
SYMPOSIUM

A Review of the Relation of Aerobic Fitness and Physical Activity to Brain Structure and Function in Children

Laura Chaddock,^{1,2} Matthew B. Pontifex,³ Charles H. Hillman,^{2,3} AND Arthur F. Kramer^{1,2}

¹Department of Psychology, University of Illinois at Urbana-Champaign, Urbana, Illinois

²Beckman Institute, University of Illinois at Urbana-Champaign, Urbana, Illinois

³Department of Kinesiology & Community Health, University of Illinois at Urbana-Champaign, Urbana, Illinois

(RECEIVED December 23, 2010; FINAL REVISION March 16, 2011; ACCEPTED March 17, 2011)

Abstract

A growing number of schools have increasingly de-emphasized the importance of providing physical activity opportunities during the school day, despite emerging research that illustrates the deleterious relationship between low levels of aerobic fitness and neurocognition in children. Accordingly, a brief review of studies that link fitness-related differences in brain structure and brain function to cognitive abilities is provided herein. Overall, the extant literature suggests that childhood aerobic fitness is associated with higher levels of cognition and differences in regional brain structure and function. Indeed, it has recently been found that aerobic fitness level even predicts cognition over time. Given the paucity of work in this area, several avenues for future investigations are also highlighted. (*JINS*, 2011, 17, 1–11)

Keywords: Academic achievement, Cognition, Cognitive control, ERPs, Exercise, MRI, Plasticity

INTRODUCTION

Inactivity among America's youth is a growing public health and educational concern. During the past several decades, children have become increasingly sedentary. This lifestyle change is associated with substantial increases in obesity, such that 17% of children between the ages of 2 and 19 years are labeled as obese (Ogden & Carroll, 2010). Sedentary behavior during childhood also relates to an increased risk for high blood pressure, high cholesterol, type II diabetes, and coronary heart disease throughout the lifespan (Anderson, Crespo, Barlett, Cheskin, & Pratt, 1998; Freedman, Khan, Dietz, Srinivasan, & Berenson, 2001; Sisson et al., 2009), and these "adult-onset" diseases have become more prevalent during childhood (Department of Health and Human Services & Department of Education, 2000). As a result, recent estimates suggest that younger generations may live less healthy and shorter lives than their parents (Olshansky et al., 2005). It is also possible that human evolution, which has been shaped by an active lifestyle, will be maladapted by the

sedentary behaviors of today (Booth & Lees, 2006; Vaynman & Gomez-Pinilla, 2006).

A sedentary lifestyle during childhood not only influences physical health, but cognitive and brain health as well. That is, accumulating evidence suggests that low levels of physical activity and aerobic fitness are associated with declines in academic achievement, cognitive abilities, brain structure, and brain function (Castelli, Hillman, Buck, & Erwin, 2007; Chaddock, Erickson, Prakash, Kim, et al., 2010; Chaddock, Erickson, Prakash, VanPatter, et al., 2010; Hillman, Buck, Themanson, Pontifex, & Castelli, 2009; Hillman, Erickson, & Kramer, 2008; Pontifex et al., 2010; Sibley & Etnier, 2003). Measures of physical activity and aerobic fitness have been related to childhood neurocognition, but their distinct contributions to cognitive health during development are still under investigation. Physical activity is defined as bodily movement that requires energy expenditure above normal physiological demands, and measurements include daily activity logs, number of physical education classes, and data collected with pedometers and accelerometers. Aerobic fitness refers to the maximal capacity of the cardiorespiratory system to use oxygen and can be measured by VO_2 max testing or the PACER test of the Fitnessgram. Aerobic fitness is one element of the multifaceted concept of physical fitness,

Correspondence and reprint requests to: Arthur F. Kramer, Beckman Institute for Advanced Science and Technology, University of Illinois at Urbana-Champaign, 405 North Mathews Avenue, Urbana, IL 61801. E-mail: a-kramer@illinois.edu

a set of health and skill-related attributes associated with one's ability to perform physical activities, which also includes muscular strength, muscle flexibility, and body composition (Buckworth & Dishman, 2002). Accordingly, fitness is best construed as a set of attributes, while physical activity more generally refers to behavioral actions.

In this review, we will discuss the associations between aerobic fitness, physical activity, brain, and cognition in children. Despite the reported positive associations among these variables, school administrators continue to de-emphasize the importance of physical activity during the school day. Educators are under increased pressure to improve academic achievement of their pupils as well as reduce educational spending. These pressures, coupled with the popular belief that physical education is of less educational value than formal academic topics, have led to the reduction or elimination of physical activity opportunities during the school day. In particular, schools have decreased opportunities for play by 25% and unstructured outdoor activities by 50% (Juster, Stafford, & Ono, 2004). This research review raises the possibility that physical activity during childhood may be important for cognitive and brain health.

Given recent societal trends, the investigation of the relationship between an inactive lifestyle and cognition in school-aged children is of great importance. A better understanding of the implications of these trends may be gained by examining the relationships between physical activity, aerobic fitness, cognition, scholastic achievement, and brain structures and processes. A growing body of literature highlights the brain-body interaction in children and suggests that low levels of physical activity and aerobic fitness may be detrimental to the developing brain and cognition.

ACADEMIC ACHIEVEMENT

Findings from reviews of the relationship between physical activity and academic achievement have concluded that providing children the opportunity to be periodically active during the school day (through classroom based activities, physical education curriculum, and recess) can improve scholastic performance, or at the very least, not detract from academic performance, while at the same time promoting better physical health (Centers for Disease Control and Prevention [CDC], 2010; Peligrini & Smith, 1993). A recent report by the CDC (2010) also noted that children's attention, attitudes, behaviors, and academic performance were positively influenced by physical activity opportunities during the school day.

Several cross-sectional evaluations have observed that poorer aerobic fitness is associated with decreased academic achievement in the areas of reading and mathematics (Castelli et al., 2007; Chomitz et al., 2009; Grissom, 2005; Roberts, Freed, & McCarthy, 2010). Specifically, Castelli et al. (2007), Chomitz et al. (2009), Grissom (2005), and Roberts et al. (2010) each examined the relationship of fitness, using the Fitnessgram (Cooper Institute for Aerobics Research, 1999), which assesses fitness in the areas of aerobic capacity, body composition, muscle strength, and muscle flexibility, with

academic achievement using statewide achievement tests (i.e., the California Achievement Tests, the Illinois Standardized Achievement Test, and the Massachusetts Comprehensive Assessment System Achievement Test). Together, findings from these investigations, which used samples ranging from 259 to 884,715 children, identified positive associations between components of aerobic fitness and overall academic achievement, reading achievement, and mathematics achievement across grade levels (ranging from 3rd to 9th grade) (Castelli et al., 2007; Chomitz et al., 2009; Grissom, 2005; Roberts et al., 2010).

Findings from randomized controlled trials provide additional support for the positive relationship between aerobic fitness and achievement, with physical activity interventions serving to improve or maintain academic performance (Donnelly et al., 2009; Sallis et al., 1999) and reduce off-task behaviors (Mahar et al., 2006). For example, Donnelly and colleagues (2009) conducted a 2-year randomized controlled trial in a sample of 1490 preadolescent children. The intervention group, which completed 90 min a week of moderate to vigorous physical activity using the Physical Activity Across the Curriculum program, exhibited increased performance on measures of overall academic achievement, and achievement in the areas of reading, spelling, and arithmetic using the Wechsler Individual Achievement Test – 2nd edition (The Psychological Corporation, 2001); an effect not observed for the standard curriculum control group. Accordingly, these findings illustrate the link between physically active behaviors, and attributes such as aerobic fitness, and academic achievement (Donnelly et al., 2009).

COGNITIVE CONTROL

Previous research has demonstrated a relationship between scholastic achievement and several cognitive processes, such as processing speed and cognitive control (Jensen, 1992, 1998; Rohde & Thompson, 2007). In particular, cognitive control (also known as “executive control”) refers to a set of higher-order processes, which serve to regulate goal-directed interactions within the environment (Botvinick, Braver, Barch, Carter, & Cohen, 2001; MacDonald, Cohen, Stenger, & Carter, 2000; Meyer & Kieras, 1997; Norman & Shallice, 1986) that are optimized through the selection, scheduling, coordination, and maintenance of computational processes underlying aspects of perception, memory, and action (Botvinick et al., 2001; Meyer & Kieras, 1997; Miyake, Friedman, Emerson, Witzki, & Howerter, 2000; Norman & Shallice, 1986). Several meta-analyses report a positive relationship between aerobic fitness and cognition across the lifespan (Colcombe & Kramer, 2003; Etner et al., 1997; Sibley & Etner, 2003; Smith et al., 2010), and further research suggests that the fitness-cognition association is disproportionately larger for tasks or task components that require extensive amounts of cognitive control (Chaddock, Erickson, Prakash, VanPatter, et al., 2010; Colcombe & Kramer, 2003; Hillman, Kramer, Belopolsky, & Smith, 2006; Pontifex et al., 2010). Of specific interest to this review, a positive association between aerobic fitness and cognitive control

exists in children (Chaddock, Erickson, Prakash, VanPatter, et al., 2010; Hillman et al., 2009; Pontifex et al., 2010).

Two of the sub-processes of cognitive control, inhibition and working memory, have been implicated in the achievement of mathematics and reading (Bull & Scerif, 2001; DeStefano & LeFevre, 2004; St. Clair-Thompson & Gathercole, 2006). Inhibition involves the ability to filter irrelevant environmental information, override a prepotent response, and selectively focus on important information in memory, processes central for sustaining attention and maintaining control over one's actions (Diamond, 2006). Inhibition is thought to be especially important for the effective functioning of cognitive control in children (Barkley, 1997; Brocki & Brohlin, 2004), given that it relates to the ability to act on the basis of choice rather than impulse (Davidson, Amso, Anderson, & Diamond, 2006). Working memory relates to the ability to temporarily store and manage information while learning and performing cognitive challenges (Baddeley, 2007; Bunge & Crone, 2009). The third component of cognitive control, cognitive flexibility, refers to an ability to restructure knowledge and information based on changing situational demands (Diamond, 2006), and there is a lack of consensus regarding the functional role of this cognitive process in academic achievement (Bull & Scerif, 2001; DeStefano & LeFevre, 2004; St. Clair-Thompson & Gathercole, 2006).

During maturation, the development of a neural network involving the frontal lobes is said to relate to substantial improvements in cognitive control (Bunge, Mackey, & Whitaker, 2009). Over the course of childhood and adolescence, cognitive control function improves dramatically, with an increased ability to manage interference (Cepeda, Kramer, & Gonzalez de Sather, 2001; Ridderinkhof & van der Molen, 1995; Travis, 1998), inhibit prepotent response tendencies, and hold multiple pieces of information in the mind (Diamond & Taylor, 1996). These improvements in cognitive control are said to parallel the maturation of networks in the brain, specifically the prefrontal cortex (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Travis, 1998), the anterior cingulate cortex (ACC), and the basal ganglia, with additional contributions from the insular and parietal cortices as well as the superior frontal sulcus (Bunge & Crone, 2009; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Rueda, Rothbart, McCandliss, Saccamanno, & Posner, 2005). Given that cognitive control has been implicated as a necessary component of academic performance, and that cognitive control relates to specific brain regions, an examination of the association between physical activity/aerobic fitness and neural structures and processes underlying behavioral performance may provide additional insights into the relationship between physical activity/aerobic fitness and cognition in children.

BRAIN STRUCTURE

Neuroimaging methods (e.g., magnetic resonance imaging [MRI]; event related brain potentials [ERP]) have been used to identify potential mechanisms involved in the relationship between childhood aerobic fitness and cognitive health. In

elderly adults, MRI techniques demonstrate that participation in physical activity and increased aerobic fitness enhance brain structure and function (Colcombe & Kramer, 2003; Colcombe et al., 2004, 2006; Erickson et al., 2009, 2011), and two recent investigations were the first to use MRI methodology in a youth population to explore the relationship between aerobic fitness, brain structure, and cognition during childhood (Chaddock, Erickson, Prakash, Kim, et al., 2010; Chaddock, Erickson, Prakash, VanPatter, et al., 2010).

Specifically, recent findings from Chaddock, Erickson, Prakash, VanPatter, and colleagues (2010) suggest that deficits in cognitive control associated with poorer aerobic fitness may relate to differences in the volume of specific regions of the basal ganglia. The basal ganglia are a group of subcortical structures subdivided into the dorsal striatum, which is implicated in stimulus-response challenges that require cognitive control, and the ventral striatum, part of an affect and reward pathway (Aron, Poldrack, & Wise, 2009; Casey, Getz, & Galvan, 2008; Di Martino et al., 2008; Draganski et al., 2008; Graybiel, 2005, 2008; Ragozzino, Jih, & Tzavos, 2002). In a sample of 55 higher- and lower-fit preadolescent children ($M_{\text{age}} = 10$ years), fitness-related differences in specific volumes of the basal ganglia were examined and related to differences in a flanker task of cognitive control. The flanker task requires participants to attend to a centrally presented stimulus amid laterally presented flanking stimuli (Eriksen & Eriksen, 1974; Kramer, Humphrey, Larish, Logan, & Strayer, 1994), with greater inhibitory control requirements necessitated in response to incongruent flanking stimuli (e.g., HSHH, <<>><<) relative to congruent flanking stimuli (e.g., HHHHH, >>>>>).

Consistent with predictions, lower-fit children exhibited decreased inhibitory control coupled with a smaller dorsal striatum (Chaddock, Erickson, Prakash, VanPatter, et al., 2010). In addition, a positive association between aerobic fitness, inhibition, and volume of the globus pallidus, an "output" region of the basal ganglia (Aron et al., 2009; Di Martino et al., 2008; Draganski et al., 2008), was reported. No relationship was found between fitness, task performance, and volume of the ventral striatum, a region with functions less involved in cognitive control (Aron et al., 2009; Casey et al., 2008; Graybiel, 2005, 2008). The researchers concluded that aerobic fitness differences in flanker task performance may relate to differences in the volume of specific regions of the basal ganglia (Chaddock, Erickson, Prakash, VanPatter, et al., 2010). Of particular interest to this review, the study suggested that the dorsal striatum, a vital structure for cognitive control, motor integration, and response resolution (Aron et al., 2009), may be particularly sensitive to physical activity behaviors in children. The findings also extend non-human animal research, which has observed exercise-induced changes in the basal ganglia, to a preadolescent human population (Aguiar, Speck, Prediger, Kapczynski, & Pinho, 2008; Ding et al., 2004; Li et al., 2005; Marais, Stein, & Daniels, 2009; Marques et al., 2008; Shi, Luo, Woodward, & Chang, 2004; Tillerson et al., 2001).

In addition to the basal ganglia, volumes of other brain structures are related to aerobic fitness. Specifically, the

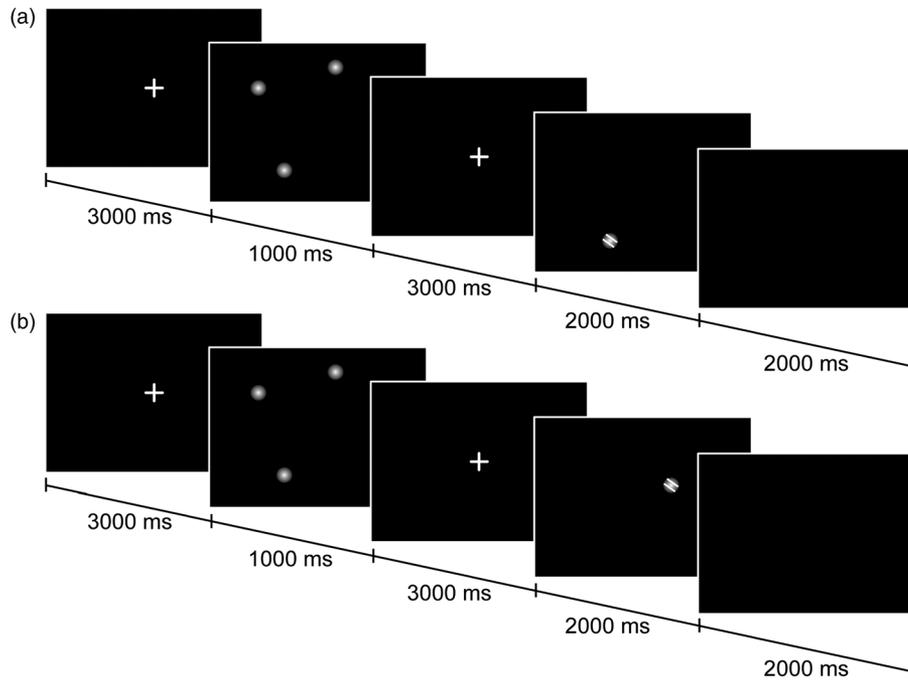


Fig. 1. Spatial Memory Task. Spatial memory is associated with hippocampal function. In the task, participants were instructed to attend to the spatial location of either one, two, or three gray circles presented for 1000 ms on a black background. Following a 3000-ms (fixation) delay, subjects were instructed to determine if a single probe red circle (illustrated via a stripped gray circle) presented for 2000 ms on a black background was in one of the same locations as the gray circle(s) (“match” condition) (a) or in a different location (“non-match” condition) (b). Participants were given 4000 ms to respond. Five blocks of 30 trials were presented with equally probable set sizes (one, two, three dots) and equally probable match/non-match conditions.

relationship between physical activity and aerobic fitness to the hippocampus has been studied in animal and human models across the lifespan (Chaddock, Erickson, Prakash, Kim, et al., 2010; Colcombe & Kramer, 2003; Cotman & Berchtold, 2002; Erickson et al., 2009, 2011; Pereira et al., 2007). The hippocampus is a subcortical brain region located in the temporal lobe, which plays a role in spatial memory as well as in the formation of new relational memories via the “binding” of individual items (Eichenbaum & Cohen, 2001). Findings from rodent models have demonstrated that wheel running positively impacts hippocampal structure and function (Cotman & Berchtold, 2002; Vaynman & Gomez-Pinilla, 2006). Furthermore, in older humans, lower levels of aerobic fitness have been associated with smaller hippocampal volumes and poorer spatial memory performance (Erickson et al., 2009).

Accordingly, Chaddock, Erickson, Prakash, Kim, et al. (2010) assessed the relationship between aerobic fitness, hippocampal volume and memory in a sample of 49 higher- and lower-fit preadolescent children (age, 9–10 years). The authors reported that lower-fit children had smaller bilateral hippocampal volumes and poorer relational memory task performance compared to higher-fit children. Bilateral hippocampal volume also served to partially mediate the relationship between childhood fitness and relational memory performance. Furthermore, hippocampal volume was positively associated with performance on the relational but not

the non-relational memory task. The specificity of the hippocampal-memory relationship (Cohen & Eichenbaum, 1993; Eichenbaum & Cohen, 2001) supports a study indicating that lower-fit preadolescents had poorer memory recognition performance when memory items were studied relationally compared to non-relationally (Chaddock, Hillman, Buck, & Cohen, 2011). More recently, we have examined whether the initial aerobic fitness level of the children in this study and their initial hippocampal volume would also predict performance on a spatial memory task (see Figure 1) 1 year later. As indicated in Figure 2, this was indeed the case. That is, both initial aerobic fitness classification and hippocampal volume predicted performance over time. Hence, fitness effects appear to extend over time in childhood. Note that the findings differ from the results of studies used in Sibley and Etnier’s (2003) meta-analysis, which suggested that physical activity is unrelated to general memory abilities in children between the ages of 4 and 18. The specific investigation of hippocampal-dependent memory and the limited age range of the samples may explain the discrepancy.

Collectively, the structural MRI results provide a starting point for a greater understanding of the neural underpinnings of cognitive enhancement through physical activity and increased aerobic fitness in preadolescent children as well as potential neural correlates of the positive associations between aerobic fitness, cognitive control (Hillman et al., 2009; Hillman, Castelli, & Buck, 2005; Pontifex et al., 2010),

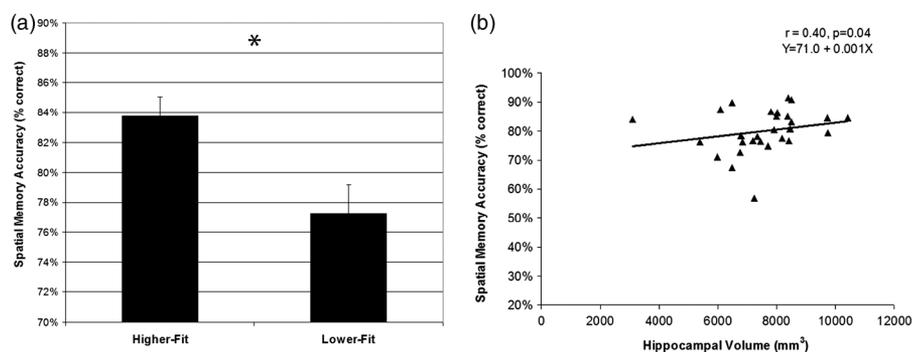


Fig. 2. Results. Children classified as higher-fit showed higher accuracy across all dot conditions of the spatial memory task one year later (a). Error bars represent standard error. * $p < .05$. Initial hippocampal volume also predicted future spatial memory accuracy (b).

and memory (Chaddock et al., 2011) in children. It is possible that cognitive enhancement through increased aerobic fitness relates to differential volumes of specific brain regions involved in cognitive function.

BRAIN FUNCTION

Beyond aerobic fitness-related differences in brain structures underlying aspects of cognition, investigations examining a class of electroencephalographic activity known as event-related brain potentials (ERPs) have suggested a positive association between aerobic fitness and neurocognitive processes that occur between stimulus engagement and response execution in preadolescent children (Hillman et al., 2005, 2009; Pontifex et al., 2010).

In particular, an ERP component called the P3 (also known as the “P300” or “P3b”) has been extensively used to characterize physical activity and aerobic fitness related differences and changes in cognition across the lifespan, with reductions in amplitude and slowing of latency associated with lower levels of fitness (Hillman, Belopolsky, Snook, Kramer, & McAuley, 2004; Hillman et al., 2006; Hillman, Weiss, Hagberg, & Hatfield, 2002; Polich & Lardon, 1997; Pontifex, Hillman, & Polich, 2009). Consonant with the hypothesis that neural inhibition underlies P3 generation (Polich, 2007), component amplitude serves to index the suppression of extraneous neuronal activity to facilitate attentional processing (Azizian & Polich, 2007; Kok, 2001; Polich, 1987; Polich & Heine, 1996), while P3 latency serves to index stimulus classification and evaluation speed independent of response selection and action (Duncan-Johnson, 1981; Verleger, 1997). Accordingly, lower levels of physical activity and aerobic fitness, which have been associated with a smaller and prolonged P3, may reflect a reduced ability to inhibit extraneous neuronal operations and delays in the processing and classification of information.

Only recently has research begun to assess the relationship between aerobic fitness and neuroelectric indices of cognition in children. In an initial investigation, Hillman and colleagues (2005) recorded neuroelectric and behavioral indices of

performance during a visual oddball task in which participants were instructed to respond to infrequent target stimuli and ignore frequent non-target stimuli. A sample of 24 pre-adolescent children ($M_{\text{age}} = 9.5$ years) and 27 young adults ($M_{\text{age}} = 19.3$ years) were divided into higher-fit and lower-fit groups based on aerobic capacity using the PACER test from the Fitnessgram (Welk, Morrow, & Falls, 2002). Findings from this investigation revealed that lower levels of aerobic fitness in children were associated with longer reaction time (RT) and decreased response accuracy, while higher-fit children were not behaviorally different than either adult group. In addition, lower aerobic fitness levels, regardless of age, were associated with longer P3 latency, with decreased P3 amplitude evidenced only for lower-fit children. Of interest, recent evidence from Hillman et al. (manuscript submitted for publication) suggests that the P3 may be a neuroelectric biomarker for academic achievement in children, with larger amplitude reflecting increased inhibitory and working memory capacities in the service of mathematics and reading achievement. Together, the reported relation of childhood fitness to P3 (Hillman et al., 2005) replicates findings observed in younger and older adults (Hillman et al., 2002, 2004, 2006; Polich & Lardon, 1997; Pontifex et al., 2009), and suggests that poorer aerobic fitness is associated with failures in attentional processes, which may relate to scholastic achievement.

Building from these investigations, Hillman et al. (2009) and Pontifex et al. (2010) examined the relation of aerobic fitness to neuroelectric indices of cognitive control in 9- to 10-year-old children. Using a cross-sectional design, Hillman et al. (2009) examined neuroelectric and behavioral indices of cognition in response to a modified flanker task in a sample of 38 higher- and lower-fit children ($M_{\text{age}} = 9.4$ years), who were assigned based on aerobic capacity as measured by the PACER test from the Fitnessgram (Welk et al., 2002). As an extension of this research, Pontifex et al. (2010) assessed neuroelectric and behavioral indices of cognitive control in response to stimulus-response compatible and incompatible conditions of the modified flanker task (Friedman, Nessler, Cyncowicz, & Horton, 2009) in a sample of 48 higher- and

lower-fit preadolescent children ($M_{\text{age}} = 10.1$ years), assigned based on aerobic capacity. The addition of the incompatible condition of the flanker task served to manipulate task difficulty between the stimulus-response compatible and incompatible conditions through multiple levels of perceptual and response conflict. Findings from these investigations indicated that poorer aerobic fitness was associated with decreased overall response accuracy (Hillman et al., 2009; Pontifex et al., 2010), as well as a selectively larger reduction in response to the most cognitively demanding task condition (Pontifex et al., 2010), with no changes in reaction time. In contrast, higher-fit participants were able to maintain a high level of performance across variable task demands (Pontifex et al., 2010). Furthermore, lower amounts of fitness were associated with smaller P3 amplitude (Hillman et al., 2009; Pontifex et al., 2010) and longer P3 latency (Pontifex et al., 2010), with higher-fit participants exhibiting a greater modulation of P3 amplitude to meet increased task demands (Pontifex et al., 2010).

In addition, lower-fit children demonstrated increased amplitude for the response-locked error-related negativity component (ERN; Hillman et al., 2009; Pontifex et al., 2010). The ERN, which neuroimaging research has indicated is generated in the dorsal portion of the ACC (Carter et al., 1998; Dehaene, Posner, & Tucker, 1994; Miltner et al., 2003; van Veen & Carter, 2002), is believed to reflect initiation of action monitoring processes in response to conflicting or erroneous behaviors to activate top-down compensatory processes (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring & Knight, 2000; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). This increase in ERN amplitude with poorer aerobic fitness corroborates previous investigations in adult populations, which have observed larger ERN and increased ACC activation for lower-fit participants, relative to their aerobically trained counterparts (Colcombe et al., 2004; Themanson & Hillman, 2006; Themanson, Hillman, & Curtin, 2006; Themanson, Pontifex, & Hillman, 2008). Further replicating findings in adults (Themanson et al., 2008), higher-fit participants exhibited a greater ability to flexibly modulate action monitoring processes in response to increasing task demands (Pontifex et al., 2010).

Together, studies using neuroelectric methods suggest that lower levels of aerobic fitness are associated with poorer integrity of cognitive control processes, with a decreased ability to begin the cascade of processes required to signal the need for additional top-down control, allocate attention toward actions, efficiently process environmental information, and flexibly modulate cognitive control processes to optimize behavioral interactions within the environment. Preliminary functional MRI (fMRI) data support the ERP findings by demonstrating that lower-fit children have increased activity in prefrontal brain regions associated with response execution, attentional control, and inhibition (e.g., middle frontal gyrus, ACC) under greater cognitive control demands, coupled with a disproportionate flanker performance cost in accuracy with increasing task difficulty, relative to higher-fit children (Voss et al., submitted).

FUTURE DIRECTIONS

Despite the research reviewed above, there are still several gaps in our understanding of the relation of physical activity and fitness to cognitive and brain health in children. Several avenues for future research are suggested below, which may provide greater understanding of the relationship between childhood health behaviors, brain health, and cognitive function.

Research is needed to understand the optimal physical activity criteria that target cognitive and brain health in children. That is, the frequency, intensity, duration, and mode of physical activity that provides the greatest synergistic benefit for scholastic achievement and neurocognitive health during childhood remain unknown. It would also be interesting to examine the relationship between other facets of physical fitness (e.g., muscular strength) and childhood neurocognition. Furthermore, the extent to which other interventional techniques (e.g., nutrition, social interaction) should be combined with physical activity to maximize long-term benefits for cognitive health and to create more permanent changes in childhood behavior also remains to be investigated.

To date, the majority of research studies assessing fitness and cognition in children have been cross-sectional in nature. Longitudinal randomized controlled trials are necessary to elucidate the causal influence between physical activity, brain structure, and brain processes. In older adults, several clinical trials in which sedentary individuals are randomized to an aerobic training group and a control group of nonaerobic activity demonstrate that aerobic exercise training can improve cognitive task performance, increase the efficiency of brain function, and moderate the trajectory of age-related brain tissue loss (Colcombe et al., 2003, 2004; Colcombe & Kramer, 2003; Heyn, Abreu, & Ottenbacher, 2004; Kramer et al., 1999; Pereira et al., 2007). Similar designs with a childhood population would significantly extend cross-sectional studies of the positive relationship between physical activity, aerobic fitness, brain, cognition, and scholastic achievement during development. In addition, the relationship between fitness, exercise, and cognition in children with cognitive and social disorders (e.g., attention deficit disorder) is an important topic for future research.

Another avenue for study involves the specific cognitive abilities that relate most to physical activity and fitness during childhood. For example, more research is required to conclude a general association between physical activity and all aspects of cognitive function (Sibley & Etnier, 2003) or for tasks with increased cognitive control (Pontifex et al., 2010). It is also important to explore whether the benefits of aerobic fitness in children extend outside the laboratory to everyday functioning such as street-crossing abilities and learning in a didactic environment.

Additional neuroimaging techniques should be used to gain insight into the relationships between childhood fitness and brain health, including white matter tract conductivity, functional connectivity, and cortical brain volume measures. The role of genetic profiles may also be assessed to determine if children with certain genetic profiles show greater benefits

from aerobic exercise. Variations in the brain-derived neurotrophic factor (BDNF) gene, for example, may play a role in determining the efficacy of high levels of aerobic fitness or physical activity participation given that the proteins and mRNA levels of this gene are affected by exercise in animal models (Vaynman, Ying, & Gomez-Pinilla, 2004). It would also be interesting to explore the relationship between childhood resistance training and levels of IGF-1 (insulin-like growth factor-1), a hormone involved in growth during development, given an association between these variables in an elderly population (Liu-Ambrose & Donaldson, 2009).

Finally, while some understanding of the mechanisms supporting exercise-induced changes in cognition is provided through research using animal models, many of the molecular and cellular details for aerobic fitness differences in the human brain remain to be discovered. Findings in rodent models have observed that wheel-running serves to increase cellular proliferation and survival in the dentate gyrus of the hippocampus in young adulthood through old age (Eadie et al., 2005; van Praag, Christie, Sejnowski, & Gage, 1999; van Praag, Shubert, Zhao, & Gage, 2005), enhance hippocampal-dependent learning and memory (Fordyce & Wehner, 1993; van Praag et al., 2005; Vaynman et al., 2004), and increase hippocampal levels of neural molecules involved in neuronal survival, synaptic development, learning, and angiogenesis (Barde, 1994; Berchtold, Chinn, Chou, Kessler, & Cotman, 2005; Cotman & Berchtold, 2002; Lopez-Lopez, LeRoith, & Torres-Aleman, 2004; Lu & Chow, 1999; Neeper, Gomez-Pinilla, Choi, & Cotman, 1995; Vaynman et al., 2004). Rodent wheel-running has also been found to influence the striatum via an increase in the production and secretion of striatal brain-derived neurotrophic factor (Aguiar et al., 2008; Marais et al., 2009), dopamine (Marques et al., 2008; Tillerson et al., 2001), astrocyte proliferation (Li et al., 2005), neural activity (Shi et al., 2004), and angiogenesis (Ding et al., 2004). Given that these neurochemical processes are critical to human brain development and organization, which involve changes in cell proliferation/apoptosis, dendritic branching/pruning, synaptic formation/elimination, growth factors, and myelination (Anderson, 2003; Giedd et al., 1996, 1999; Gogtay et al., 2004), it seems possible that aerobic fitness may impact the brain during childhood, a period of significant cognitive and neural development (Caviness, Kennedy, Richelme, Rademacher, & Filipek, 1996; Casey, Tottenham, Liston, & Durston, 2005). Further research is necessary to elucidate the extent to which findings from animal models translate to human models.

CONCLUSION

Collectively, the reviewed findings converge across multiple domains to suggest the potentially deleterious effects of physical inactivity and poorer aerobic fitness on brain structures and functions, which underlie aspects of school-based scholastic performance. The data speak to the importance of physical activity and aerobic fitness for maximizing brain health and cognitive function during development. Since

physical activity behaviors are often established during pre-adolescent childhood (Pate, Baranowski, Dowda, & Trost, 1996), the creation and maintenance of physical activity opportunities within school—where children spend the majority of their day—may provide a means of increasing and/or maintaining health and effective functioning across the lifespan. Indeed, as reviewed above aerobic fitness level at one point in time can predict cognition in the future. In summary, the extant literature highlights the interaction between physical health, brain, and cognitive abilities underlying aspects of academic achievement, which with further research may serve to promote legislative changes directed at the creation of more physical activity opportunities for our children and the promotion of increased quality of life.

ACKNOWLEDGMENTS

Support for our research and the preparation of this manuscript was provided by grants from the National Institute on Aging to Arthur Kramer (RO1 AG25667 and RO1 AG25302), the National Institute of Child Health and Human Development (NICHD) to Charles Hillman (RO1 HD055352), and a fellowship awarded to Matthew Pontifex through the NICHD Developmental Psychobiology and Neurobiology Training Grant at the University of Illinois (2 T32 HD007333).

REFERENCES

- Aguiar, A.S., Speck, A.E., Prediger, R.D., Kapczynski, F., & Pinho, R.A. (2008). Downhill training upregulates mice hippocampal and striatal brain-derived neurotrophic factor levels. *Journal of Neural Transmission*, *115*, 1251–1255.
- Anderson, S.L. (2003). Trajectories of brain development: Point of vulnerability or window of opportunity? *Neuroscience & Biobehavioral Reviews*, *27*, 3–18.
- Anderson, R.E., Crespo, C.J., Barlett, S.J., Cheskin, L.J., & Pratt, M. (1998). Relationship of physical activity and television watching with body weight and level of fatness among children. *The Journal of the American Medical Association*, *279*, 938–942.
- Aron, A.R., Poldrack, R.A., & Wise, S.P. (2009). Cognition: Basal ganglia role. *Encyclopedia of Neuroscience*, *2*, 1069–1077.
- Azizian, A., & Polich, J. (2007). Evidence for attentional gradient in the serial position memory curve from event-related potentials. *Journal of Cognitive Neuroscience*, *19*, 2071–2081.
- Baddeley, A.D. (2007). *Working Memory, Thought and Action*. Oxford: Oxford University Press.
- Barde, Y.A. (1994). Neurotrophins: A family of proteins supporting the survival of neurons. *Progress in Clinical Biological Research*, *390*, 45–56.
- Barkley, R.A. (1997). Behavioral inhibition, sustained attention, and executive functions. *Psychological Bulletin*, *121*, 65–94.
- Berchtold, N.C., Chinn, G., Chou, M., Kessler, J.P., & Cotman, C.W. (2005). Exercise primes a molecular memory for brain-derived neurotrophic factor protein induction in the rat hippocampus. *Neuroscience*, *133*, 853–861.
- Booth, F.W., & Lees, S.J. (2006). Physically active subjects should be the control group. *Medicine & Science in Sports & Exercise*, *38*, 405–406.

- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., & Cohen, J.D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*, 624–652.
- Brocki, K.C., & Brohlin, G. (2004). Executive functions in children aged 6–13: A dimensional and developmental study. *Developmental Neuropsychology*, *26*, 571–593.
- Buckworth, J., & Dishman, R.K. (2002). *Exercise Psychology*. Champaign, IL: Human Kinetics.
- Bull, R., & Scerif, G. (2001). Executive functioning as a predictor of children's mathematics ability: Inhibition, switching, and working memory. *Developmental Neuropsychology*, *19*, 273–293.
- Bunge, S.A., & Crone, E.A. (2009). Neural correlates of the development of cognitive control. In J.M. Rumsey & M. Ernst (Eds.), *Neuroimaging in Developmental Clinical Neuroscience*. Cambridge, UK: Cambridge University Press.
- Bunge, S.A., Dudukovic, N.M., Thomason, M.E., Vaidya, C.J., & Gabrieli, J.D. (2002). Immature frontal lobe contributions to cognitive control in children: Evidence from fMRI. *Neuron*, *33*, 301–311.
- Bunge, S.A., Mackey, A.P., & Whitaker, K.J. (2009). Brain changes underlying the development of cognitive control and reasoning. In M.S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (4th ed.). Cambridge, MA: MIT Press.
- Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D., & Cohen, J.D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, *280*, 747–749.
- Casey, B.J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review*, *28*, 62–77.
- Casey, B.J., Tottenham, N., Liston, C., & Durston, S. (2005). Imaging the developing brain: What have we learned about cognitive development? *Trends in Cognitive Sciences*, *9*, 104–110.
- 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*, 239–252.
- Caviness, V.S., Kennedy, D.N., Richelme, C., Rademacher, J., & Filipek, P.A. (1996). The human brain age 7–11 years: A volumetric analysis based on magnetic resonance images. *Cerebral Cortex*, *6*, 726–736.
- Centers for Disease Control and Prevention. (2010). *The Association Between School Based Physical Activity, Including Physical Education, and Academic Performance*. Atlanta, GA: Department of Health and Human Services.
- Cepeda, N.J., Kramer, A.F., & Gonzalez de Sather, J.C. (2001). Changes in executive control across the lifespan: Examination of task switching performance. *Developmental Psychology*, *37*, 715–730.
- Chaddock, L., Erickson, K.I., Prakash, R.S., Kim, J.S., Voss, M.W., VanPatter, M., ... Kramer, A.F. (2010). 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.V., Pontifex, M.B., ... Kramer, A.F. (2010). Basal ganglia volume is associated with aerobic fitness in preadolescent children. *Developmental Neuroscience*, *32*, 249–256.
- Chaddock, L., Hillman, C.H., Buck, S.M., & Cohen, N.J. (2011). Aerobic fitness and executive control of relational memory in preadolescent children. *Medicine & Science in Sports & Exercise*, *43*, 344–349.
- Chomitz, V.R., Slining, M.M., McGowan, R.J., Mitchell, S.E., Dawson, G.F., & Hacker, K.A. (2009). Is there a relationship between physical fitness and academic achievement?: Positive results from public school children in the northeastern United States. *Journal of School Health*, *79*, 30–37.
- Cohen, N.J., & Eichenbaum, H. (1993). *Memory, Amnesia, and the Hippocampal System*. Cambridge, MA: MIT Press.
- Colcombe, S.J., Erickson, K.I., Raz, N., Webb, A.G., Cohen, N.J., McAuley, E., & Kramer, A.F. (2003). Aerobic fitness reduces brain tissue loss in aging humans. *Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *58*, 176–180.
- Colcombe, S.J., Erickson, K.I., Scalf, P.E., Kim, J.S., Prakash, R., McAuley, E., ... Kramer, A.F. (2006). Aerobic exercise training increases brain volume in aging humans. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *61*, 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*, 125–130.
- Colcombe, S.J., Kramer, A.F., Erickson, K.I., Scalf, P., McAuley, E., Cohen, N.J., ... Elavsky, S. (2004). Cardiovascular fitness, cortical plasticity, and aging. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 3316–3321.
- Cooper Institute for Aerobics Research (1999). *Fitnessgram: Test administration manual*. Champaign, IL: Human Kinetics.
- Cotman, C.W., & Berchtold, N.C. (2002). Exercise: A behavioral intervention to enhance brain health and plasticity. *Trends in Neurosciences*, *25*, 295–301.
- Davidson, M.C., Amso, D., Anderson, L.C., & Diamond, A. (2006). Development of cognitive control and executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and task switching. *Neuropsychologia*, *44*, 2037–2078.
- Dehaene, S., Posner, M.I., & Tucker, D.M. (1994). Localization of a neural system for error detection and compensation. *Psychological Science*, *5*, 303–305.
- Department of Health and Human Services [DHHS] and Department of Education [DOE]. (2000). Promoting better health for young people through physical activity and sports. *A Report to the President from the Secretary of Health and Human Services and the Secretary of Education*. Silver Spring, MD: Centers for Disease Control.
- DeStefano, D., & LeFevre, J.A. (2004). The role of working memory in mental arithmetic. *European Journal of Cognitive Psychology*, *16*, 353–386.
- Di Martino, A., Scheres, A., Margulies, D.S., Kelly, A.M., Uddin, L.Q., Shehzad, Z., ... Milham, M.P. (2008). Functional connectivity of human striatum: A resting state fMRI study. *Cerebral Cortex*, *18*, 2735–2747.
- Diamond, A. (2006). The early development of executive functions. In E. Bialystok, & F.I.M. Craik (Eds.), *Lifespan Cognition: Mechanisms of Change*. New York: Oxford University Press.
- Diamond, A., & Taylor, C. (1996). Development of an aspect of executive control: Development of the abilities to remember what I say and to “do as I say, not as I do”. *Developmental Psychobiology*, *29*, 315–334.
- Ding, Y.H., Luan, X.D., Li, J., Rafols, J.A., Guthinkonda, M., Diaz, F.G., & Ding, Y. (2004). Exercise-induced overexpression of angiogenic factors and reduction of ischemia/reperfusion injury in stroke. *Current Neurovascular Research*, *1*, 411–420.
- Donnelly, J.E., Greene, J.L., Gibson, C.A., Smith, B.K., Washburn, R.A., Sullivan, D.K., ... Williams, S.L. (2009). Physical activity

- across the curriculum (PAAC): A randomized controlled trial to promote physical activity and diminish overweight and obesity in elementary school children. *Preventative Medicine*, *49*, 336–341.
- Draganski, B., Kherif, F., Klöppel, S., Cook, P.A., Alexander, D.C., Parker, G.J., ... Frackowiak, R.S. (2008). Evidence for segregated and integrative connectivity patterns in the human basal ganglia. *The Journal of Neuroscience*, *28*, 7143–7152.
- Duncan-Johnson, C.C. (1981). P3 latency: A new metric of information processing. *Psychophysiology*, *18*, 207–215.
- Eadie, B.D., Redilla, V.A., & Christie, B.R. (2005). Voluntary exercise alters the cytoarchitecture of the adult dentate gyrus by increasing cellular proliferation, dendritic complexity, and spine density. *The Journal of Comparative Neurology*, *486*, 39–47.
- Eichenbaum, H., & Cohen, N.J. (2001). *From Conditioning to Conscious Recollection: Memory Systems of the Brain*. New York: Oxford University Press.
- Erickson, K.I., Prakash, R.S., Voss, M.W., Chaddock, L., Hu, L., Morris, K.S., ... Kramer, A.F. (2009). Aerobic fitness is associated with hippocampal volume in elderly humans. *Hippocampus*, *19*, 1030–1039.
- Erickson, K.I., Voss, M., Prakash, R., Basak, C., Chaddock, L., Kim, J., ... Kramer, A.F. (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), 3017–3022.
- Eriksen, B.A., & Eriksen, C.W. (1974). Effects of noise letters on the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, *16*, 143–149.
- Etnier, J.L., Salazar, W., Landers, D.M., Petruzello, S.J., Han, M., & Nowell, P. (1997). The influence of physical fitness and exercise upon cognitive functioning: A meta-analysis. *Journal of Sport and Exercise Psychology*, *19*, 249–277.
- Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalography and Clinical Neurophysiology*, *78*, 447–455.
- Fordyce, D.E., & Wehner, J.M. (1993). Physical activity enhances spatial learning performance with an associated alteration in hippocampal protein kinase C activity in C57BL/6 and DBA/2 mice. *Brain Research*, *619*, 111–119.
- Freedman, D.S., Khan, L.K., Dietz, W.H., Srinivasan, S.R., & Berenson, G.S. (2001). Relationship of childhood obesity to coronary heart disease risk factors in adulthood: The Bogalusa heart study. *Pediatrics*, *108*, 712–718.
- Friedman, D., Nessler, D., Cycowicz, Y.M., & Horton, C. (2009). Development of and change in cognitive control: A comparison of children, young adults, and older adults. *Cognitive, Affective, & Behavioral Neuroscience*, *9*, 91–102.
- Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, *4*, 385–390.
- Gehring, W.J., & Knight, R.T. (2000). Prefrontal-cingulate interactions in action monitoring. *Nature Neuroscience*, *3*, 516–520.
- Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Liu, H., Zijdenbos, A., ... Rapoport, J.L. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, *2*, 861–863.
- Giedd, J.N., Snell, J.W., Lange, N., Rajapakse, J.C., Casey, B.J., Kozuch, P.L., ... Rapoport, J.L. (1996). Quantitative magnetic resonance imaging of human brain development: Ages 4–18. *Cerebral Cortex*, *6*, 551–560.
- Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzid, A.C., ... Thompson, P.M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 8147–8179.
- Graybiel, A.M. (2005). The basal ganglia: Learning new tricks and loving it. *Current Opinion in Neurobiology*, *15*, 638–644.
- Graybiel, A.M. (2008). Habits, rituals and the evaluative brain. *Annual Review of Neuroscience*, *31*, 359–387.
- Grissom, J.B. (2005). Physical fitness and academic achievement. *Journal of Exercise Physiology Online*, *8*, 11–25.
- Heyn, P., Abreu, B.C., & Ottenbacher, K.J. (2004). The effects of exercise training on elderly persons with cognitive impairment and dementia: A meta-analysis. *Archives of Physical Medicine and Rehabilitation*, *85*, 1694–1704.
- 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*, 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 of executive control in preadolescent children. *Developmental Psychology*, *45*, 114–129.
- Hillman, C.H., Castelli, D.M., & Buck, S.M. (2005). Aerobic fitness and neurocognitive function in healthy preadolescent children. *Medicine & Science in Sports & Exercise*, *37*, 1967–1974.
- 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*, 58–65.
- Hillman, C.H., Kramer, A.F., Belopolsky, A.V., & Smith, D.P. (2006). 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*, 30–39.
- Hillman, C.H., Pontifex, M.B., Motl, R.W., O’Leary, K.C., Johnson, C.R., Scudder, M.R., ... Castelli, D.M. (submitted). From ERPs to academics.
- Hillman, C.H., Weiss, E.P., Hagberg, J.M., & Hatfield, B.D. (2002). The relationship of age and cardiovascular fitness to cognitive and motor processes. *Psychophysiology*, *39*, 303–312.
- Jensen, A.R. (1992). The importance of intraindividual variation in reaction time. *Personality and Individual Differences*, *13*, 869–881.
- Jensen, A.R. (1998). *The g factor: The science of mental ability*. Westport, CT: Praeger.
- Juster, T.F., Stafford, F., & Ono, H. (2004). *Major changes have taken place in how children and teens spend their time: Child development supplement*. Ann Arbor, MI: Institute for Social Research, University of Michigan.
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*, 557–577.
- Kramer, A.F., Hahn, S., Cohen, N., Banich, M., McAuley, E., Harrison, C., ... Colcombe, A. (1999). Aging, fitness, and neurocognitive function. *Nature*, *400*, 418–419.
- Kramer, A.F., Humphrey, D.G., Larish, J.F., Logan, G.B., & Strayer, D.L. (1994). Aging and inhibition: Beyond a unitary view of inhibitory processing in attention. *Psychology and Aging*, *9*, 491–512.
- Li, J., Ding, Y.H., Rafols, J.A., Lai, Q., McAllister, J.P., & Ding, Y. (2005). Increased astrocyte proliferation in rats after running exercise. *Neuroscience Letters*, *386*, 160–164.

- Liu-Ambrose, T., & Donaldson, M. (2009). Exercise and cognition in older adults: Is there a role for resistance training programmes? *British Journal of Sports Medicine, 43*, 25–27.
- Lopez-Lopez, C., LeRoith, D., & Torres-Aleman, I. (2004). Insulin-like growth factor I is required for vessel remodeling in the adult brain. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 9833–9838.
- Lu, B., & Chow, A. (1999). Neurotrophins and hippocampal synaptic transmission and plasticity. *Journal of Neuroscience Research, 58*, 176–180.
- MacDonald, A.W., Cohen, J.D., Stenger, V.A., & Carter, C.S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science, 288*, 1835–1838.
- Mahar, M.T., Murphy, S.K., Rowe, D.A., Golden, J., Shields, A.T., & Raedeke, T.D. (2006). Effects of a classroom-based program on physical activity and on-task behavior. *Medicine & Science in Sports & Exercise, 38*, 2086–2094.
- Marais, L., Stein, D.J., & Daniels, W.M. (2009). Exercise increases BDNF levels in the striatum and decreases depressive-like behavior in chronically stressed rats. *Metabolic Brain Disease, 24*, 587–597.
- Marques, E., Vasconcelos, F., Rolo, M.R., Pereira, F.C., Silva, A.P., Macedo, T.R., & Ribeiro, C.F. (2008). Influence of chronic exercise on the amphetamine-induced dopamine release and neurodegeneration in the striatum of the rat. *Annals of the New York Academy of Sciences, 1139*, 222–231.
- Meyer, D.E., & Kieras, D.E. (1997). A computational theory of executive cognitive processes and multi-task performance: Part 1. Basic Mechanisms. *Psychological Review, 104*, 3–65.
- Miltner, W.H., Lemke, U., Weiss, T., Holroyd, C., Scheffers, M.K., & Coles, M.G. (2003). Implementation of error-processing in the human anterior cingulate cortex: A source analysis of the magnetic equivalent of the error-related negativity. *Biological Psychology, 64*, 157–166.
- Miyake, A., Friedman, N.P., Emerson, M.J., Witzki, A.H., & Howerter, A. (2000). The unity and diversity of executive functions and their contributions to complex “frontal lobe” tasks: A latent variable analysis. *Cognitive Psychology, 41*, 49–100.
- Neeper, S., Gomez-Pinilla, F., Choi, J., & Cotman, C.W. (1995). Exercise and brain neurotrophins. *Nature, 373*, 109.
- Nieuwenhuis, S., Ridderinkhof, K.R., Blom, J., Band, G.P., & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task. *Psychophysiology, 38*, 752–760.
- Norman, D.A., & Shallice, T. (1986). Attention to action: Willed and automatic control of behavior. In R.J. Davidson G.E. Schwartz & D. Shapiro (Eds.), *Consciousness and Self-Regulation: Vol. 4. Advances in Research and Theory*. New York: Plenum Press.
- Ogden, C., & Carroll, M. (2010). Prevalence of Obesity Among Children and Adolescents: United States, Trends 1963–1965 Through 2007–2008. Retrieved from http://www.cdc.gov/nchs/data/hestat/obesity_child_07_08/obesity_child_07_08.pdf
- Olshansky, S.J., Passaro, D.J., Hershow, R.C., Layden, J., Carnes, B.A., Brody, J., ... Ludwig, D.S. (2005). A potential decline in life expectancy in the United States in the 21st century. *The New England Journal of Medicine, 352*, 1138–1143.
- Pate, R.R., Baranowski, T., Dowda, M., & Trost, S. (1996). Tracking of physical activity in young children. *Medicine & Science in Sports & Exercise, 28*, 92–96.
- Peligrini, A.D., & Smith, P.K. (1993). School recess: Implications for education and development. *Review of Educational Research, 63*, 51–67.
- Pereira, A.C., Huddleston, D.E., Brickman, A.M., Sosunov, A.A., Hen, R., McKhann, G.M., ... Small, S.A. (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*, 5638–5643.
- Polich, J. (1987). Task difficulty, probability and inter-stimulus interval as determinants of P300 from auditory stimuli. *Electroencephalography and Clinical Neurophysiology, 63*, 251–259.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology, 118*, 2128–2148.
- Polich, J., & Heine, M.R. (1996). P3 topography and modality effects from a single-stimulus paradigm. *Psychophysiology, 33*, 747–752.
- Polich, J., & Lardon, M. (1997). P300 and long-term physical exercise. *Electroencephalography and Clinical Neurophysiology, 103*, 493–498.
- Pontifex, M.B., Hillman, C.H., & Polich, J. (2009). Age, physical fitness, and attention: P3a and P3b. *Psychophysiology, 46*, 379–387.
- Pontifex, M.B., Raine, L.B., Johnson, C.R., Chaddock, L., Voss, M.W., Cohen, N.J., ... Hillman, C.H. (2010). Cardiorespiratory fitness and the flexible modulation of cognitive control in preadolescent children. *Journal of Cognitive Neuroscience*, [Epub ahead of print].
- Ragozzino, M.E., Jih, J., & Tzavos, A. (2002). Involvement of the dorsomedial striatum in behavioral flexibility: Role of muscarinic cholinergic receptors. *Brain Research, 953*, 205–214.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science, 306*, 443–447.
- Ridderinkhof, K.R., & van der Molen, M.W. (1995). A psychophysiological analysis of developmental differences in the ability to resist interference. *Child Development, 66*, 1040–1056.
- Roberts, C.K., Freed, B., & McCarthy, W.J. (2010). Low aerobic fitness and obesity are associated with lower standardized test scores in children. *The Journal of Pediatrics, 156*, 711–718.
- Rohde, T.E., & Thompson, L.A. (2007). Predicting academic achievement with cognitive ability. *Intelligence, 35*, 83–92.
- Rueda, M.R., Rothbart, M.K., McCandliss, B.D., Saccomanno, L., & Posner, M.I. (2005). Training, maturation, and genetic influences on the development of executive attention. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 14931–14936.
- Sallis, J.F., McKenzie, T.L., Kolody, B., Lewis, M., Marshall, S., & Rosengard, P. (1999). Effects of health-related physical education on academic achievement: Project SPARK. *Research Quarterly for Exercise and Sport, 70*, 127–134.
- Shi, L.H., Luo, F., Woodward, D.J., & Chang, J.Y. (2004). Neural responses in multiple basal ganglia regions during spontaneous and treadmill locomotion tasks in rats. *Experimental Brain Research, 157*, 303–314.
- Sibley, B.A., & Etnier, J.L. (2003). The relationship between physical activity and cognition in children: A meta-analysis. *Pediatric Exercise Science, 15*, 243–256.
- Sisson, S.B., Church, T.S., Martin, C.K., Tudor-Locke, C., Smith, S.R., Bouchard, C., ... Katzmarzyk, P.T. (2009). Profiles of sedentary behavior in children and adolescents: The US national health and nutrition examination survey, 2001–2006. *International Journal of Pediatric Obesity, 4*, 353–359.

- Smith, P.J., Blumenthal, J.A., Hoffman, B.M., Cooper, H., Strauman, T.A., Welsh-Bohmer, K., ... Sherwood, A. (2010). Aerobic exercise and neurocognitive performance: A meta-analytic review of randomized controlled trials. *Psychosomatic Medicine*, *72*, 239–252.
- St. Clair-Thompson, H.L., & Gathercole, S.E. (2006). Executive functions and achievements in school: Shifting, updating, inhibition, and working memory. *The Quarterly Journal of Experimental Psychology*, *59*, 745–759.
- The Psychological Corporation. (2001). *WIAT-II-A: Wechsler Individual Achievement Test-Second Edition*. San Antonio: The Psychological Corporation.
- Themanson, J.R., & Hillman, C.H. (2006). Cardiorespiratory fitness and acute aerobic exercise effects on neuroelectric and behavioral measures of action monitoring. *Neuroscience*, *141*, 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*, 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*, 319–328.
- Tillerson, J.L., Cohen, A.D., Philhower, J., Miller, G.W., Zigmond, M.J., & Schallert, T. (2001). Forced limb-use effects on the behavioral and neurochemical effects of 6-hydroxydopamine. *The Journal of Neuroscience*, *21*, 4427–4435.
- Travis, F. (1998). Cortical and cognitive development in 4th, 8th, and 12th grade students: The contribution of speed of processing and executive functioning to cognitive development. *Biological Psychology*, *48*, 37–56.
- van Praag, H., Christie, B.R., Sejnowski, T.J., & Gage, F.H. (1999). Running enhances neurogenesis, learning, and long-term potentiation in mice. *Neurobiology*, *96*, 13427–13431.
- van Praag, H., Shubert, T., Zhao, C., & Gage, F.H. (2005). Exercise enhances learning and hippocampal neurogenesis in aged mice. *The Journal of Neuroscience*, *25*, 8680–8685.
- van Veen, V., & Carter, C.S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*, *14*, 593–602.
- Vaynman, S., & Gomez-Pinilla, F. (2006). Revenge of the “sit”: How lifestyle impacts neuronal and cognitive health through molecular systems that interface energy metabolism with neuronal plasticity. *Journal of Neuroscience Research*, *84*, 699–715.
- Vaynman, S., Ying, Z., & Gomez-Pinilla, F. (2004). Hippocampal BDNF mediates the efficacy of exercise on synaptic plasticity and cognition. *European Journal of Neuroscience*, *20*, 2580–2590.
- Verleger, R. (1997). On the utility of P3 latency as an index of mental chronometry. *Psychophysiology*, *34*, 131–156.
- Voss, M.W., Chaddock, L., Kim, J.S., VanPatter, M., Pontifex, M.B., Raine, L.B., ... Kramer, A.F. (submitted). Aerobic fitness is associated with greater efficiency of the network underlying cognitive control in preadolescent children. *Journal of Neuroscience*.
- Welk, G.J., Morrow, J.R.J., & Falls, H.B. (2002). *Fitnessgram Reference Guide*. Dallas, TX: The Cooper Institute.