/day, 3 days/week, 4 months	CS	After training, aerobic exercise group showed:	No difference in RT or accuracy	No difference in ERP measures		n.s.
SELECTIVE ATTENTION AND INHIBITION										
Stroop	Smiley-Oyen et al., 2008	64–74	28	Aerobic exercise (brisk walking) 30 min/day, 3 days/week, 10 months	RCT	After training, aerobic exercise group showed:	Reduced interference			***
	Prakash et al., 2011	60–75	70	Aerobic exercise (VO _{2max} estimate, Rockport test)	RCT	Association between VO _{2max} and:	Reduced interference Improved accuracy			***
	Buck et al., 2008	7–12	74	Aerobic fitness (PACER test)	CS	Association between aerobic fitness and:	Less interference Higher accuracy			**
	Castelli et al., 2011	7–9	59	Aerobic fitness (various) ~75 min/day, 5 days/week, 9 months	CS	Association between aerobic fitness and:	Items reported in 45 sec across conditions			*
	Colcombe et al., 2004 Study 1	55+	41	Aerobic fitness (VO _{2max} estimate, Rockport test)	RUT	Association between increased aerobic fitness and:	Interference effect			n.s.
	Colcombe et al., 2004 Study 2	58–77	29	Aerobic exercise (brisk walking)	RCT	Compared to low fit, high fit (median split) showed:	Items reported in 45 sec			n.s.
Flanker	Colcombe et al., 2004 Study 1	55+	41	Aerobic fitness (VO _{2max} estimate, Rockport test)	CS	Compared to low fit, high fit (median split) showed:	Smaller flanker effects			*
	Colcombe et al., 2004 Study 2	58–77	29	Aerobic exercise (brisk walking)	RCT	After training, aerobic exercise group showed:	Smaller flanker effects			*
								Greater task-relevant activation in MFG, SFG, SPL; less activation in ACC		**
								Greater task-relevant PFC activation		**

Table 1 (continued)

Task	Study	Ages	N	Exercise type or measure	De-sign	Results	Behavioural	EEG	fMRI	p
				40 min/day, 3 days/week, 6 months						
	Hillman et al., 2006b	15–71	241	Self-reported PA that induced sweating	CS	Association between frequency/week and:	Smaller flanker effects in participants over 40			**
	Thermonson et al., 2008	18–25	72	Aerobic fitness (VO _{2max} test)	CS	Association between VO _{2max} and:	Greater post-error accuracy when instructed to maximize accuracy	Larger ERN when instructed to maximize accuracy		*
	Voss et al., 2011b	9–10	36	Aerobic fitness (VO _{2max} test)	CS	Compared to low fit (<30th percentile), high fit (>70th percentile) children showed:	Higher accuracy rates, particularly on incompatible trials			*
	Chaddock, Erickson, et al., 2012a	9–10	32	Aerobic fitness (VO _{2max} test)	CS	Compared to low fit (<30th percentile), high fit (>70th percentile) children showed:	Maintenance of accuracy rates on incompatible trials across the test blocks			*
	Chaddock et al., 2010a	9–10	55	Aerobic fitness (VO _{2max} test)	CS	Compared to low fit (<30th percentile), high fit (>70th percentile) children showed:	Smaller flanker effects (based on proportional interference scores)			*
	Pontifex et al., 2011; Wu et al., 2011	8–11	48	Aerobic fitness (VO _{2max} test)	CS	Compared to low fit (<30th percentile), high fit (>70th percentile) children showed:	Higher accuracy rates and less variable response latencies	Faster, smaller N2; faster, larger P3; smaller ERN		***
Arbitrary stimulus–response mapping (e.g., letters)	Kramer et al., 2001	60–75	58	Aerobic exercise (brisk walking) 3 days/week, 6 months	RCT	After training, aerobic exercise group showed:	Smaller flanker effects			*
	Voelcker-Rehage et al., 2010	62–79	72	Aerobic fitness (VO _{2max} test)	CS	Association between VO _{2max} and:	RTs on incompatible trials			**
	Hillman et al., 2004	~67	24	Self-reported PA (Yale Survey for Older Adults)	CS	Comparison of low, moderate, and high fit showed:	No differences in RTs or accuracy			n.s.
	Thermonson & Hillman, 2006	~20	28	Aerobic fitness (VO _{2max} test)	CS	Compared to low fit, high fit (>80th percentile) showed:	More post-error slowing	Smaller ERN		**
	Hillman et al., 2009	8–11	38	Aerobic fitness (PACER test)	CS	Compared to low fit (bottom 10%), high fit (top 10%) showed:	Higher accuracy rates	Larger P _e Larger P3 Smaller ERN		** * *
Stop-signal	Kramer et al., 2001	60–75	58	Aerobic exercise (brisk walking), 3 days/week, 6 months	RCT	After training, aerobic exercise group showed:	Reduced stop signal RTs	Larger P _e		**
Go/no-go	Smiley-Oyen et al., 2008	64–74	28	Aerobic exercise (brisk walking) 30 min/day, 3 days/week, 10 months	RCT	After training, aerobic exercise group showed:	No change in go/no-go RT			n.s.

Table 1 (continued)

Task	Study	Ages	N	Exercise type or measure	De-sign	Results	Behavioural			p
							EEG	fMRI	p	
WORKING MEMORY										
N-back task										
2-back	Voelcker-Rehage et al., 2010	62–79	72	Aerobic fitness (VO ₂ max test)	CS	Association between VO ₂ max and: After training, aerobic exercise group showed.	Accuracy		*	
2-back	Hansen et al., 2004	18–22	21	Aerobic exercise (unspecified) 3 hours/week, 2 months	NCT	After training, aerobic exercise group showed.	Improved accuracy		***	
2-back	Stroth et al., 2010	17–47	47	Aerobic exercise (running) on ~3 days/week, 4 months	NCT	After training, aerobic exercise group showed.	Faster RTs		*	
Digit Span										
Forward & Backward	Blumenthal et al., 1991	60–83	33	Aerobic exercise (cycling, walking, jogging) 45 min/day, 3 days/week, 4 months	RCT	After training, aerobic exercise group showed.	No change in forward or backward digit span		n.s.	
Forward	Williams & Lord, 1997	60+	71	Aerobic exercise (see paper) 60 min/day, 2 days/week, 12 months	RCT	After training, aerobic exercise group showed.	Longer forward digit spans		**	
Backward	Weuve et al., 2004	70+	16382	Telephone survey of PA levels	CS	Association between higher levels of PA and:	Longer backward digit spans		***	
Sternberg task										
	Kamijo et al., 2010	~20	64	Aerobic fitness (VO ₂ max test)	CS	Compared to low fit, high fit (median split) showed:	No difference in RT or accuracy		n.s.	Smaller CNV under speed instructions **
	Kamijo et al., 2011	7–9	20	Aerobic exercise (various) ~75 min/day, 5 days/week, 9 months	RCT	After training, aerobic exercise group showed:	Improved accuracy		**	Larger initial CNV **

Note. CS = cross-sectional; RCT = randomized controlled trial; NCT = non-randomized controlled trial; PA = physical activity; VO₂max = maximal oxygen uptake; PFC = prefrontal cortex; MFG = middle frontal gyrus; SFG = superior frontal gyrus; SPL = superior parietal lobule; ACC = anterior cingulate cortex; RT = reaction time; ERN = error-related negativity; P_e = error positivity; CNV = contingent negative variation

n.s. = not significant

* $p < .05$

** $p < .01$

*** $p < .001$

order to respond correctly, participants have to selectively attend to the color of the ink and inhibit the prepotent response of reading the word (Miyake et al., 2000). The task is particularly difficult because the distracting information appears in the same spatial location as the target information; as a result, participants cannot divert their attention away from the location of the distracting information to aid performance. Children and older adults frequently show impaired performance on Stroop tasks, as compared with young adults (regarding development, see Ikeda, Okuzumi, Kokubun, & Haishi, 2011; regarding aging, see West & Alain, 2000).

A recent cross-sectional study involving older adults performing a Stroop task indicated that higher aerobic fitness was associated with smaller amounts of interference (based on reaction times in the interference condition), greater accuracy, and greater task-relevant activation in the prefrontal cortex (based on fMRI data; Prakash et al., 2011). Importantly, findings from two randomized controlled trials in older adults investigating the effects of aerobic exercise on Stroop task performance support these results. In the first study, sedentary older adults were assigned to one of three conditions: (1) aerobic exercise (fast walking), (2) strength and flexibility training, or (3) no exercise (sedentary controls; Dustman et al., 1984). Those in the two exercise groups met with the researchers and trained for three 1-h sessions per week for 4 months. Performance on a Stroop task (as well as other nonexecutive control tasks) was assessed before and after the intervention. Comparisons of participants' pre- and posttraining reaction times revealed that only the aerobic exercise group showed a reliable reduction in Stroop interference after the intervention. In the second study, sedentary older adults were assigned to either aerobic exercise or strength and flexibility training (Smiley-Oyen, Lowry, Francois, Kohut, & Ekkekakis, 2008). Participants exercised under supervision for 30 min a day, three times a week for 10 months. A Stroop test (along with other cognitive tests) was administered before, during, and at the end of the exercise program. After about 5 months of exercise, response accuracy in the interference condition improved only in the aerobic exercise group. Moreover, after 10 months of exercise, postintervention analyses revealed robust improvements in response speed and accuracy in the interference condition only in the aerobic exercisers. Taken together, the results of these studies support the idea that the ability of older adults to selectively attend and to inhibit prepotent responses may benefit from regular engagement in aerobic exercise.

Studies in children utilizing Stroop tasks have yielded far less promising results (Buck, Hillman, & Castelli, 2008; Castelli, Hillman, Hirsch, Hirsch, & Drollette, 2011). Although these studies provided some indication of an association between aerobic fitness and faster performance,

there was no indication that executive function was influenced (i.e., the effects did not differentially involve the interference condition). It may be the case that the lack of an association in children in part reflects word reading being less automatized in this group due to limited experience, and thus there should be less of a need to recruit controlled processes to avoid being influenced by the distracting word. Alternatively, Buck et al. suggested that, in contrast to older adults, functions requiring higher levels of executive control in children may not be preferentially benefited by increased fitness.

Research investigating inhibitory control over prepotent responses, using tasks that do not involve selective attention, has produced inconsistent results. For example, in Kramer and colleagues' (2001) randomized controlled trial, older adults in an aerobic exercise group showed a significantly greater reduction in stop signal reaction times than did those in a stretching and toning group at the end of a 6-month intervention. In contrast, in Smiley-Oyen and colleagues' (2008) randomized controlled trial referred to above, the older adults in the aerobic exercise group showed no improvement in go/no-go reaction times after the 10-month intervention. Thus, it appears from these data in older adults, that regular engagement in aerobic exercise may benefit only select inhibitory control processes, presumably due to process-specific reliance on select brain regions that benefit most from aerobic exercise.

Several studies investigating links between exercise and selective attention or inhibitory control have employed variations of the Eriksen flanker task (Eriksen & Eriksen, 1974). In a typical flanker paradigm, participants indicate the identity of a centralized stimulus while ignoring distracting stimuli appearing in the periphery. There are two main trial types: compatible and incompatible. On compatible trials, the distractors are associated with the same response as the target; on incompatible trials, the distractors are associated with a response different from that required by the target. Successful performance on flanker tasks involves selectively attending and responding to the target stimulus, while simultaneously inhibiting distractor-related activity (Machado, Wyatt, Devine, & Knight, 2007). Despite efforts to selectively process the target, the distracting stimuli tend to influence a person's ability to respond effectively to the target, resulting in worse performance (longer reaction times and/or more errors) on incompatible than on compatible trials. This difference in performance is referred to as the *flanker effect*, with smaller flanker effects reflecting more efficient executive control (Callejas, Lupiáñez, & Tudela, 2004). Although flanker and Stroop tasks tap similar cognitive functions (i.e., selective attention and inhibition), a key point of difference is that in flanker tasks, the distracting information appears in the periphery, away from the focus of attention. Furthermore, the distracting information is not

necessarily associated with a prepotent response; indeed, in the seminal flanker task, stimulus–response associations were assigned arbitrarily during the testing session.

The most common version of the flanker task employed by exercise–cognition researchers involves presenting participants with five arrowheads and asking them to indicate the direction of the central arrowhead by pressing the button on the left- or right-hand side (e.g., left button for <). On compatible trials, all arrowheads face in the same direction (e.g., > > > > >); on incompatible trials, the distractor arrowheads face in the opposite direction to the central target arrowhead (e.g., > > < > >). Because indicating the direction of an arrowhead is a relatively automatic response, the incompatible trials on this task are thought to require strong inhibitory control over motor activity (Eimer et al., 1995). As with switching costs and Stroop interference, flanker effects caused by arrows increase with advancing age (Zhu, Zacks, & Slade, 2010), and inflated effects have also been reported in children (see van Meel, Heslenfeld, Rommelse, Oosterlaan, & Sergeant, 2012; see also Voss, Chaddock, et al., 2011).

Exercise-related research utilizing arrow versions of the flanker task suggests that exercise attenuates age-related decline. In one cross-sectional study involving 241 healthy adults 15–71 years of age, the frequency with which the participants over 40 reported engaging in physical activity sufficient to induce sweating was associated with smaller flanker effects (based on accuracy rates; Hillman, Motl, et al., 2006), which suggests that higher levels of physical activity may lead to better attentional and/or motor control in relatively older adults. Consistent with this possibility, in another study involving 41 healthy older adults, those with high scores on an aerobic fitness test had smaller flanker effects than did those who scored poorly on the fitness test (Colcombe et al., 2004, Study 1). Furthermore, fMRI data from that study indicated that, during performance of the flanker task, fit older adults exhibited greater activation in areas of the brain associated with regulating attention (middle and superior frontal gyri, superior parietal lobule) and less activation in areas related to response interference (anterior cingulate cortex). Importantly, similar results were reported in a follow-up randomized controlled study involving 29 older adults, with those who had been aerobically exercising for 6 months replicating the reduced flanker effects and the changes in the pattern of fMRI activation, whereas those in the strength and flexibility control group showed no improvement and no changes in activation patterns (Colcombe et al., 2004, Study 2). Together, these studies provide evidence that regular aerobic exercise benefits control over responses during selective attention in older adults.

Evidence in developing children is much weaker due to a lack of studies addressing engagement in aerobic exercise, but cross-sectional fitness studies provide some support for

superior performance on flanker arrow tasks in fit (above the 70th percentile), as compared with unfit (below the 30th percentile), children, evidenced by smaller proportional flanker effects (Chaddock, Erickson, Prakash, VanPatter, et al., 2010), higher accuracy rates (Pontifex et al., 2011; see also Voss, Chaddock, et al., 2011), maintenance of accuracy rates across test blocks (Chaddock, Erickson, et al., 2012a), and less variable response latencies (Wu et al., 2011). Furthermore, fMRI data from 28 of the children in the Voss, Chaddock, et al. study indicated that the unfit children showed greater differential activation in association with incompatible versus compatible trials in brain areas linked to cognitive control, including the prefrontal, supplementary motor, and anterior cingulate cortices (note that the task in this study involved fish directed toward the left or right, instead of arrows). In the Chaddock, Erickson, et al. (2012a) study, fMRI data showed that fit, as compared with unfit, children exhibited an initial activity increase, followed by a decrease in activity in the later test block in the frontal (middle frontal gyrus and supplementary motor area) and superior parietal cortex. ERP data from the Pontifex et al. study showed that fit, as compared with unfit, children exhibited shorter latency and smaller amplitude N2, shorter latency and larger amplitude P3, and smaller amplitude error-related negativity. Together, these functional imaging and neuroelectric data are consistent with superior cognitive control in fit children. Additional evidence supporting superior cognitive control in fit, as compared with unfit, children arose in the Pontifex et al. study when participants were asked to respond on the side *opposite* the direction of the arrow; fit children exhibited higher accuracy rates as well as stronger modulation of P3 and error-related negativity in the anti than in the pro task. Developmental studies assessing engagement in aerobic exercise are now needed to determine the extent of its contribution to these fitness findings.

Although healthy young adults generally outperform older adults and children on tasks that depend on inhibitory control, there is some evidence in young adults to suggest that aerobic fitness might still confer a benefit for top-down control in the context of arrow versions of the flanker task. In 2008, Themanson and colleagues had 72 young adults perform an arrow flanker task before undergoing an aerobic fitness test. In one condition of the flanker task, participants were instructed to focus on responding as quickly as possible on each trial; in another condition, participants were instructed to focus on responding accurately. Regression analyses revealed that aerobic fitness was not associated with reaction time on either compatible or incompatible trials, in either the speed or the accuracy condition. However, in the accuracy condition, fit young adults tended to be more accurate on trials that immediately followed an error. Furthermore, ERP data collected during task

performance showed that fit young adults had greater error-related negativity during the accuracy condition. The authors interpreted these converging findings as evidence for better top-down modulation of motor responses in fit young adults.

Another version of the Eriksen flanker task employed by exercise–cognition researchers involves stimuli that have been arbitrarily assigned to responses. For example, participants are asked to indicate the identity of a central letter by pressing one of two buttons (e.g., left button if “F,” right button if “X”). On compatible trials, distractor letters are the same as the target (e.g., F F F); on incompatible trials, distractor letters differ from the target and are associated with the incorrect response (e.g., F X F). Because the association of left/right buttonpresses to arbitrary letters is less prepotent than that to left-/right-pointing arrowheads, letter versions of the flanker task presumably depend more on effective selective attention than on strong response inhibition. As with flanker effects based on prepotent stimulus–response mappings, flanker effects based on arbitrary stimulus–response mappings increase with advancing age (Machado et al., 2009). Whether children also show inflated effects for stimuli with arbitrary response links has not yet been reported to our knowledge.

A small cross-sectional study that used a letter version of the flanker task found that low, moderate, and highly active older adults did not differ in performance, but it should be noted that each group included just 8 participants, so the lack of significant differences could reflect a lack of power (Hillman, Belopolsky, Snook, Kramer, & McAuley, 2004). ERP recordings taken while participants performed the task indicated that older adults who reported regularly engaging in moderate to high levels of physical activity exhibited on the incompatible trials of the task better attentional focus (as indicated by larger P3 amplitude), than did 7 young adults, but no differences emerged in comparison with their less active peers. In addition, in contrast to the less active older adult groups, highly active older adults did not exhibit the typical age-related increase in cognitive processing speed (measured by P3 latency), but note that P3 latency did not differ between the older adult groups. Another cross-sectional study using a larger sample size of older adults and measuring aerobic fitness yielded evidence that fitness predicts at least some aspects of performance in a flanker task involving arbitrary response associations (Voelcker-Rehage, Godde, & Staudinger, 2010). Specifically, the authors of that study found a small but reliable association between older adults’ physical fitness and their reaction times on the incompatible trials of a color version of the flanker task, such that fit older adults responded faster than their unfit peers. Finally, a 6-month intervention study in older adults revealed significantly greater reductions in the size of the flanker effect (letter version) for aerobic

exercisers, as compared with stretchers and toners (Kramer et al., 2001). Overall, these findings suggest that regular aerobic exercise in older adulthood could be beneficial for performance on an executive control task that requires resolution of the interference arising from competing distractors with arbitrary response links.

Although data in young adults are sparse, one study suggests that there may be some benefits of aerobic fitness on participants’ reaction times in a letter version of the flanker task (Themanson & Hillman, 2006). In that study, 28 young adults were categorized as either highly fit or of lower fitness on the basis of whether their score on an aerobic fitness test was above or below the 80th percentile for their age. The authors reported that there were no differences in the size of the flanker effect between the two fitness groups. However, they also reported that fit individuals exhibited significantly more slowing on trials following commission of an error. This posterror slowing effect was interpreted as evidence for better top-down control of attentional processes because it reflects effortful modulation of responses in order to avoid making another error. Furthermore, ERP data from that study suggested that, as compared with their less fit peers, highly fit individuals exhibited less neural conflict on incompatible trials and greater attentional focus after receiving error feedback (as indicated by error-related negativity and error positivity). Thus, the authors concluded that aerobically fit young adults are better able to use executive control processes to modulate their neural responses in a selective attention task.

Data in children are also sparse, but again one cross-sectional fitness study provided some evidence of superior performance in fitter children on a letter version of the flanker task (Hillman, Buck, Themanson, Pontifex, & Castelli, 2009). In that study, 38 children were selected from a pool of 592 on the basis of ranking in the top or bottom 10 % on an aerobic fitness test (Progressive Aerobic Cardiovascular Endurance Run). Although the size of the flanker effect did not differ between the two fitness groups, overall accuracy rates were higher in the fit group. Furthermore, ERP data suggested that fit participants exhibited superior cognitive control, including better allocation of attention (evidenced by larger amplitude P3) and posterror modulation (evidenced by smaller amplitude error-related negativity and larger amplitude error positivity).

Taken together, the research presented here provides compelling evidence for exercise-related benefits on selective attention and inhibitory control in older adults. To summarize, studies in older adults indicate that aerobic fitness is a good predictor of performance on tasks that rely relatively heavily on inhibitory control over prepotent responses (e.g., Colcombe et al., 2004, Study 1; Prakash et al., 2011) and also that regular aerobic exercise *improves* performance on such tasks (e.g., Colcombe et al., 2004,

Study 2; Dustman et al., 1984). In addition, there is some evidence that regular aerobic exercise improves older adults' performance on tasks that rely more on selective attention than on inhibitory motor control (e.g., Kramer et al., 2001). In contrast, current research in young adults and children provides only limited support for exercise-related benefits in selective attention and inhibitory control via associations with fitness levels, with the bulk of the supportive evidence relating to accuracy rates and indices of posterror behavior (e.g., Hillman et al., 2009; Themanson & Hillman, 2006; Themanson et al., 2008; Voss, Chaddock, et al., 2011). Clearly, intervention studies are needed in children and young adult populations to determine whether the reported associations with fitness relate specifically to regular engagement in aerobic exercise.

Working memory

Working memory tasks involve holding information in mind for a short period of time and rapidly updating that information in order to respond correctly (Baddeley & Hitch, 1974). One working memory task commonly used in the exercise–cognition literature is the two-back task, in which participants are asked to press a button whenever the currently displayed stimulus matches the stimulus that appeared two stimuli back in a sequential presentation (Cohen et al., 1994). Since this task requires participants to keep a relatively small amount of information in mind, it is presumed to rely heavily on the updating component of working memory (E. E. Smith & Jonides, 1997), and performance depends on the lateral prefrontal cortex (Muller, Machado, & Knight, 2002). In older adults, cross-sectional research has shown that physical fitness is a significant predictor of accuracy on the two-back task (Voelcker-Rehage et al., 2010). In relatively young adults, training studies have shown that aerobic exercise programs can increase two-back accuracy (Hansen et al., 2004) and reduce reaction times (Stroth et al., 2010). Together, these findings suggest that both aerobic fitness (in older adulthood) and regular engagement in aerobic exercise (in young adulthood) are beneficial for the updating component of working memory.

Other paradigms used to assess the effects of regular exercise on working memory include digit span and Sternberg tasks. Forward span tests involve presenting numbers to participants one at a time and then asking them to report the whole sequence to the experimenter in the correct order. Backward span tests are identical, except that participants are asked to report the sequence in the *reverse* order. In both tasks, the sequence length is gradually increased until participants can no longer correctly recall all of the digits. While span tests rely on mental updating to some degree (particularly backward versions), they mainly test the amount of information that a person can hold in mind at one

time. Although an early study indicated no effect of regular exercise on older adults' forward or backward digit spans (Blumenthal et al., 1991), more recent research suggests that exercise can be beneficial for this type of working memory. For example, data from a large-scale cross-sectional study showed that higher levels of physical activity in older women are associated with longer backward digit spans (Weuve et al., 2004). Furthermore, a 12-month intervention study involving 187 older women revealed that aerobic exercise can significantly increase older adults' forward digit spans (Williams & Lord, 1997).

In contrast to the span tasks, the modified Sternberg tasks used by exercise–cognition researchers involved simultaneous presentation of a memory set of variable size (e.g., three, five, or seven letters) followed, after a short delay, by a single probe stimulus; participants indicated whether the probe was present in the memory set. Given the relatively low requirement for updating in this task, performance presumably depends primarily on memory capacity. One cross-sectional fitness study in 64 young adults that used a median split to categorize participants into higher and lower fitness groups found no differences in Sternberg task performance between the fitness groups; however, ERP data showed that fitter participants exhibited smaller amplitude frontal contingent negative variation when instructed to maximize speed, which could be interpreted as an indication of more efficient preparation processes (Kamijo, O'Leary, Pontifex, Themanson, & Hillman, 2010). By comparison, a 9-month intervention study in 20 children did find performance differences, with accuracy improved after aerobic training, and this was accompanied by an increase in the amplitude of initial frontal contingent negative variation, which was interpreted as an indication of superior cognitive control, given past findings regarding this ERP subcomponent (Kamijo et al., 2011). Overall, the results from the span and Sternberg tasks suggest that regular exercise can also confer benefits for the volume of information that children and older adults can hold in mind at one time.

Conclusions

In this review, we examined evidence in healthy populations supporting links between regular aerobic exercise and specific components of executive functioning, including task switching, selective attention, inhibitory control, and working memory. In older adults, intervention studies indicate that regular aerobic exercise can improve task switching, selective attention, inhibition of prepotent responses, and working memory span. Furthermore, cross-sectional data indicate that aerobic fitness predicts better working memory updating, but further research is needed to determine whether this relationship reflects engagement in exercise. In

young adults, the scarcity of data to date makes it difficult to determine the specific benefits that aerobic exercise may have on different aspects of executive functioning; however, some evidence indicates that higher physical activity levels are associated with better task switching when the upcoming switch is predictable, that aerobic fitness is associated with top-down modulation of responses in tasks that rely on selective attention and inhibitory control, and that regular aerobic exercise can improve the updating component of working memory. In children, working memory capacity is the only executive function shown to benefit from chronic exercise, but fitness studies suggest potential benefits for selective attention and inhibitory control.

Although the evidence to date supports a wider range of executive functions benefitting from regular exercise in older adults, the relative lack of supportive evidence in young adults and children may, in part, reflect a poverty of studies, especially controlled trials, in these age groups. While more research is clearly needed to fully characterize the benefits that can be gained through regular exercise in younger healthy populations, the indications reported thus far that regular exercise can benefit brains even when they are in their prime developmentally warrant more rigorous investigation, particularly in the context of society becoming increasingly sedentary, which of course may augment the room for improvement in executive functioning.

Acknowledgments We thank the University of Otago for funding this work and Cathleen Moore and two anonymous reviewers for providing us with valuable comments and suggestions.

References

- Åberg, M. A. I., Pedersen, N. L., Torén, K., Svartengren, M., Bäckstrand, B., Johnsson, T., et al. (2009). Cardiovascular fitness is associated with cognition in young adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(49), 20906–20911.
- Ainslie, P. N., Cotter, J. D., George, K. P., Lucas, S., Murrell, C., Shave, R., et al. (2008). Elevation in cerebral blood flow velocity with aerobic fitness throughout healthy human ageing. *The Journal of Physiology*, *586*(16), 4005–4010.
- Albinet, C., Boucard, G., Bouquet, C., & Audiffren, M. (2010). Increased heart rate variability and executive performance after aerobic training in the elderly. *European Journal of Applied Physiology*, *109*(4), 617–624.
- Angevaren, M., Aufdemkampe, G., Verhaar, H. J. J., Aleman, A., & Vanhees, L. (2008). Physical activity and enhanced fitness to improve cognitive function in older people without known cognitive impairment. *Cochrane Database Systematic Reviews*, (2), CD005381.
- Anstey, K. J., & Wood, J. (2011). Chronological age and age-related cognitive deficits are associated with an increase in multiple types of driving errors in late life. *Neuropsychology*, *25*(5), 613–621.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 8, pp. 47–89). New York: Academic Press.
- Banich, M. T. (2009). Executive function: The search for an integrated account. *Current Directions in Psychological Science*, *18*(2), 89–94.
- Barnes, D. E., Yaffe, K., Satariano, W. A., & Tager, I. B. (2003). A longitudinal study of cardiorespiratory fitness and cognitive function in healthy older adults. *Journal of the American Geriatrics Society*, *51*(4), 459–465.
- Best, J. R., Miller, P. H., & Naglieri, J. A. (2011). Relations between executive function and academic achievement from ages 5 to 17 in a large, representative national sample. *Learning and Individual Differences*, *21*(4), 327–336.
- Blumenthal, J. A., Emery, C. F., Madden, D. J., Schniebolck, S., Walsh-riddle, M., George, L. K., et al. (1991). Long-term effects of exercise on psychological functioning in older men and women. *Journal of Gerontology*, *46*(6), 352–361.
- Brown, A. D., McMorris, C. A., Longman, R. S., Leigh, R., Hill, M. D., Friedenreich, C. M., et al. (2010). Effects of cardiorespiratory fitness and cerebral blood flow on cognitive outcomes in older women. *Neurobiology of Aging*, *31*(12), 2047–2057.
- Buck, S. M., Hillman, C. H., & Castelli, D. M. (2008). The relation of aerobic fitness to stroop task performance in preadolescent children. *Medicine and Science in Sports and Exercise*, *40*(1), 166–172.
- Callejas, A., Lupiáñez, J., & Tudela, P. (2004). The three attentional networks: On their independence and interactions. *Brain and Cognition*, *54*(3), 225–227.
- Castelli, D. M., Hillman, C. H., Buck, S. M., & Erwin, H. E. (2007). Physical fitness and academic achievement in third- and fifth-grade students. *Journal of Sport & Exercise Psychology*, *29*(2), 239–252.
- Castelli, D. M., Hillman, C. H., Hirsch, J., Hirsch, A., & Drollette, E. (2011). FIT Kids: Time in target heart zone and cognitive performance. *Preventive Medicine*, *52*(Suppl 1), S55–S59.
- Cepeda, N. J., Kramer, A. F., & Gonzalez de Sather, J. C. (2001). Changes in executive control across the life span: Examination of task-switching performance. *Developmental Psychology*, *37*(5), 715–730.
- Chaddock, L., Erickson, K. I., Prakash, R. S., Kim, J. S., Voss, M. W., Vanpatter, M., et al. (2010a). A neuroimaging investigation of the association between aerobic fitness, hippocampal volume, and memory performance in preadolescent children. *Brain Research*, *1358*, 172–183.
- Chaddock, L., Erickson, K. I., Prakash, R. S., VanPatter, M., Voss, M. W., Pontifex, M. B., et al. (2010b). Basal ganglia volume is associated with aerobic fitness in preadolescent children. *Developmental Neuroscience*, *32*(3), 249–256.
- Chaddock, L., Erickson, K. I., Prakash, R. S., Voss, M. W., VanPatter, M., Pontifex, M. B., et al. (2012a). A functional MRI investigation of the association between childhood aerobic fitness and neurocognitive control. *Biological Psychology*, *89*(1), 260–268.
- Chaddock, L., Neider, M. B., Lutz, A., Hillman, C. H., & Kramer, A. F. (2012b). Role of childhood aerobic fitness in successful street crossing. *Medicine & Science in Sports & Exercise*, *44*(4), 749–753.
- Chan, R. C. K., Shum, D., Touloupoulou, T., & Chen, E. Y. H. (2008). Assessment of executive functions: Review of instruments and identification of critical issues. *Archives of Clinical Neuropsychology*, *23*(2), 201–216.
- Chodzko-Zajko, W. J., & Moore, K. A. (1994). Physical fitness and cognitive functioning in aging. *Exercise and Sport Sciences Reviews*, *22*(1), 195–220.
- Cohen, J. D., Forman, S. D., Braver, T. S., Casey, B., Servan Schreiber, D., & Noll, D. C. (1994). Activation of the prefrontal cortex in a

- nonspatial working memory task with functional MRI. *Human Brain Mapping*, 1(4), 293–304.
- Colcombe, S. J., Erickson, K. I., Raz, N., Webb, A. G., Cohen, N. J., McAuley, E., et al. (2003). Aerobic fitness reduces brain tissue loss in aging humans. *Journals of Gerontology Series A-Biological Sciences and Medical Sciences*, 58(2), 176–180.
- Colcombe, S. J., Erickson, K. I., Scalf, P. E., Kim, J. S., Prakash, R., McAuley, E., et al. (2006). Aerobic exercise training increases brain volume in aging humans. *Journals of Gerontology Series A-Biological Sciences and Medical Sciences*, 61(11), 1166–1170.
- Colcombe, S. J., & Kramer, A. F. (2003). Fitness effects on the cognitive function of older adults: A meta-analytic study. *Psychological Science*, 14(2), 125–130.
- Colcombe, S. J., Kramer, A. F., Erickson, K. I., Scalf, P., McAuley, E., Cohen, N. J., et al. (2004). Cardiovascular fitness, cortical plasticity, and aging. *Proceedings of the National Academy of Sciences of the United States of America*, 101(9), 3316–3321.
- Dustman, R. E., Ruhling, R. O., Russell, E. M., Shearer, D. E., Bonekat, H. W., Shigeoka, J. W., et al. (1984). Aerobic exercise training and improved neuropsychological function of older individuals. *Neurobiology of Aging*, 5(1), 35–42.
- Eimer, M., Hommel, B., & Prinz, W. (1995). S-R compatibility and response selection. *Acta Psychologica*, 90(1–3), 301–313.
- Erickson, K. I., Prakash, R. S., Voss, M. W., Chaddock, L., Hu, L., Morris, K. S., et al. (2009). Aerobic fitness is associated with hippocampal volume in elderly humans. *Hippocampus*, 19(10), 1030–1039.
- Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., et al. (2011). Exercise training increases size of hippocampus and improves memory. *Proceedings of the National Academy of Sciences of the United States of America*, 108(7), 1–6.
- Eriksen, B. A., & Eriksen, C. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, 16(1), 143–149.
- Etnier, J. L., & Chang, Y. K. (2009). The effect of physical activity on executive function: A brief commentary on definitions, measurement issues, and the current state of the literature. *Journal of Sport & Exercise Psychology*, 31(4), 469–483.
- Etnier, J. L., Nowell, P. M., Landers, D. M., & Sibley, B. A. (2006). A meta-regression to examine the relationship between aerobic fitness and cognitive performance. *Brain Research Reviews*, 52(1), 119–130.
- Etnier, J. L., Salazar, W., Landers, D. M., Petruzzello, S. J., Han, M., & Nowell, P. (1997). The influence of physical fitness and exercise upon cognitive functioning: A meta-analysis. *Journal of Sport & Exercise Psychology*, 19, 249–277.
- Flöel, A., Ruscheweyh, R., Kruger, K., Willemer, C., Winter, B., Volker, K., et al. (2010). Physical activity and memory functions: Are neurotrophins and cerebral gray matter volume the missing link? *NeuroImage*, 49(3), 2756–2763.
- Gondoh, Y., Sensui, H., Kinomura, S., Fukuda, H., Fujimoto, T., Masud, M., et al. (2009). Effects of aerobic exercise training on brain structure and psychological well-being in young adults. *The Journal of Sports Medicine and Physical Fitness*, 49(2), 129–135.
- Gordon, B. A., Rykhlevskaia, E. I., Brumback, C. R., Lee, Y., Elavsky, S., Konopack, J. F., et al. (2008). Neuroanatomical correlates of aging, cardiopulmonary fitness level, and education. *Psychophysiology*, 45(5), 825–838.
- Hansen, A. L., Johnsen, B. H., Sollers, J. J., Stenvik, K., & Thayer, J. F. (2004). Heart rate variability and its relation to prefrontal cognitive function: The effects of training and detraining. *European Journal of Applied Physiology*, 93(3), 263–272.
- Hawkins, H. L., Kramer, A. F., & Capaldi, D. (1992). Aging, exercise, and attention. *Psychology and Aging*, 7(4), 643–653.
- Hillman, C. H., Belopolsky, A. V., Snook, E. M., Kramer, A. F., & McAuley, E. (2004). Physical activity and executive control: Implications for increased cognitive health during older adulthood. *Research Quarterly for Exercise and Sport*, 75(2), 176–185.
- Hillman, C. H., Buck, S. M., Themanson, J. R., Pontifex, M. B., & Castelli, D. M. (2009). Aerobic fitness and cognitive development: Event-related brain potential and task performance indices of executive control in preadolescent children. *Developmental Psychology*, 45(1), 114–129.
- Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: Exercise effects on brain and cognition. *Nature Reviews Neuroscience*, 9(1), 58–65.
- Hillman, C. H., Kramer, A. F., Belopolsky, A. V., & Smith, D. P. (2006a). A cross-sectional examination of age and physical activity on performance and event-related brain potentials in a task switching paradigm. *International Journal of Psychophysiology*, 59(1), 30–39.
- Hillman, C. H., Motl, R. W., Pontifex, M. B., Posthuma, D., Stubbe, J. H., Boomsma, D. I., et al. (2006b). Physical activity and cognitive function in a cross-section of younger and older community-dwelling individuals. *Health Psychology*, 25(6), 678–687.
- Ikeda, Y., Okuzumi, H., Kokubun, M., & Haishi, K. (2011). Age-related trends of interference control in school-age children and young adults in the Stroop color-word test. *Psychological Reports*, 108(2), 577–584.
- Johnson, N. F., Kim, C., Clasey, J. L., Bailey, A., & Gold, B. T. (2012). Cardiorespiratory fitness is positively correlated with cerebral white matter integrity in healthy seniors. *NeuroImage*, 59(2), 1514–1523. doi:10.1016/j.neuroimage.2011.08.032
- Kamijo, K., O'Leary, K. C., Pontifex, M. B., Themanson, J. R., & Hillman, C. H. (2010). The relation of aerobic fitness to neuroelectric indices of cognitive and motor task preparation. *Psychophysiology*, 47(5), 814–821.
- Kamijo, K., Pontifex, M. B., O'Leary, K. C., Scudder, M. R., Wu, C. T., Castelli, D. M., et al. (2011). The effects of an afterschool physical activity program on working memory in preadolescent children. *Developmental Science*, 14(5), 1046–1058.
- Kamijo, K., & Takeda, Y. (2010). Regular physical activity improves executive function during task switching in young adults. *International Journal of Psychophysiology*, 75(3), 304–311.
- Kramer, A. F., Erickson, K. I., & Colcombe, S. J. (2006). Exercise, cognition, and the aging brain. *Journal of Applied Physiology*, 101(4), 1237–1242.
- Kramer, A. F., Hahn, S., Cohen, N. J., Banich, M. T., McAuley, E., Harrison, C. R., et al. (1999). Ageing, fitness and neurocognitive function. *Nature*, 402(6763), 418–419.
- Kramer, A. F., Hahn, S., McAuley, E., Cohen, N. J., Banich, M. T., Harrison, C., et al. (2001). Exercise, aging and cognition: Healthy body, healthy mind. In A. D. Fisk & W. Rogers (Eds.), *Human factors interventions for the health care of older adults* (pp. 91–120). Hillsdale, N.J.: Erlbaum.
- Kray, J., Karbach, J., & Blaye, A. (2012). The influence of stimulus-set size on developmental changes in cognitive control and conflict adaptation. *Acta Psychologica*, 140(2), 119–128.
- Levine, B. D. (2008). VO₂ max: What do we know, and what do we still need to know? *The Journal of Physiology*, 586(1), 25–34.
- Machado, L., Devine, A., & Wyatt, N. (2009). Distractibility with advancing age and Parkinson's disease. *Neuropsychologia*, 47(7), 1756–1764.
- Machado, L., Wyatt, N., Devine, A., & Knight, B. (2007). Action planning in the presence of distracting stimuli: An investigation into the time course of distractor effects. *Journal of Experimental Psychology. Human Perception and Performance*, 33(5), 1045–1061.
- Mäntylä, T., Karlsson, M. J., & Marklund, M. (2009). Executive control functions in simulated driving. *Applied Neuropsychology*, 16(1), 11–18.

- Marks, B. L., Madden, D. J., Bucur, B., & Provenzale, J. M. (2007). Role of aerobic fitness and aging on cerebral white matter integrity. *Annals of the New York Academy of Sciences*, *1097*, 171.
- Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks. *Cognitive Psychology*, *41*(1), 49–100.
- Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, *7*(3), 134–140.
- Müller, N. G., Machado, L., & Knight, R. T. (2002). Contributions of subregions of the prefrontal cortex to working memory: Evidence from brain lesions in humans. *Journal of Cognitive Neuroscience*, *14*(5), 673–686.
- Netz, Y., Dwolatzky, T., Zinker, Y., Argov, E., & Agmon, R. (2010). Aerobic fitness and multidomain cognitive function in advanced age. *International Psychogeriatrics*, 1–11.
- Ogoh, S., & Ainslie, P. N. (2009). Cerebral blood flow during exercise: Mechanisms of regulation. *Journal of Applied Physiology*, *107*(5), 1370–1380.
- Pereira, A. C., Huddleston, D. E., Brickman, A. M., Sosunov, A. A., Hen, R., McKhann, G. M., et al. (2007). An in vivo correlate of exercise-induced neurogenesis in the adult dentate gyrus. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(13), 5638.
- Pontifex, M. B., Raine, L. B., Johnson, C. R., Chaddock, L., Voss, M. W., Cohen, N. J., et al. (2011). Cardiorespiratory fitness and the flexible modulation of cognitive control in preadolescent children. *Journal of Cognitive Neuroscience*, *23*(6), 1332–1345.
- Prakash, R. S., Voss, M. W., Erickson, K. I., Lewis, J. M., Chaddock, L., Malkowski, E., et al. (2011). Cardiorespiratory fitness and attentional control in the aging brain. *Frontiers in Human Neuroscience*, *4*, 1–12.
- Sanders, A. F., & Lamers, J. M. (2002). The Eriksen flanker effect revisited. *Acta Psychologica*, *109*, 41–56.
- Schulte, T., Müller-Oehring, E. M., Vinco, S., Hoefl, F., Pfefferbaum, A., & Sullivan, E. V. (2009). Double dissociation between action-driven and perception-driven conflict resolution invoking anterior versus posterior brain systems. *NeuroImage*, *48*(2), 381–390.
- Scisco, J. L., Leynes, P. A., & Kang, J. (2008). Cardiovascular fitness and executive control during task-switching: An ERP study. *International Journal of Psychophysiology*, *69*(1), 52–60.
- Shiu, L. P., & Kornblum, S. (1996). Negative priming and stimulus–response compatibility. *Psychonomic Bulletin & Review*, *3*(4), 510–514.
- Smiley-Oyen, A. L., Lowry, K. A., Francois, S. J., Kohut, M. L., & Ekkekakis, P. (2008). Exercise, fitness, and neurocognitive function in older adults: The "Selective Improvement" and "Cardiovascular Fitness" hypotheses. *Annals of Behavioral Medicine*, *36*(3), 280–291.
- Smith, P. J., Blumenthal, J. A., Hoffman, B. M., Cooper, H., Strauman, T. A., Welsh-Bohmer, K., et al. (2010). Aerobic exercise and neurocognitive performance: A meta-analytic review of randomized controlled trials. *Psychosomatic Medicine*, *72*(3), 239–252.
- Smith, E. E., & Jonides, J. (1997). Working memory: A view from neuroimaging. *Cognitive Psychology*, *33*, 5–42.
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology. General*, *18*, 643–662.
- Stroth, S., Reinhardt, R. K., Thöne, J., Hille, K., Schneider, M., Härtel, S., et al. (2010). Impact of aerobic exercise training on cognitive functions and affect associated to the COMT polymorphism in young adults. *Neurobiology of Learning and Memory*, *94*(3), 364–372.
- Themanson, J. R., & Hillman, C. H. (2006). Cardiorespiratory fitness and acute aerobic exercise effects on neuroelectric and behavioral measures of action monitoring. *Neuroscience*, *141*(2), 757–767.
- Themanson, J. R., Hillman, C. H., & Curtin, J. J. (2006). Age and physical activity influences on action monitoring during task switching. *Neurobiology of Aging*, *27*(9), 1335–1345.
- Themanson, J. R., Pontifex, M. B., & Hillman, C. H. (2008). Fitness and action monitoring: Evidence for improved cognitive flexibility in young adults. *Neuroscience*, *157*(2), 319–328.
- Tompsonowski, P. D., Lambourne, K., & Okumura, M. S. (2011). Physical activity interventions and children's mental function: An introduction and overview. *Preventive Medicine*, *52*(Suppl 1), S3–S9.
- United Nations Population Division. (2009). World population ageing 2009. Retrieved from <http://www.un.org/esa/population/publications/WPA2009/WPA2009-report.pdf>
- van Meel, C. S., Heslenfeld, D. J., Rommelse, N. N., Oosterlaan, J., & Sergeant, J. A. (2012). Developmental trajectories of neural mechanisms supporting conflict and error processing in middle childhood. *Developmental Neuropsychology*, *37*(4), 358–378.
- Voelcker-Rehage, C., Godde, B., & Staudinger, U. M. (2010). Physical and motor fitness are both related to cognition in old age. *European Journal of Neuroscience*, *31*(1), 167–176.
- Voss, M. W., Chaddock, L., Kim, J. S., Vanpatter, M., Pontifex, M. B., Raine, L. B., et al. (2011a). Aerobic fitness is associated with greater efficiency of the network underlying cognitive control in preadolescent children. *Neuroscience*, *199*, 166–176.
- Voss, M. W., Nagamatsu, L. S., Liu-Ambrose, T., & Kramer, A. F. (2011b). Exercise, brain, and cognition across the lifespan. *Journal of Applied Physiology*, *111*(5), 1505–1513.
- Voss, M. W., Prakash, R. S., Erickson, K. I., Basak, C., Chaddock, L., Kim, J. S., et al. (2010). Plasticity of brain networks in a randomized intervention trial of exercise training in older adults. *Frontiers in Aging Neuroscience*, *2*, 1–17.
- West, R., & Alain, C. (2000). Age-related decline in inhibitory control contributes to the increased Stroop effect observed in older adults. *Psychophysiology*, *37*(2), 179–189.
- Weuve, J., Kang, J. H., Manson, J. E., Breteler, M. M. B., Ware, J. H., & Grodstein, F. (2004). Physical activity, including walking, and cognitive function in older women. *JAMA: The Journal of the American Medical Association*, *292*(12), 1454–1461.
- Williams, P., & Lord, S. R. (1997). Effects of group exercise on cognitive functioning and mood in older women. *Australian and New Zealand Journal of Public Health*, *21*(1), 45–52.
- World Health Organization. (2012a). Physical inactivity: A global public health problem. Retrieved from http://www.who.int/dietphysicalactivity/factsheet_inactivity/en/
- World Health Organization. (2012b). Prevalence of insufficient physical activity. Retrieved from http://www.who.int/gho/ncd/risk_factors/physical_activity_text/en/
- Wu, C. T., Pontifex, M. B., Raine, L. B., Chaddock, L., Voss, M. W., Kramer, A. F., et al. (2011). Aerobic fitness and response variability in preadolescent children performing a cognitive control task. *Neuropsychology*, *25*(3), 333–341.
- Yogev-Seligmann, G., Hausdorff, J. M., & Giladi, N. (2008). The role of executive function and attention in gait. *Movement Disorders*, *23*(3), 329–342.
- Zhu, D. C., Zacks, R. T., & Slade, J. M. (2010). Brain activation during interference resolution in young and older adults: An fMRI study. *NeuroImage*, *50*(2), 810–817.