CHAPTER 6

Physical Activity and Neurocognitive Function Across the Life Span

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In recent years, there has been growing interest in the relationship between physical activity and cognition. Researchers have sought to determine the exact nature of this relationship to better understand factors that relate to increased health and effective functioning. The issue of cognitive health and function becomes especially relevant for individuals in the late stages of the human life span. A wealth of evidence now exists that demonstrates both general and selective decrements in cognition associated with advanced aging. Thus the investigation of lifestyle factors that may ameliorate or protect against cognitive loss during aging has gained interest among researchers and practitioners across a variety of health-related fields.

One aspect of cognition that is particularly amenable to physical activity intervention is executive control (see Colcombe & Kramer, 2003 for review). Researchers have outlined a number of cognitive processes that are influenced by aerobic exercise participation. Of interest, older adults exhibit disproportionate decrements in executive control relative to other types of cognition. The determination of lifestyle factors that protect against loss of executive function is particularly relevant. Accordingly, one purpose of this chapter is to review the executive control literature and describe the relationship of aging to this aspect of cognition.

Beyond behavioral measures of cognition, a growing literature base has emerged that incorporates neuroimaging to better determine the functional neuroanatomy and specific cognitive processes involved in information processing that are influenced by physical activity participation. One such measure is that of event-related brain potentials (ERPs), which index neuroelectric activation associated with specific cognitive processes. The main focus of this chapter is to examine physical activity effects on ERP indices of cognition. Although a number of other neuroimaging and behavioral techniques have been used to examine this relationship, they are beyond the scope of the chapter and therefore are not discussed in extensive detail (see Kramer & Hillman, 2006 for review of these other neuroimaging techniques).

Before turning attention to the relationship of physical activity to the brain and cognition, we provide background on the literature pertaining to executive control, cognitive aging, and the neuroelectric system to offer a rationale for why physical activity may be well suited to increasing the cognitive health and effective functioning of individuals during the late stages of the human life span. We then present an argument for providing physical activity interventions earlier in the life span, since recent evidence from our laboratory indicates that physical activity participation is related to cognitive health and function in preadolescent children. The chapter concludes with discussion on the limitations of the empirical research completed thus far and suggests several directions to guide future research efforts.

Executive Control

The term "executive control" has been used to describe a subset of processes concerned with the selection, scheduling, and coordination of the computational processes responsible for perception, memory, and action (Meyer & Keiras, 1997; Norman & Shallice, 1986). Executive processes require conscious awareness, are functionally distinct from the processes they organize, and are limited in their resources (Rogers & Monsell, 1995). Because of these characteristics, tasks requiring executive processes do not habituate or become automatic over time.

One proposed theoretical model of executive control (Norman & Shallice, 1986) assumes a top-down approach to cognitive processing and action execution. This model suggests that multiple subsystems interact and are under the control of two distinct mechanisms: contention scheduling and the supervisory attentional system (SAS). Contention scheduling is the lower-order level of control, which automatically selects action schemas to execute well-learned processes that are active until goal attainment or inhibition by a competing schema or supervisory control. Thus, adoption of the appropriate response to a task (i.e., a task-set or action schema) does not typically involve the intervention of the executive mechanism. In most instances, the suitable task-set can be automatically selected through the contention scheduling process. However, in some instances an action schema or task-set may not be available to achieve control of the desired behavior, especially when tasks are novel or complex. On these occasions, additional control is provided through the SAS (Norman & Shallice, 1986). The SAS operates by providing increased inhibition or activation to competing schemas to bias the selection of schemas through the contention scheduling mechanism. In this manner, the individual's component processes can be reorganized to meet the current demands and objectives of the task. Thus, the SAS is an attentional control process that modulates, biases, or even restarts the selection process and is primarily related to the initiation rather than the execution of action (Norman & Shallice, 1986).

Cognitive Control

Within the framework of executive control is the online implementation of one's thoughts, actions, and emotions, which is often referred to as cognitive control. That is, cognitive control is a subset of executive processes responsible for adjustments in perceptual selection, biasing of responses, and online maintenance of contextual information (Botvinick et al., 2001). Thus, cognitive control processes are often associated with a "central executive" in theoretical models. This executive is responsible for the adaptability of the cognitive system and is often specified similarly to the SAS (Baddeley, 1996; Norman & Shallice, 1986).

However, cognitive control processes are not unitary; and the adaptability of the cognitive system needs to be understood not only in terms of what increases control influences in an individual's interaction with the environment, but also in terms of how increased control is implemented or brought about to intervene under the appropriate circumstances. To address these issues, researchers have suggested that there are at least two functionally linked but dissociable systems of cognitive control, termed evaluative and regulative (see Botvinick et al., 2001 for review).

The evaluative system of cognitive control monitors for instances of conflict during information-processing events. More specifically, the evaluative system detects the occurrence of conflict during cognitive processing and sends signals to processing centers responsible for providing compensatory adjustments of top-down control that are necessary for successful adaptations to task demands (Botvinick et al., 2001). Neuroimaging research has suggested that the anterior cingulate cortex (ACC) is involved in the evaluative system and the signaling and detection of conflict. Most notably, results indicate that ACC activation is largest when cognitive control is weak (Botvinick et al., 1999; Carter et al., 2000). Further, increased ACC activation in conjunction with weak cognitive control may indicate the signaling for adjustments in control to more strongly engage the strategic processes necessary for improvements in subsequent behavior (MacDonald et al., 2000).

The regulative system exerts top-down control during ongoing information processing. That is, flexible adjustments in strategic support are provided for task-relevant interactions within the stimulus environment, allowing for improved representations and active attentional maintenance of task demands. Available neuroimaging research indicates that this regulative support is likely provided, at least in part, by the dorsolateral prefrontal cortex (DLPFC; MacDonald et al., 2000). Thus, the two components of cognitive control interact as part of a negative feedback loop to optimize performance (MacDonald et al., 2000). In this loop, the DLPFC implements cognitive control for task-related behaviors; the ACC monitors for conflict during task execution and signals for the increased engagement of control in instances of conflict; and the DLPFC responds to signals of conflict with an adaptive adjustment to upregulate control in an attempt to improve subsequent behavioral interactions with the environment.

Cognitive Aging

With aging come changes in brain structure and function. Coupled with these age-related changes in the neurobiology are changes in cognitive functions associated with the affected brain structures. Responsible for changes in brain structure are well-documented age-related reductions in brain volume and ventricular enlargement (Davis & Wright, 1977). Brain volume reductions are due to reductions in the volume of gray matter (Salat et al., 2004). However, reductions in white matter volume, related to decreases in the number of synapses and the atrophy of dendritic processes, are also evident with advancing age (West, 1996). Changes in neurotransmitter function have also been observed with age. Recent evidence suggests that these age-related decrements begin during early adulthood, with an acceleration of loss occurring during later adulthood (Fotenos et al., 2005). Although age-related decrements have been observed across multiple brain structures (Raz, 2000), substantial decrements in two distinct anatomical circuits have been identified. The first involves the frontal cortex and basal ganglia, and the other involves the hippocampal formation and related medial temporal lobe structures (Buckner, Head, & Lustig, 2006). Accordingly, functions subserved by these brain structures have been found to be especially susceptible to cognitive aging.

Relative to young adults, older adults exhibit performance deficits across a wide variety of tasks that tap a number of cognitive processes including visuospatial and verbal memory (Park et al., 2002), working memory (Hasher & Zacks, 1988), long-term memory (Zacks & Hasher, 2006), attention (Kramer & Kray, 2006), and executive control (Kramer et al., 1994), among other cognitive functions.[A] Thus it appears that age-related changes in brain structure and function lead to general decrements in cognition during later stages of the life span. However, Kramer and his colleagues (1994) have indicated that cognitive aging is not unitary, as disproportionately larger deficits in cognitive performance have been found for tasks or task components requiring greater amounts of executive control. Further, certain executive functions are more susceptible to age-related decline than others. Given that the frontal lobe also exhibits a disproportionate loss of function relative to other brain regions (Haug & Eggers, 1991), it is not surprising that processes mediated by this region of the cortex would evidence disproportionate loss during aging. Dempster (1992) reviewed the role of the frontal lobes in cognitive development and stated that they are among the earliest to show signs of deterioration due to age, with that area of brain tissue characterized by a significant decrease in blood flow, weight, and cortical thickness during the later stages of the life span.

Specifically, Kramer and his colleagues (Kramer, Hahn, & Gopher, 1999; Kramer et al., 1994) used several tests of executive control (e.g., task-switching, Wisconsin Card Sorting Task, negative priming, response compatibility, stopping) to further understand the affects of aging on inhibitory processes. Their findings indicated that older, compared to younger, adults exhibited decreased performance (i.e., reaction time [RT], error rate) on certain tasks (e.g., response compatibility, stopping) but were equivalent for other tasks (e.g., negative compatibility), indicating that age-related decrements in executive control are not unitary. The authors interpreted their findings by suggesting that age-related deficits in performance are specific to certain failures in inhibitory processes rather than a more general failure in overall inhibitory control. Interestingly, the tasks that elicited the largest age-related performance differences were those that are mediated, in large part, by the frontal lobes, whereas the tasks in which aging differences were not observed were mediated by other regions of the brain. This would suggest that aging might specifically compromise inhibitory processes mediated by the frontal lobe (Kramer et al., 1994).

Although a wealth of other data also point to selectively larger age-related decrements for (executive) tasks subserved by the frontal lobe, the purpose of this chapter is not to provide an exhaustive review of cognitive aging. However, germane to the chapter is that cognitive performance decreases during later stages of the life span, and further, that tasks mediated by specific brain regions exhibit disproportionately larger decrements. Accordingly, one guiding framework for the literature examining physical activity effects on cognitive aging as described here is that tasks (or task components) engaging the frontal lobe may be especially responsive to lifestyle factors that promote increased health and function, compared to tasks that are mediated by other brain regions and exhibit fewer signs of cognitive aging. The body of research we describe is limited in scope to the neuroelectric system. Compared to a growing literature base addressing general and selective physical activity effects on cognitive function (see Colcombe & Kramer, 2003 for review), the literature base on the neuroelectric system remains considerably smaller. Accordingly, the goal of this chapter is to provide a detailed review of the relationship between physical activity participation and neuroelectric concomitants of cognition during performance of tasks that require variable amounts of executive control, thus allowing for greater understanding of the general and selective influence of physical activity on cognitive aging.

Neuroelectric Measurement

Electroencephalographic (EEG) activity is a recording of the difference in electrical potentials between various locations on the scalp.[B] When electrodes are placed on the scalp, the EEG reflects activity of large populations of neurons firing in sync (Hugdahl, 1995). The dipoles from the individual neurons must be spatially aligned perpendicular to the scalp in order to be detected (Luck, 2005). Thus, EEG measurement is most likely to result from cortical pyramidal cells, which are aligned perpendicular to the cortex surface (Luck, 2005). This type of measurement has long been used to assess cognition and more recently to identify potential physiological mechanisms underlying the beneficial relationship between fitness and cognition. In particular, ERPs, which are a class of EEG activity, appear to be susceptible to the effects of exercise (Polich & Lardon, 1997), and refer to fluctuations in neuroelectric activity that are related to the occurrence of a stimulus or event. Event-related potentials may be classified as either exogenous (i.e., obligatory responses dependent upon the physical properties of the eliciting stimulus) or endogenous (i.e., higher-order cognitive processes that often require active participation from the subject, but are independent of the physical properties of the stimulus environment). Given the direction of previous research on physical activity and neurocognition, this chapter focuses solely on endogenous components of an ERP.[C]

Stimulus-locked ERP components are named based on their polarity (i.e., negative or positive deflections of the waveform) and ordinal position along the waveform. The typical ERP to a visual stimulus consists of a complex of several components, with earlier components (P1, N1, P2) relating to aspects of spatial attention and later components (N2, P3 or P3b) relating to various facets of cognitive function (e.g., detection of deviant stimuli, working memory; Luck, 2005). For more extensive descriptions of the stimulus-locked ERP components, the interested reader is referred to a review by Coles and Rugg (1995).

Response-locked components, including the error-related negativity (ERN) and the error positivity (Pe), are thought to be related to neural correlates of action monitoring and error awareness, respectively. The ERN is a negative deflection of the waveform at frontal and central electrode sites that begins just after an incorrect response is made. The Pe is a positive deflection of the waveform at centroparietal sites occurring approximately 300 ms after an incorrect response. Physical activity, fitness, or both appear to relate to changes in various components of an ERP waveform, including the P3, ERN, and Pe.

Having provided a rationale for the need to better understand factors that may ameliorate or protect against cognitive aging, as well as a brief description of disproportionate loss of executive control during older adulthood, in the remainder of the chapter we examine the relationship between physical activity and neurocognition. We specifically focus on the neuroelectric system by first reviewing the literature on stimulus-locked ERPs and then the literature on response-locked ERPs. Finally, we discuss extensions of this work to cognitive development.

Physical Activity Influences on Stimulus-Locked ERPs

In this section we focus on the P3 component (also known as the P300 or P3b), which has been examined most commonly in studies using simple discrimination tasks. The neuroelectric literature has provided strong support for age-related deficits in the expression of P3. In adult populations, however, a number of studies have demonstrated a positive relationship between physical activity and decreased P3 latency, as well as between physical activity and increased P3 amplitude.[D]

The P3 Component

The P3 is a positive deflection in an ERP (Sutton et al., 1965) that peaks approximately 300 to 1000 ms after stimulus onset, depending on task complexity and individual characteristics in the sample tested. Because of its relation to aspects of information processing, this endogenous component has captured considerable attention in the literature. Although the P3 may be recorded using a variety of tasks and paradigms, it has most commonly been elicited by simple discrimination tasks, such as an oddball task in which individuals must discriminate between two stimuli that are presented in a long and random series. The participants' task is to respond to one or to both stimuli, which occur with differing probabilities (see Polich, 2004 for review).

The precise neural tissue mediating the P3 response is unknown, since this ERP component likely reflects a network of neural circuitry and generators. However, discrimination tasks requiring attentional focus are thought to elicit frontal lobe activation (Posner, 1992; Posner & Petersen, 1990), with ERP (i.e., P3a) and functional magnetic resonance imaging (fMRI) studies demonstrating greater frontal lobe activity in response to rare or alerting stimuli (Polich, 2004). The ACC is activated when working memory representations of the stimulus environment change, which in turn signals the inferotemporal lobe for stimulus maintenance (i.e., memory storage). The P3 (i.e., P3b) component is elicited when attentional resources are allocated for subsequent memory updating after stimulus evaluation. This is thought to occur when memory storage operations initiated in the hippocampal formation are transmitted to the parietal cortex, which is typically where the P3 exhibits maximal amplitude in the scalp distribution (Squire & Kandell, 1999; Knight, 1996). Thus, the neuroelectric events that underlie P3 generation occur from the interaction between frontal lobe and hippocampal/temporal-parietal function (Knight, 1996; Polich, 2004) to modulate attentional control over the contents of working memory (Polich, 2004).[E]

The P3 has been examined extensively in order to investigate aspects of information processing related to stimulus engagement. That is, the P3 has been hypothesized to represent the allocation of attentional resources involved in working memory operations during context updating of the stimulus environment once sensory information has been analyzed (Donchin, 1981; Donchin & Coles, 1988). The amplitude of the P3 component is thought to reflect changes in the neural representation of the stimulus environment and is proportional to the amount of attentional resources needed to engage a given stimulus or task, with greater attentional allocation increasing P3 amplitude (Polich & Heine, 1996). The latency of the P3 component is a measure of stimulus evaluation or cognitive processing speed (Duncan-Johnson, 1981), with longer latencies reflecting increased processing time.

Decreases in P3 amplitude elicited during paradigms with short interstimulus intervals have been observed during tasks or task conditions requiring more extensive amounts of executive control. For example, smaller P3 amplitude has been found during the incongruent, relative to the congruent, condition for a flanker task in both younger and older adults (Hillman et al., 2004; Hillman, Snook, & Jerome, 2003); this is due to the increased need for interference control in the incongruent condition and additional demands placed upon the recovery cycle that underlie the mechanisms responsible for generation of the P3 component (Gonsalvez & Polich, 2002). In a flanker task, participants are required to discriminate between target stimuli that are flanked by an array of other stimuli with which different responses are associated. Differences in response accuracy and speed are observed between congruent (e.g., HHHHH) and incongruent (e.g., HHSHH) conditions, with the former eliciting faster and more accurate responses than the latter (Eriksen & Schultz, 1979). The incongruent task requires greater amounts of interference control (one aspect of executive control) to inhibit task-irrelevant stimuli and execute the correct response. Specifically, the flanking stimuli activate the incorrect response to the task, which competes with the correct response elicited by the centrally placed target stimulus (Spencer & Coles, 1999).

Other research has evidenced topographic differences in P3 amplitude during a Go/NoGo task, which manipulates stimulus probability and requires variable amounts of response inhibition, with maximal amplitude observed parietally during the Go condition and frontocentrally during the NoGo condition (Tekok-Kilic, Shucard, & Shucard, 2001). Given that the NoGo condition requires greater amounts of inhibitory control due to the need to suppress a prepotent motor response, these findings again suggest that P3 amplitude is sensitive to task conditions requiring variable amounts of executive control. Further, the findings reflect deficits or inefficiencies (i.e., decreased amplitude or shifts in scalp topography) in neuroelectric resource allocation associated with attention during tasks that have larger executive control requirements. P3 latency may also be used to index neurocognitive deficits in information processing during executive control operations, as longer P3 latency has been observed during task components with greater executive requirements in older and younger adults (Hillman et al., 2004, 2006). This robust finding indicates that P3 latency measures alterations in cognitive processing speed associated with task requirements, and suggests decreases in the efficiency of the neuroelectric system during tasks necessitating greater amounts of executive control (Hillman et al., 2006; Zeef et al., 1996). Given these findings, the P3 is considered a useful tool for understanding covert alterations in information processing, even in the absence of changes in overt performance across experimental manipulations.

Aging and P3

One of the most robust findings in the neuroelectric literature is age-related deficits in the expression of the P3 component (Fabiani & Friedman, 1995; Fabiani, Friedman, & Cheng, 1998; Picton et al., 1984; Polich, 1997). Picton and colleagues (1984) used auditory stimuli to elicit the P3 from participants of different age groups (20-79 years, 12 participants from each decade). P3 amplitude declined with age at a rate of 0.18 μV/year, and the scalp distribution became more frontal due to age-related decreases in amplitude at the vertex of the scalp. Thus the observed similarity across electrode sites on the scalp that accompany aging may relate to an inefficiency of neuroelectric processes underlying cognitive function.[F] Other researchers have used dipole modeling techniques to localize the neural generators of the P3, with results supporting increased frontal lobe involvement during aging (Friedman, Simpson, & Hamberger, 1993). This finding suggests that older adults may exert greater amounts of executive control during tasks that do not normally require extensive top-down executive control support in younger individuals. Accordingly, age-related decrements in the cognitive processes indexed by P3 scalp distribution are suggestive of alterations in neurobiological integrity. That is, the observed similarity across electrode sites on the scalp that accompany aging may relate to the decreased efficiency of these processes. Given that there is an overall reduction of P3 amplitude for older compared to younger adults, one might speculate that the increased similarity observed in the topographic distribution is indicative of some compensatory mechanism that helps older adults meet the demands of the imposed challenge. These aging differences would be expected to emerge more frequently when greater amounts of executive control (which has been shown to be subserved by the frontal lobe) are required.

Brain lesion data further support the differential activation of the frontal lobe during aging. Specifically, Knight (1984, 1997) used common (frequent, ignored), rare (in which participants responded)^{G}, and novel (uninstructed, task irrelevant) stimuli to examine differences in scalp distribution between patients with lesions in the DLPFC and nonlesion controls. Results indicated that during the novelty condition, control participants exhibited frontally distributed P3 responses compared to lesion patients, who showed parietally distributed P3 responses. Since the DLPFC has been implicated in orienting behavior (Luria, 1973), Knight's findings suggest that the DLPFC is involved in the modulation or generation of novelty P3 (i.e., P3a). Further, these data support the importance of the frontal lobe in stimulus evaluation processes, suggesting that if these regions are compromised during advanced aging, biases in stimulus engagement and response selection may occur.

With regard to the latency of P3, Picton and colleagues (1984) reported an increase of 1.36 ms/year beginning in early adulthood. Workers in other laboratories have corroborated these results and found similar latency decrements (O'Donnell et al., 1992). O'Donnell and his colleagues (1992) suggested that cognitive processing speed, measured via P3 latency, contributes to decreased task performance (e.g., RT) of older individuals. P3 latency measured during a flanker task, which manipulated interference control requirements, was longer for older compared to younger participants and for the incongruent relative to the congruent condition. However, latency differences for age and congruency did not interact, suggesting that age-related decrements in processing speed during tasks that require interference control may not be related to stimulus evaluation; rather, age-related differences may be due to other ongoing executive processes (Zeef et al., 1996). Taken together, the cognitive aging data regarding the P3 component indicate deficits in the allocation of neuroelectric resources in terms of the amount and topography of the amplitude, as well as the speed at which cognitive processing occurs during stimulus engagement. As such, these age-related deficits in cognitive function increase the reliance upon executive control operations, even when characteristics of the stimulus environment would not normally require such top-down control during earlier periods of the adult life span.

Physical Activity and the P3 Component in Adult Populations

Currently, an abundance of evidence indicates that physical activity, aerobic exercise in particular, benefits cognition on the cellular, systems, and behavioral levels, with research showing that cognitive function of older adults is especially amenable to physical activity intervention (Colcombe & Kramer, 2003; Bashore, 1989; Dustman et al., 1990; Kramer et al., 1999). Habitual participation in aerobic exercise, which leads to improvements in cardiorespiratory fitness, has been found to decrease neuroelectric performance differences between older and younger adults, indicating that exercise may help to maintain overall cognitive health (Dustman, Shearer, & Emmerson, 1993; Hillman et al., 2002, 2004, 2006).

P3 Latency

Some of the earliest research examining aerobic exercise effects on ERPs was performed by Dustman and his colleagues (Dustman et al., 1985, 1990), who observed that P3 latency was faster in aerobically trained compared to sedentary older males performing an oddball task. The reduction was great enough to lead to nonsignificant differences between the older fit males and younger adults, whereas older sedentary males exhibited significantly longer P3 latencies. These data indicated that aerobic exercise improved cognitive processing speed or protected against age-related decrements in processing speed in older men. Other researchers have corroborated or extended Dustman's findings using tasks with small executive control requirements (Bashore, 1989; Hillman et al., 2002).

Given the recent findings of disproportionately larger age-related deficits in executive control processes that are subserved by the frontal lobe, the relationship of physical activity to these processes is of great interest from the viewpoint of determining means for protecting against cognitive aging and maintaining cognitive health during the later stages of the life span. Accordingly, Hillman and colleagues (2004, 2006) used various executive control tasks to determine the relationship between physical activity and neurocognitive performance during older adulthood. Findings indicated that greater amounts of physical activity were associated with faster P3 latency (Hillman et al., 2004, 2006). From these studies, two important findings were obtained. First, greater amounts of aerobic activity in older adults were related to linear decreases in P3 latency. Specifically, faster latency was observed for high-active older adults relative to their moderate- and low-active peers (Hillman et al., 2004). Secondly, the relationship between physical activity and P3 latency is selectively greater for task components requiring greater amounts of executive control (Hillman et al., 2006). That is, during task conditions requiring individuals to hold two rule sets in working memory and flexibly shift between rule sets, high-active individuals exhibited faster P3 latency than low-active individuals. However, during task conditions requiring individuals to hold only one rule set in working memory without the need to shift between sets, no physical activity–related differences were observed (Hillman et al., 2006). Taken together, these findings indicate the disproportionately larger relationship between physical activity and cognitive processing speed during executive control tasks and suggest a linear relationship between physical activity participation and benefits in older adults' processing speed.

P3 Amplitude

In addition to improvements in cognitive processing speed, physical activity has been related to differential allocation of neuroelectric resources during older adulthood. Most notably, active individuals exhibit increased P3 amplitude when compared to their sedentary counterparts, and these findings are indicative of greater allocation of attentional resources with physical activity participation. Early researchers employed oddball (Polich & Lardon, 1997) and other speeded perceptual (Bashore, 1989) tasks to examine physical activity effects on P3 amplitude, with results indicating a positive relationship. More recent investigations have corroborated these findings (McDowell et al., 2003) and extended them to include somatosensory oddball tasks in which participants received electrical stimulation to their index fingers (Hatta et al., 2005). Importantly, Hatta and colleagues (2005) also observed greater heterogeneity across midline scalp sites for high-active, relative to low-active, older participants, suggesting greater specificity of neuroelectric resource allocation with increased amounts of physical activity. However, other research has failed to examine physical activity effects on P3 amplitude in older adults using simple stimulus discrimination tasks (Dustman et al., 1990; Hillman et al., 2002).

On the basis of the inconsistent findings indicating that physical activity either has a positive effect on or is unrelated to P3 amplitude and its topographic distribution during older adulthood, research in our laboratory been aimed at determining whether the relation of physical activity to P3 (and the processes subsumed by it) would be more robust when examined within the context of tasks that are dependent upon the frontal lobe, since this region of the brain exhibits a disproportionate loss of structure and function during aging. As described previously in connection with P3 latency, we conducted two studies that used task conditions requiring variable amounts of executive control. Both studies included older and younger participants so that we could determine not only the influence of physical activity participation on P3, but also whether the relationship changes with age during adulthood. As predicted, higher-active older adults exhibited increased P3 amplitude at electrode sites over the frontal region of the scalp (Hillman et al., 2004, 2006). Specifically, moderate- and high-active older adults had larger P3 amplitude relative to younger adults during tasks requiring greater amounts of executive control (i.e., incongruent flanker conditions that necessitate greater interference control). This relationship was not observed for low-active older participants, and no such effect was observed during task conditions requiring smaller amounts of interference control (Hillman et al., 2004). These findings suggest that physical activity is associated with increased allocation of attentional resources during task performance, and that this relationship is selectively greater during tasks that necessitate increases in frontally mediated executive control function.

Additional support for these findings was obtained using a task-switching paradigm, which as already described manipulates working memory load and requires cognitive flexibility during switching between rule sets. The comparison of older and younger adults who varied in their physical activity participation corroborated our earlier efforts (Hillman et al., 2004) and extended them to an additional aspect of executive control. In particular, older active adults exhibited larger P3 amplitude over frontally placed scalp sites relative to their sedentary peers and to both physically active and sedentary younger adult groups. However, shifts in scalp topography were observed that were dependent upon both age and physical activity participation, such that both older and younger active participants exhibited larger P3 amplitude than their sedentary peers at central scalp sites. Further, younger active participants exhibited larger amplitude over parietal scalp sites relative to the other three groups. Given that younger adults exhibited the classic and robust P3 topography, which includes a parietal maximum (i.e., P3 amplitude is largest over parietal scalp sites), the increase in P3 amplitude for high-active older adults may reflect compensatory neural function during stimulus engagement to improve or maintain task performance. Task performance data supported this hypothesis, as faster RTs were observed for physically active relative to sedentary participants, regardless of age. Additional support was garnered from the sedentary participants, who exhibited smaller amplitude and decreased heterogeneity of scalp topography, which indicated smaller and less efficient allocation of neuroelectric resources during a task requiring variable amounts of executive control.

Data from these two studies reveal that physical activity may benefit a subset of processes involved in information processing that occur between stimulus engagement and response production. Further, the influence of physical activity on these neuroelectric processes appears to benefit the allocation and efficiency of cognitive processing in this system and has implications for task performance. Taken together, these findings suggest that physical activity may help to ameliorate or protect against cognitive aging, and they support cardiorespiratory fitness as a potential mediator for cognitive aging. Lastly, the data also indicate that physical activity is beneficial to cognition during young adulthood, suggesting that the adoption of a physically active lifestyle may be associated with improved cognitive health and function during earlier stages of the life span.

Physical Activity Influences on Response-Locked ERPS

In this section we look at research that has addressed the influence of physical activity and fitness on action monitoring and error correction processes and their neural correlates, the ERN and the Pe. The ERN appears to be more efficient in physically active compared to sedentary older adults, and higher-fit individuals exhibit both smaller ERN amplitude and larger Pe amplitude than individuals with lower levels of fitness.[H]

Action Monitoring

People are typically aware of the consequences of their actions. Specifically, when individuals make an incorrect judgment or an error in a cognitive task, they often have an awareness of the error and react out of frustration in a visible or audible way (Yeung, Cohen, & Botvinick, 2004). Further, the participant is often able to specify the error that was made with the appropriate response (Rabbitt, 1966).[I] According to Rabbitt (2002), this explicit detection and specification of the error is mostly accurate (79% of errors are detected by young adults) and often deliberate and effortful (700 ms latency following error commission). However, behavioral correction of an error is fast and relatively automatic (Yeung, Cohen, & Botvinick, 2004). Participants are able to produce a corrective response (i.e., the response they initially should have made to complete the task correctly) anywhere between 20 ms (Rabbitt, Cumming, & Vyas, 1978) and 250 ms (Rabbitt, 2002) following the error response. Thus, errors provide individuals with an important source of information in relation to their subsequent interaction with the environment and the corrective actions or processes that need to occur for performance to improve. These corrective actions can be fast and automatic, or they can be more deliberate and related to conscious recognition of error commission.

These behavioral findings and the related investigation of action monitoring and error correction processes have gained interest in recent years with the discovery of neural correlates of action monitoring. In particular, studies of ERPs have revealed neural indices of both fast and relatively automatic action monitoring processes (i.e., ERN) and corrective action monitoring processes that are more deliberate and related to error awareness (i.e., Pe).

Error-Related Negativity

One neural response following error commission is the error-related negativity (ERN: Gehring et al., 1993; or Ne: Falkenstein et al., 1991). The ERN is a negative-going component observed in response-locked ERP averages of incorrect responses. It is maximal over frontocentral recording sites and peaks shortly after incorrect responses in speeded RT tasks (Falkenstein et al., 1991; Gehring et al., 1993). The ERN has been shown to be evident regardless of an individual's awareness of error commission (Nieuwenhuis et al., 2001), and it is reduced following error responses to infrequent stimuli (Holroyd & Coles, 2002). Further, researchers have localized the source of the ERN at or very near the dorsal ACC using dipole localization techniques (Dehaene, Posner, & Tucker, 1994; van Veen & Carter, 2002), and corroborating evidence has come from both neuroimaging (Carter et al., 1998) and magnetoencephalography studies (Miltner et al., 2003). Neuroimaging findings have established that the functional significance of ACC activation is related to action monitoring and evaluation during tasks requiring extensive executive control (Carter et al., 2000). Further, Gehring and Knight (2000) have shown that the ACC exhibits a functional interaction with the prefrontal cortex during action monitoring processes and compensatory or corrective actions following error responses.

Though the ERN is generally believed to reflect a cognitive learning mechanism used to correct an individual's responses during subsequent environmental interactions, the specific functional significance of the ERN remains unresolved. Two distinct theories have suggested differential processes that relate to ERN activation. One theory holds that the ERN measures error detection and monitoring (Berstein, Scheffers, & Coles, 1995; Falkenstein et al., 1991; Scheffers et al., 1996). More specifically, this reinforcement learning model (Holroyd & Coles, 2002) proposes that the ERN is part of a system that detects the occurrence of an error and uses that information to improve task performance. The ERN is evidenced on error trials through a reduction in dopaminergic activity that disinhibits the ACC, which in turn selects the appropriate motor controllers to successfully complete the task based upon this input (Holroyd & Coles, 2002).

An alternative theory suggests that the ERN reflects a conflict monitoring process (Botvinick et al., 2001). This process is part of a system involving the ACC that detects (or monitors) levels of response conflict. This information is then transmitted from the ACC to processing control centers, which triggers adjustments in relative influences on processing among the control centers (Botvinick et al., 2001). Although the true function of the ERN is debated, there is consensus that the ACC is the primary structure driving the ERN signal (Carter et al., 1998; Miltner et al., 2003).

Error Positivity

A second ERP component related to action monitoring processes following error responses is the error positivity (Pe: Falkenstein et al., 1990, 2000). The Pe is a positive-going component observed in response-locked ERP averages of incorrect responses. It is maximal over centroparietal recording sites and peaks after the ERN (about 300 ms following an incorrect response). Further, research using dipole localization techniques has identified generators of the Pe in the rostral ACC (van Veen & Carter, 2002). Although both the ERN and Pe are associated with neural processes in the ACC, the two components have distinct neural generators and are believed to be independent of each other (Herrmann et al., 2004).

The Pe has been described as an emotional reaction to the commission of an error (Falkenstein et al., 2000; van Veen & Carter, 2002), as a postresponse evaluation of an error (Davies et al., 2001; Falkenstein et al., 1990), and as the allocation of attentional resources toward an error following error commission (Mathewson, Dywan, & Segalowitz, 2005). More specifically, Davies and colleagues (2001) found strong correlations between Pe and P3 amplitude, suggesting that the Pe could be a P3-like response to the internal detection of an error, with the error response being the salient stimulus to which attentional resources are allocated. Additionally, Mathewson and coworkers (2005) found that both increased P3 and Pe amplitudes were associated with better task performance (i.e., fewer errors) across multiple cognitive tasks, though these relationships were different across age groupings. The finding of an association between increased P3 amplitude and improved task performance has been verified independently (Falkenstein et al., 2000) and provides support for the notion that the Pe may be a neuroelectric index of compensatory actions following the commission of an error through the increase of attentional control (Themanson & Hillman, 2006).

Physical Activity and Action Monitoring

Currently, only two published studies have addressed physical activity and fitness in relation to response-locked ERPs. The initial study (Themanson, Hillman, & Curtin, 2006) assessed the relationship between self-reported physical activity behavior, ERN amplitude, and posterror behavior for 53 older and younger adults during a task requiring variable amounts of executive control (i.e., task-switching) in which participants were instructed to respond as quickly as possible. Physical activity was assessed using the

Yale Physical Activity Survey for Older Adults (YPAS; DiPietro et al., 1993), which measures activities of daily living and comprises three subscales: total hours of activity, kilocalorie expenditure, and the Yale Summary Index (YSI). The YSI estimates the average amount of physical activity during the previous month and is highly correlated with $\dot{V}O_2$peak in older adults (Young, Jee, & Appel, 2001). The results from this initial study indicated that older adults exhibited a greater relative slowing in RT during switch blocks and smaller ERN amplitude compared to younger adults; both of these findings corroborated previous aging research.

However, physical activity differences were also observed that revealed a relatively smaller switch cost (i.e., RT on switch trials – RT on nonswitch trials) for physically active older adults, indicating better performance during tasks that place an increased load on working memory. Further, decreased ERN amplitude for older and younger physically active participants and relatively greater response slowing following commission of errors were observed when compared with values for the sedentary counterparts (Themanson, Hillman, & Curtin, 2006). Given that posterror response slowing is a behavioral indicator of increased recruitment and implementation of top-down attentional control to improve performance on subsequent environmental interactions (Gehring et al., 1993; Kerns et al., 2004), these findings suggest increased attentional control among physically active individuals regardless of age (Themanson, Hillman, & Curtin, 2006). This increase in top-down attentional control not only improves behavioral performance, but also decreases the activation associated with the evaluative component of action monitoring processes during speeded task performance. Thus, the resulting neuroelectric signal (i.e., ERN) indicative of response monitoring may be described as more efficient in physically active adults, and may relate to increases in top-down adjustments used to correct behavior following error commission.

Fitness and Action Monitoring

A second study examined the influence of cardiorespiratory fitness on ERP components related to action monitoring, using two groups of young adults that exhibited large differences in their respective levels of fitness (Themanson & Hillman, 2006). The study focused on neuroelectric (i.e., ERN, Pe) and behavioral (i.e., posterror slowing) indices of action monitoring processes acquired during the completion of a flanker task in which 28 higher- and lower-fit young adult participants were required to respond as quickly as possible. Participants completed a graded exercise test to assess their level of cardiorespiratory fitness through measurement of maximal oxygen consumption ($\dot{V}O_2$max). Additionally, cognitive testing was conducted for each individual on two separate, and counterbalanced, occasions: once after a 30 min period of rest and once after a 30 min bout of hard but submaximal (83.5% maximal heart rate) treadmill exercise (Themanson & Hillman, 2006). Findings demonstrated a relationship between levels of cardiorespiratory fitness and indices of action monitoring such that the higher-fit group exhibited smaller ERN amplitude than the lower-fit group, suggesting a relative reduction in the conflict-related neuroelectric index of action monitoring associated with error responses. Additionally, higher-fit individuals exhibited both larger Pe amplitude and greater posterror response slowing than lower-fit individuals, which indicated an increase in both neural and behavioral posterror adjustments in top-down attentional control.

Together, these two studies indicate that individuals with greater levels of fitness or physical activity participation are exerting increased levels of top-down attentional control during task execution. This increase in top-down attentional control is associated with a reduced activation of the neuroelectric system designed to respond to indicants of task performance conflicts, resulting in an overall reduced ERN amplitude (Themanson & Hillman, 2006; Themanson, Hillman, & Curtin, 2006). Finally, given current views of posterror slowing as a behavioral indicator of the implementation of top-down attentional control (Gehring et al., 1993; Kerns et al., 2004), and of Pe amplitude as a neuroelectric index of postresponse evaluation of an error (Davies et al., 2001; Falkenstein et al., 1990) or the allocation of attentional resources toward an error (Mathewson et al., 2005), Themanson and Hillman (2006) have argued that this increase in top-down attentional control is associated with an increased corrective response following error commission, through the observed increase in both posterror slowing and Pe amplitudes for higher-fit individuals.

The observed reductions in ERN amplitude and increase in Pe amplitude with greater levels of fitness or physical activity involvement corroborate research on the relationship between aerobic training and ACC activation (Colcombe et al., 2004). Using neuroimaging measures, Colcombe and colleagues (2004) found that aerobically trained older adults, compared to nonaerobically trained control participants, evidenced greater activation of task-related prefrontal and parietal brain regions involved with inhibitory functioning. This increase in the recruitment of relevant brain regions for higher-fit individuals suggests "an increase in the ability of the frontal attentional circuitry to bias task-related activation in posterior regions of cortex" (Colcombe et al., 2004, p. 3320), which might be indicative of an increase in Pe amplitude.

Further, reduced ACC activation was observed for aerobically trained older adults compared to their sedentary counterparts, suggesting a decrease in behavioral conflict for these individuals (Colcombe et al., 2004). This finding strongly suggests a reduction in ERN amplitude for aerobically fit individuals according to the conflict monitoring hypothesis proposed by

Botvinick and colleagues (2001). The reinforcement learning model of ERN activation (Holroyd & Coles, 2002) might also predict a relative reduction in ERN amplitude for individuals with greater levels of cardiorespiratory fitness. According to this model, a phasic reduction in dopaminergic activity is associated with the modulation of ERN amplitude. Interestingly, both animal and human studies have shown that regular aerobic exercise leads to increases in dopaminergic activity (Farrell et al., 1986; Gullestad et al., 1997; MacRae et al., 1987; Meeusen et al., 1997; Van Loon, Schwartz, & Sole, 1979; but see also Wang et al., 2000), which, according to this model, would suggest that aerobic fitness may be associated with a relative decrease in ERN amplitude through increased inhibition of the ACC.

Physical Activity Influences on Neurocognitive Function During Preadolescent Development

Given that a positive relationship has been established between fitness and cognition in older adults (see Colcombe & Kramer, 2003 for review), more attention has begun to shift toward the investigation of a similar relationship between fitness and cognitive health during earlier periods of the human life span. Preliminary findings in school-aged children indicate a comparable relationship (Sibley & Etnier, 2003), although gaps in the literature exist regarding the particular types of cognition affected and the mechanisms underlying such findings. With an increasing percentage of children living an inactive lifestyle, a greater understanding of the benefits of fitness for cognition during this period of the life span is both timely and relevant.

Sibley and Etnier (2003) conducted a meta-analysis on the relationship between physical activity and school-aged children.[J] Forty-four studies that differed in design (i.e., true, quasi-, cross-sectional), age of participants (4-18), type of physical activity behavior (i.e., acute, chronic), training characteristics (i.e., resistance, aerobic, perceptual-motor, physical education program), and cognitive assessment (i.e., perceptual skills, intelligent quotient, achievement, verbal tests, math tests, memory, developmental level or academic readiness, and other) were included in the analyses. A significant positive relationship between physical activity and cognition was found, such that increased physical activity was related to cognitive performance along the eight measurement categories; the relationship was beneficial in all categories (Sibley & Etnier, 2003). Although this relationship was seen across all age groups, it was stronger for children in the 4- to 7- and 11- to 13-year-old groups compared to the 8- to 10- and 14- to 18-year-old groups (Sibley & Etnier, 2003).

In order to better understand some of the potential mechanisms underlying the cognitive improvements observed in children, Hillman, Castelli, and Buck (2005) examined neuroelectric indices (P3-ERP) of attentional allocation during a visual oddball task. Neuroelectric data were collected on 51 higher- and lower-fit (n = 12-15 per group, approximately equal male-to-female ratio per group) preadolescent children (M = 9.5 years, SD = 0.9 years) and young adults (M = 19.3 years, SD = 1.4 years). Participants were screened for aerobic capacity using the Progressive Aerobic Cardiovascular Endurance Run (PACER) subtest of the *Fitnessgram* (Welk, Morris, & Falls, 2002), which is a field test that assesses aerobic, strength, and flexibility fitness. Cognitive function was measured using ERPs and behavioral responses (accuracy, RT). During the oddball task, participants responded to infrequent target stimuli (i.e., clip-art drawing of a cat) and were told not to respond to frequent nontarget stimuli (i.e., clip-art drawing of a dog) that were presented at a rate of 20% and 80%, respectively. Results indicated a positive relationship between fitness and cognitive function linked to the allocation of attentional resources to working memory in preadolescent children, as measured by the P3 potential. That is, higher-fit children evidenced larger P3 amplitude compared to the other three groups, which were not different from each other (Hillman, Castelli, & Buck, 2005).

Further, participants with greater aerobic fitness, regardless of age, evidenced faster P3 latency than sedentary participants, indicating that fitness was positively associated with cognitive processing speed (Hillman, Castelli, & Buck, 2005). Notably, fitness was also associated with task performance, as shorter RT was observed in higher-fit, compared to lower-fit, participants. Response accuracy was also greater in higher-fit children relative to lower-fit children and did not differ from either adult group.[K] These findings indicate that aerobic fitness may be related to improvements in cognitive processes associated with attentional allocation during stimulus discrimination in preadolescent children, and provide a convincing argument for further investigation of underlying mechanisms that may be responsible for fitness effects on cognitive function in this population.

Although these data suggest a positive relationship between fitness and cognition, no published research has addressed the relationship between fitness and executive control during cognitive development. According to Piaget, executive function begins to formulate around 8 to 9 months of age during the sensorimotor stage when goal-directed behavior becomes evident (Siegler, 1998). By the second year, children begin to grasp the concept of abstract rules. The comprehension of abstract rules allows for greater success on tests of working memory, processing speed, and interference control (Diamond, Towle, & Boyer, 1994). Early childhood (ages 3-7) is characterized by a marked improvement in certain executive control functions, such as inhibition and cognitive flexibility (Diamond, 2006), due to the development of the frontal lobes (e.g., Miyake et al., 2000; West, 1996). Executive control processes, including working memory, selective attention, and inhibitory control, improve throughout childhood and adolescence (Luciana & Nelson, 1998; Klenberg, Korkman, & Lahti-Nuuttila, 2001; Zelazo, Craik, & Booth, 2004), although performance relying on these processes remains poorer than that of young adults.

One task frequently used to study executive control is the Stroop Color-Word Task, which entails multiple cognitive processes including selective attention, response inhibition, interference control, and speeded responding (Adleman et al., 2002). The basic tenet underlying Stroop performance is that individuals must inhibit their prepotent response to read the words and activate a normally inhibited response to name the ink color in which the word is printed, thus resolving interference associated with reading the word (Adleman et al., 2002; Demetriou et al., 2002; MacLeod, 1991). Accordingly, participants read fewer words in the incongruent word-color condition due to response competition. In a study designed to gain understanding of the potential relationship between fitness and executive control, 74 preadolescent children between the ages of 7 and 12 years (37 boys; M = 9.4 years) completed a paper-and-pencil version of the Stroop Color-Word Task and completed the *Fitnessgram* (Buck, Hillman, & Castelli, 2005). During each of the three conditions of the Stroop task (word, color, color-word), participants were instructed to read aloud as many words as possible in 45 s. Results indicated that better performance on each of the three Stroop conditions was associated with age, IQ, and fitness. Specifically, older children and those with higher IQ read more words aloud correctly during each of the three conditions. Further, those children who completed more laps on the PACER test, indicating higher levels of aerobic fitness, correctly read more words during each condition.

These findings suggest that increased levels of fitness may benefit cognition during maturation and also that fitness may have a global relationship with cognition during this period of the life span.[L] Interestingly, this contradicts previous literature with adult populations, which has indicated both a general and a selective relationship between fitness and cognition (Colcombe & Kramer, 2003; Kramer et al., 2005). That is, although research in adults has demonstrated general improvements in cognition with greater amounts of aerobic fitness, the relationship was disproportionately larger for tasks requiring extensive amounts of executive control (Colcombe & Kramer, 2003). However, the mechanisms underlying the relationship between aerobic fitness and improved cognitive performance remain poorly understood for both children and adults. In any case, these preliminary findings are encouraging and suggest that a more sensitive examination is warranted to achieve a better understanding of the relationship between fitness and cognition during different periods of the life span.

Accordingly, a second study from our laboratory examined neuroelectric concomitants of cognition in preadolescent children during performance of a task requiring variable amounts of executive control (Buck et al., 2006). Neuroelectric data were collected on 44 preadolescent children who were placed into higher (n = 22; 11 males) or lower (n = 22; 12 males) fitness groups based on aerobic capacity as measured by the PACER test of the *Fitnessgram* (Welk, Morris, & Falls, 2002). Participants completed congruent (i.e., HHHHH or SSSSS) and incongruent (i.e., HHSHH or SSHSS) conditions of the Eriksen flanker task (Eriksen & Eriksen, 1974[M]), which required them to respond as quickly as possible to an array of letters presented on a computer monitor. Results indicated that P3 amplitude was larger over the parietal region of the scalp for higher- compared to lower-fit children across both conditions (Buck et al., 2006). Further, higher-fit children performed more accurately across conditions than lower-fit children, while group differences were not observed for RT latency. These findings indicate that fitness may be associated with better interference control in children and also—since they were obtained across conditions requiring variable amounts of interference control—that these cognitive benefits are nonselective during preadolescent childhood.

One translational ramification of the positive relationship between aerobic fitness and cognitive performance observed in the laboratory may relate to academic achievement testing, a common measure of cognitive performance in school-aged children. Castelli and colleagues (in press) investigated the relationship between different components of fitness (i.e., aerobic, muscle strength, flexibility) and academic achievement (Illinois State Achievement Test, ISAT) in 259 elementary school children in the 3rd and 5th grades (M = 9.5 years, female = 127). The *Fitnessgram* (Welk, Morris, & Falls, 2002) was administered to each student during regularly scheduled physical education classes. Children recruited for the study were representative of the population of the community along measures of race/ethnicity, socioeconomic status, and achievement test performance for the school district. The ISAT scores, administered each spring to children in 3rd through 8th grade, were collected with the *Fitnessgram* data. The ISAT tests grade-level student achievement in reading, writing, and mathematics for grades 3, 5, and 7 and science and social studies for grades 4, 6, and 8. Results indicated that only aerobic fitness was positively related to academic performance on mathematics and reading achievement, while body mass index was negatively related to scores on these achievement tests, independent of other variables (Castelli et al., in press). Strength and flexibility fitness were not related to achievement test performance. These data provide preliminary evidence to suggest that higher aerobic fitness in school-age children may be associated with better academic performance, lend further support to the notion that fitness may be important to the development of cognitive health in this population, and provide additional evidence of a general relationship between fitness and cognition during development.

Potential Mechanisms for the Relationship Between Physical Activity and Neurocognitive Function

The underlying mechanisms by which physical activity affects cognitive function are not well understood. However, our understanding of the influences of physical activity on brain structure and function has significantly increased through human neuroimaging and animal model research. With regard to human neuroimaging research, the frontal regions of the brain have been heavily implicated in the modulation of top-down control on tasks requiring variable amounts of executive control. Specifically, disproportionate changes in brain structure with aging have been associated with age-related changes in executive control that are supported in large part by prefrontal and temporal regions of the brain (Robbins et al., 1998; Schretlen et al., 2000). Executive control function is inefficient and variable during the preadolescent years (Rueda et al., 2004) and has been related to immaturity of the frontal lobes during this period of the life span (Bunge et al., 2002). However, physical activity and aerobic exercise training have been related to changes in both structure and function of the prefrontal, frontal, and parietal cortices in older adults (Colcombe et al., 2004). Interestingly, selective improvements in executive control have been observed for aerobically trained adults, which may relate to changes in the health of these neural structures.

With regard to animal research, recent advancements have demonstrated several exercise-related changes at the molecular, vascular, and cellular levels of the brain. For example, aerobic exercise has been shown to increase neurochemicals such as brain-derived neurotrophin factor (BDNF; Neeper et al., 1995), insulin-like growth factor 1 (IGF1; Carro et al., 2001), serotonin (Blomstrand et al., 1989), and dopamine (Spirduso & Farrar, 1981), which have been found to improve plasticity and neuronal survival and underlie learning and memory in adult rats (Cotman & Berchtold, 2002) and neonatal rat pups (Parnpiansil et al., 2003). Other animal research has evidenced the development of new capillaries in the cerebellum with aerobic exercise, presumably to support increased neuronal firing, in rodents (Black et al., 1990; Isaacs et al., 1992) and primates (Rhyu et al., 2003). Importantly, these exercise-induced changes in neural structures have been linked to greater resting blood flow and an increased ability to respond to greater oxygen demands in comparison to values in sedentary controls (Swain et al., 2003).

The relationship between physical activity–induced changes in the basic neurobiology and neuroelectric (i.e., ERP) correlates of human cognition is tenuous. However, several brain structures (i.e., prefrontal, frontal, temporal, parietal) and neurochemicals (i.e., dopamine) most influenced by physical activity have also been related to the modulation of ERP components. The precise neural tissue mediating the P3 response is unknown, since this ERP component likely reflects a network of neural circuitry and generators. However, discrimination tasks requiring attentional focus are thought to elicit frontal lobe activation (Posner, 1992; Posner & Petersen, 1990), with ERP (i.e., P3a) and fMRI studies demonstrating greater frontal lobe activity in response to rare or alerting stimuli (Polich, 2004). The ACC is activated when working memory representations of the stimulus environment change, which in turn signals the inferotemporal lobe for stimulus maintenance (i.e., memory storage). The P3 (i.e., P3b) component is elicited when attentional resources are allocated for subsequent memory updating after stimulus evaluation (Polich, 2004). It is hypothesized that this occurs when memory storage operations initiated in the hippocampal formation are transmitted to the parietal cortex, which is typically where the P3 exhibits maximal amplitude in the scalp distribution (Squire & Kandell, 1999; Knight, 1996). Thus, the neuroelectric events that underlie P3 generation occur from the interaction between frontal lobe and hippocampal/temporal-parietal function (Knight, 1996; Polich, 2004) to modulate attentional control over the contents of working memory (Polich, 2004).[N]

More is known about the neural circuitry underlying the response-locked ERN and Pe components. As discussed previously, the source of the ERN has been localized to the dorsal ACC, and the source of the Pe has been localized to the rostral ACC using several imaging measures. The Pe and P3 components are strongly correlated and are thought to reflect similar attentional processes (Davies et al., 2001). Gehring and Knight (2000) have also observed that the ACC exhibits a functional interaction with the prefrontal cortex during action monitoring processes. In addition, Holroyd and Coles' (2002) reinforcement learning model suggests that the ERN is modulated through a reduction in dopaminergic activity that disinhibits the ACC. Given the early developmental and age-related changes in the structure and function of the frontal lobe, changes in dopamine levels (Brozoski et al., 1979) during preadolescence and older adulthood, and the functional interaction between the ACC and prefrontal cortex, processes subserved by these brain regions may be especially amenable to intervention during these periods of the life span. Interestingly, researchers have suggested that aerobic exercise affects both activation of the ACC (Colcombe et al., 2004) and dopaminergic activity (Wang et al., 2000), indicating that aerobic exercise training may be one such intervention leading to improvements in cognitive performance—which can easily be monitored through the modulation of various ERP components.

Future Directions

Despite the growing body of literature on the relationship between physical activity and neuroelectric indices of cognition that has emerged in recent years, there is a need to gain a better understanding of this relationship. Specifically, since physical activity participation has been found to benefit cognitive function during earlier periods of the human life span, most notably during preadolescent development, future research efforts must focus on how early in the life span these differences emerge. Further, from a life span perspective, it is important to determine the time course of this relationship, as there appears to be a shift during maturation in which physical activity effects change from global to selective aspects of cognition. That is, research with adult populations clearly indicates that physical activity effects on cognition are disproportionately larger for executive control tasks, whereas in children the data indicate a more global relationship across tasks and task types. A better understanding of this relationship may also provide information to cognitive neuroscientists about important developmental changes in brain structure and function that coincide with the development of higher-level cognitive functioning, such as executive control.

Several other important aspects of this relationship have not been thoroughly investigated. For example, the amount, intensity, and duration of physical activity necessary to provide positive changes in cognitive function are as yet unknown. Given that the various cognitive functions are mediated by different brain structures, it is obvious that this relationship is not straightforward. Since executive control deteriorates more extensively than other types of cognition, determining the amount, intensity, and duration of physical activity needed to improve this aspect of cognition is of the utmost importance. However, executive control in and of itself is not unitary, and thus determining this relationship within the subset of processes that comprise executive control will prove challenging. Future examinations of this topic will also have to involve more rigorous scientific methods than those reviewed in this chapter. That is, the vast majority of research to date has utilized cross-sectional designs involving groups that fall along the extremes of the physical activity or aerobic fitness continuum. Further efforts will need to employ randomized controlled designs so that causality in this relationship can be better inferred.

Finally, little is known about the majority of neuroelectric processes that occur during information processing. Most research thus far has focused on the P3 component, while a subset of studies have focused on various other ERP components. Hence, although our understanding of processes subsumed by the P3 is reasonable, little is known about other cognitive processes involved in the stimulus–response relationship. Future efforts clearly need to address this paucity in the literature to determine whether certain processes are disproportionately influenced by physical activity relative to others. Despite the need for these future research efforts, the knowledge base on physical activity and neuroelectric indices of cognition has experienced substantial growth during the last decade. These efforts have led to a deeper understanding of lifestyle factors that promote better cognitive health and function across the life span.

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Chapter 6

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Chapter 7

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