Chapter 3

Benefits of Physical Activity and Fitness for Lifelong Cognitive and Motor Development—Brain and Behavior

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In recent years, the influence of exercise and physical activity not only on physiological health and psychological well-being, but also on cognitive performance as well as on brain structure and function, has come into focus (eg, Etnier, Nowell, Landers, & Sibley, 2006; Hillman, Erickson & Kramer, 2008). In addition, studies examining the effects of exercise and physical activity on motor performance and motor learning processes (Roig, Skriver, Lundbye-Jensen, Kiens, & Nielsen, 2012) represent promising areas of research, especially for older adults and rehabilitation after stroke (Singh & Staines, 2015). The inclusion of brain research methods such as electroencephalography (EEG) or functional and structural magnetic resonance imaging (MRI) provide valuable information on how exercise and physical activity affect brain structure and function and which possible mechanisms might underlie their relationship with cognition/motor performance.

One line of research focuses on the immediate effects of acute bouts of exercise. Studies that fall into this category can be further divided into approaches measuring cognitive or motor performance during or directly after exercising. These studies are often complemented by EEG measurements to investigate underlying neurophysiological mechanisms. Another line of research investigates chronic effects of physical activity. Investigations in this field examine either the association between an individual's overall physical fitness level with, or

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the effect of a (long-term) exercise intervention on cognitive or motor performance. Only long-term intervention studies are assumed to lead to structural changes in the organism (eg, increased vascularization or growth of synaptic connections). For structural changes to occur, however, physiological changes must precede. Such physiological changes, which take place while the organism adapts to the physical demands of an activity, may already positively impact specific cognitive processes directly after an acute bout of exercise. The investigated age ranges vary between studies and the underlying mechanisms are still not completely understood.

Physical activity incorporates bodily movements produced by skeletal muscles including a variety of unspecified activities in daily life domains (eg, work, household). In contrast, structured *exercise* is characterized as physical activity that is planned, repetitive, and done with the purpose to improve physical fitness level. *Physical fitness level* (or: *fitness level*) in turn refers to the actual status of someone's physical fitness, often measured by defining the maximal rate of oxygen consumption (VO_2 max) or the participant's energy expenditure by use of physical activity questionnaires.

EFFECTS OF ACUTE BOUTS OF EXERCISE

Effects of Acute Bouts of Exercise on Cognitive Performance

The relationship between acute exercise and cognition has been investigated with various physical intervention methods, sample characteristics, cognitive assessments, and timepoints of measurement (McMorris, Sproule, Turner, & Hale, 2011). There is evidence that performance on complex cognitive tasks that tap into the executive control system, that is, those cognitive functions that are related to attentional control, working memory, and cognitive flexibility, suffers when performed *during* aerobic exercise (Pontifex & Hillman, 2007). These deficits, however, dissipate and even reverse when exercise is terminated, that is, cognitive performance *following* exercise improves on average (for a review, cf. Chang et al., 2012).

Most studies on acute exercise effects have been performed with young adults. A meta-analysis by McMorris, Sproule, Turner, and Hale (2011) reveals significantly faster response times in tasks of executive functions following moderate intensity exercise. Only few studies investigated healthy older adults or children.

Key factors that add to the variation in findings on the exercise-cognition relationship are the intensity and duration of the exercise. A recent meta-analysis by McMorris and Hale (2012) supports the assumption of an inverted U-shaped relationship between arousal and performance, referring to the Yerkes–Dodson Law (Yerkes & Dodson, 1908). Accordingly, the most beneficial and robust results for acute exercise on cognitive performance (particularly executive control) are achieved at submaximal, moderate intensities with durations between 20 and 60 min (McMorris et al., 2011; Tomporowski, 2003). High-intensity exercise, on the contrary, seems to be most beneficial in highly fit subjects (Budde et al., 2012). Alves and colleagues (2014) revealed improved performance in an attention task, but not in a short-term memory task in healthy middle-aged adults (participants of a physical fitness program) after a high-intensity interval training (HIT) indicating specific effects of bouts of high-intensity exercise with respect to the cognitive task. We have shown that attention was improved after high-intensity exercise in young adults with a high participation rate in physical activity, whereas this was not the case in low active individuals. This finding indicates that a higher participation rate in physical activity might lead to neurobiological adaptations that facilitate effects of high-intensity exercise on cognitive processes (ie, attention) (Budde et al., 2012; for further specification of effects of high-intensity exercise, see section "Combination of acute and chronic exercise" in this chapter).

Further, exercise effects differ with regard to the timepoint of assessment following exercising. Post exercise effects on executive functioning are evident immediately after exercise and last up to 30 to 40 min after exercise cessation (eg, Pontifex, Hillman, Fernhall, Thompson, & Valentini, 2009), but seem to diminish after two hours (Hopkins, Davis, VanTieghem, Whalen, & Bucci, 2012).

The finding that brief, moderate-intensity exercise can improve cognitive function has important implications for various target groups. For example, for adolescents in a school setting positive effects of single bouts of exercise on cognitive performance support the argument that physical activity could help to improve scholastic performance (Budde, Voelcker-Rehage, Pietrabyk-Kendziorra, Ribeiro, & Tidow, 2008), particularly for adolescents considered low cognitive performers (Budde, Windisch, Kudielka, & Voelcker-Rehage, 2010b). In older adults it could increase daily functioning and quality of life. Within the work context these findings suggest that an active lunch break could potentially increase job performance in the second half of the workday.

Several studies applied neurophysiological methods, predominantly EEG, during or after an acute bout of exercise to better understand underlying brain processes. It has repeatedly been shown that acute bouts of exercise modulate event-related potentials (ERPs). For example, there is some indication that acute bouts of moderate-intensity exercise lead to increased P3 amplitudes and earlier peak latencies alongside behavioral benefits (Drollette et al., 2014; Kamijo, Nishihira, Higashiura, & Kuroiwa, 2007; Magnie et al., 2000; Nakamura, Nishimoto, Akamatu, Takahashi, & Maruyama, 1999; Scudder, Drollette, Pontifex, & Hillman, 2012). This enlargement of the P3 amplitude can be interpreted as an increase in attentional resources in the brain (Kamijo, 2009, for an overview). Own pilot data collected from younger adults immediately after cycling for 20 min at a moderate intensity (40–60% of individual VO_2 peak values) reveal earlier P3 peaks and a trend for increased P3 amplitudes as compared to a rest condition (Winneke, Hübner, Godde, & Voelcker-Rehage, 2016). Little is known about acute intervention effects on ERPs in older adults. Only one study reported earlier P3 latencies in older adults immediately following moderate exercise as compared to a rest condition (Kamijo, 2009), indicating that acute bouts of exercise might be able to counter age-related cognitive decline. In a recent study by Drollette et al. (2014) children (age 8–10 years) showed earlier P3 latencies in a Flanker task following moderate exercise, indicating a higher processing speed. Interestingly, children classified as low performers showed particular behavioral gains in the more difficult incongruent Flanker condition accompanied by P3 amplitude enlargements, suggesting a gain in selective attentional resource allocation (cf. Hillman, Buck, Themanson, Pontifex, & Castelli, 2009, for similar results).

Results regarding the effect of exercise on the N2 ERP component are scarce and mixed; results with older adults are lacking. Themanson and Hillman (2006) did not find effects of acute exercise on the N2. Pontifex and Hillman (2007) in young adults reported a reduction in N2 amplitude while exercising accompanied by reduced performance, whereas Drollette and colleagues (2014) in children reported a reduction in N2 amplitude after 20 min of exercise together with improvement in performance. This reduction was interpreted as an facilitation in repsonse conflict.

Crabbe and Dishman (2004) did a quantitative synthesis of EEG studies investigating oscillations in the alpha frequency band (~8–12 Hz) after acute exercise including participants ranging from young to older adults. The authors reported overall increased absolute alpha power directly after exercise. For example, in 9- to 10-year-old children, larger alpha activity was revealed in the precuneus after 15 min of moderate bike exercise (Schneider, Vogt, Frysch, Guardiera, & Strüder, 2009). This has been interpreted as a reflection of an overall state of physical relaxation, which might improve the ability to concentrate and result in better cognitive performance following an acute exercise bout. Further, decreased coherence in the lower alpha band (8–10 Hz) after acute exercise of moderate intensity as compared to rest condition was shown, which is regarded as indicator for reduced cognitive effort after acute exercise (Hogan et al., 2013). Furthermore, individual alpha peak frequency (iAPF) was increased after exhaustive exercise but not after less intense exercise in young healthy adults (Gutmann et al., 2015). The increase in iAPF is interpreted as a marker of arousal and attention and is associated with increased information-processing speed (Gutmann et al., 2015). In a study with older adults, the participants revealed a stronger decrease in alpha event-related desynchronization) during a Stroop task following 20 min of exercise at a moderate intensity (Chang, Chu, Wang, Song, & Wei, 2015). Alpha desynchronization was particularly pronounced in frontal brain regions and was interpreted as a neural marker of enhanced task performance. These findings are supported by studies using functional near-infrared spectroscopy (fNIRS), which revealed that acute exercise led to enhanced prefrontal activity after exercise in older adults (Hyodo et al., 2012; Tsujii, Komatsu, & Sakatani, 2013), reflecting improved task processing.

To sum up the electrophysiological findings, research indicates enhanced attentional capacity related to acute exercise as reflected in increased P3 amplitudes. Studies looking at EEG frequencies (alpha frequency in particular) indicate an increase in neural resources that can be devoted to the cognitive task at hand, representing enhanced attention and better cognitive task performance.

Effects of Acute Bouts of Exercise on Motor Performance and Motor Learning

Effects of acute exercise on motor performance and motor learning have been studied for decades.[a] However, conducted exercise protocols (eg, exercise intensity, termination criteria) and performed motor tasks (eg, gross or fine motor skills) or whether the focus was on performance or learning varied across studies.

When measuring effects of acute exercise on motor performance, the performance or adaptation of a motor task was measured directly after exercise (Thacker, Middleton, McIlroy, & Staines, 2014; Wegner, Koedijker, & Budde, 2014). Findings are very heterogeneous. Some findings partially supported a claim of an inverted U-shape relationship between exercise intensity and motor performance (eg, with the gross motor Bachman ladder task, Pack, Cotten, & Biasiotto, 1974). Others found improvements after intense exercise in a task requiring fine motor control in high-fit young subjects (eg, Fitts' reciprocal tapping task; Dickinson, Medhurst, & Whittingham, 1979). A recent meta-analysis of effects of acute exercise on sport-related skills like passing in soccer by McMorris, Hale, Corbett, Robertson, & Hodgson (2015) did not only disprove an inverted U-shape relationship, but also found no significant effect of moderate-intensity exercise on motor performance and a detrimental effect of intense exercise.

So far, all studies were performed with young adults, with few exceptions. Wegner, Koedijker, and Budde (2014) investigated the effects of moderate-intensity exercise on manual dexterity performance in children (flower trail) and found no effect of acute exercise on fine motor performance. An EEG study by Thacker et al. (2014) revealed that acute bouts of moderate exercise led to an earlier onset of the early readiness potential in young participants indicating a positive effect on movement preparation in a subsequent motor task (self-paced wrist extension). Effects on task performance were not reported.

When measuring the effects of acute exercise on motor learning, performance was mostly measured by use of delayed retention tests (Mang, Snow, Campbell, Ross, & Boyd, 2014; Roig et al., 2012; Skriver et al., 2014) as the motor memory needs time to be transformed in performance improvement (for a review, see Kantak & Winstein, 2012). Findings regarding the effects of acute exercise on motor learning are again inconsistent. Interestingly, contrary to studies analyzing exercise effects on cognitive or motor performance, these studies used bouts of exercise of high intensity as lactate is assumed to

[a] In early studies, acute bouts of exercise were named as physical fatigue (eg, Pack, Cotten, & Biasiotto, 1974).

be a mediating mechanism. Positive effects of a high-intensity acute exercise protocol have been found on learning an implicit motor sequence task in terms of higher temporal precision but not spatial accuracy (force tracking) (Mang et al., 2014) and on retention performance (24 h and 7 days after practice), but not immediately after exercise (Roig et al., 2012; Skriver et al., 2014) as compared to a resting control group. The latter finding reflects that motor memory needs time for consolidation to be transformed into better motor performance. Roig and colleagues (2012) did not only compare the amount of motor learning after an acute bout of exercise with the amount of learning after a rest condition, but also varied the order of acute exercise and motor task. Interestingly, both, the experimental group practicing the motor task before the acute exercise and the group practicing the motor task after intense exercise performed better in the retention test seven days after practice than a non-exercising control group, with the post-exercise group performing best (Roig et al., 2012). This finding points to the need to further investigate the best timepoint of a bout of acute exercise (before or after practicing the motor task) to facilitate consolidation of motor learning processes.

Very recent studies provided neural underpinnings for the positive impact of acute bouts of exercise on motor learning processes. They revealed that acute bouts of exercise facilitate neuroplasticity in the (primary) motor cortex (M1) induced by repetitive transcranial magnetic stimulation (rTMS, ie, a noninvasive brain stimulation technique; Singh & Staines, 2015, for a review). M1 is the most important source of ascending projections to the motor neurons and is crucial for the voluntary control of movements. This enhanced neuroplasticity might occur because acute exercise affects neurochemical processes that are in turn known to facilitate M1 excitability, like higher levels of the neurotransmitters dopamine, serotonin, norepinephrine, and lactate (Singh, Neva, & Staines, 2014). In accordance to that, Skriver and colleagues (2014) showed that the same neurochemical processes (plus increased levels of insulin-like growth factor [IGF-1], epinephrine and vascular endothelial growth factor [VEGF]) were involved in motor skill acquisition and retention. Nevertheless, more studies are needed to examine the effects of acute exercise on motor functions and, motor learning including physiological and neurochemical measures. The aim is to understand the exact mechanisms and to give recommendations about exercise intensity, duration, and timing of exercise and motor paradigms (McMorris et al., 2015).

LONG-TERM EXERCISE OR PHYSICAL ACTIVITY EFFECTS

Long-Term Exercise or Physical Activity Effects on Cognition

Meta-analyses and review articles (Colcombe & Kramer, 2003; Kramer, Erickson, & Colcombe, 2006; Voelcker-Rehage & Niemann, 2013) have shown that physical activity (cross-sectional data and intervention studies) is positively associated with cognitive functioning across the lifespan. Colcombe and

Kramer (2003) analyzed 18 intervention studies on the influence of physical activity on various cognitive tasks in adults 55 years of age and older. They found the largest benefit of physical activity on executive control functions. Independent of cognitive task, method of training, and sample characteristics, physical activity enhanced cognitive performance by 0.5 standard deviations. The effect of physical activity was influenced by the length, the extent, and the type of intervention. Not only effects on executive control, but also on perceptual speed (Colcombe & Kramer, 2003) and memory performance were repeatedly shown (Flöel et al., 2008; Hötting, Schauenburg, & Röder, 2012; Klusman et al., 2010). Positive effects of moderate physical activity on cognitive performance have been shown already after only eight to 12 weeks of exercise (Albinet, Boucard, Bouquet, & Audiffren, 2010; Fabre, Chamari, Mucci, Masse-Biron, & Prefaut, 2002) two to three times a week and even in seniors who have been rather inactive previously.

Most exercise paradigms utilized cardiovascular exercise, also referred to as aerobic or cardiorespiratory exercise, where highly automated movements like walking or cycling are performed. Fewer studies investigated other types of exercise, such as motor-coordinative or resistance exercise. Similar to cardiovascular fitness, resistance exercise (resistance training) affects metabolic and energetic processes and to some extent intramuscular coordination. Unlike metabolic exercise, motor-coordination training comprises exercises for bilateral fine and gross motor body coordination such as balance, eye-hand coordination, and leg-arm coordination, as well as spatial orientation and reaction to moving objects/persons (Voelcker-Rehage, Godde, & Staudinger, 2011). Coordination training induces less change in energy metabolism than cardiovascular and resistance exercise. Instead, coordinative movements require perceptual and higher-level cognitive processes, such as attention, that are essential for mapping sensation to action and ensuring anticipatory and adaptive aspects of coordination. Thus, changes induced by coordinative exercise are likely to be related to changes in information processing and cognitive tasks that demand, besides attention, the ability to handle visual and spatial information. By contrast, perceptual and higher-level cognitive processes are less relevant in highly automated movements like walking or cycling, as used in cardiovascular exercise. Recently, dancing has come into focus as an attractive leisure-time activity among older adults. Dancing is a multimodal type of physical activity that addresses cardiovascular as well as coordinative and cognitive demands, and it is difficult to disentangle effects of cardiovascular from other fitness effects in dancing studies. In this section, we will detail the differential effects of different types of exercise and fitness on brain and cognitive function.

Cardiovascular Exercise

As for acute effects of exercise, there is increasing evidence for fitness-related modulations of cognitive ERPs. Other studies investigated the chronic exercise-cognition relationship by use of MRI or on a behavioral level only.

Higher physical activity levels are associated with shorter P3 latencies and/or larger amplitudes in children (Hillman et al., 2014) and both younger (Kamijo & Takeda, 2010) and older adults (Fong, Chi, Li, & Chang, 2014; for reviews, cf. Kamijo et al., 2007). A cross-sectional study revealed that the amplitude of the N1 ERP component was increased in older adults participating in light and moderate aerobic exercise, as compared to a sedentary control group (Chang, Huang, Chen, & Hung, 2013b). This finding indicates that the exercise group was able to engage more attentional resources for the early stimulus encoding processes. Recent data from our lab revealed a linear positive relationship between VO_2 peak values and both behavioral performance and P3 amplitude in a working memory task in young adults (Winneke et al., 2016). Also a study with elementary school children revealed faster response times as well as shorter P3 latencies and increased P3 amplitudes on a flanker task and thereby underline the positive effect of physical activity intervention programs on attentional processes in children (Hillman et al., 2014). Interestingly, benefits of physical exercise in children were not only reported for general cognitive tasks but also for specific aspects of arithmetic problem solving (Moore, Drollette, Scudder, Bharij, & Hillman, 2014).

Findings regarding the N2 ERP component in context of physical activity are less and mixed. In a sample of middle-aged adults we showed a positive association between cardiovascular fitness levels and attentional control as well as N2 amplitudes (Fig. 3.1; Winneke, Godde, Reuter, Vieluf & Voelcker-Rehage, 2012), indicating greater conflict monitoring capacity (Yeung, Botvinick, & Cohen, 2004; for similar N2 results, cf. Gajewski & Falkenstein, 2015). Others report N2 and P2 latency reductions indicating reduced processing speed after aerobic exercise interventions (Özkaya et al., 2005). Contrary, Themanson and Hillman (2006) reported that in young adults the fitness level was not associated with modulations of the N2, but high-fit adults showed marked reductions in the amplitude of

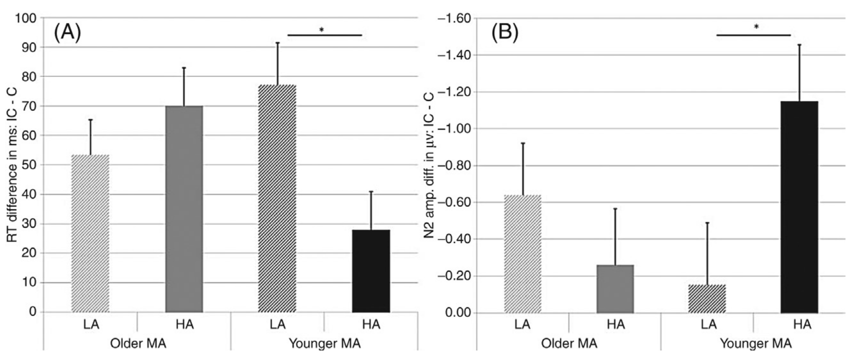

FIGURE 3.1 Interference induced by incongruent flanker (IC) quantified as (A) RT difference and (C) N2 amplitude difference at electrode Cz relative to congruent flanker (C) separated by age group and physical activity level *(LA = low active; HA = highly active)*. * $p < 0.05$. *(Original figure appeared in Winneke et al., 2012.)*

the error-related negativity (ERN; cf. Themanson, Hillman, & Courton, 2006, for similar ERP results in older adults). Findings regarding the N2 and physical fitness in children and adolescents are also mixed with some studies reporting no association (Hillman et al., 2009), others reporting smaller N2 amplitudes in high-fit children yet better performance (Pontifex et al., 2011; Stroth et al., 2009).

Given the diversity of experimental designs and testing parameters together with the small number of studies, the effects of exercise interventions on ERP components, as markers of cognitive functioning and attentional control, require further investigation. Also, differences in maturity of brain development have to be considered particularly when comparing findings in children, young adults, and seniors.

The first functional MRI study on the exercise–cognition relationship was conducted by Colcombe and colleagues (2004) on older adults. Results indicated that after cardiovascular training, older adults applied cognitive resources more effectively and cognition was improved. Using a Flanker task, the data showed significantly higher levels of brain activation for physically active as compared to inactive older participants in prefrontal and parietal regions, and significantly lower activity in the anterior cingulate cortex (ACC). The same was true for older adults participating in a six-month aerobic exercise intervention (walking training) as compared to a stretching and toning control group (Colcombe et al., 2004). Higher prefrontal activation may contribute to better performance in a range of executive control functions, including attentional selection, working memory, task switching, and inhibitory control. Parietal structures that revealed higher activation in these studies are mainly associated with visuospatial processing, but also with language and tactile processing. Less activation in the ACC, on the contrary, indicates reduced response conflict.

Other studies confirmed the findings by Colcombe and colleagues (2004) (Holzschneider, Wolbers, Röder, Hötting, 2012; Prakash et al., 2011; Rosano et al., 2010). Interestingly, some studies revealed differential activation patterns. Following a 12-month aerobic exercise intervention, high-fit as compared to low-fit older adults revealed lower activation in the prefrontal cortex but higher activation in temporal regions during performance of incongruent Flanker trials (Voelcker-Rehage, Godde, & Staudinger, 2010, 2011). In the cognitive aging literature these contradictory findings are explained twofold: On the one hand, increasing task load is associated with increased recruitment (until a critical point is reached after which a decrease occurs) and training may serve to increase the engagement of task-relevant regions. On the other hand, increased efficiency in the processes linked to these regions might lead to reduced activations, that is, fewer neural resources required albeit maintaining or even improving performance. Moreover, higher activation in frontal brain areas, in older as compared to young adults, has often been interpreted as compensation for age-related changes (for review, see Reuter-Lorenz, & Lustig, 2005). Following this view, reduced activation after training might indicate a more youth-like or efficient brain and in turn less need for compensation. Thus, overactivation might be reduced in high-fit (Prakash et al., 2011) or trained older adults during less demanding, but also during challenging (Voelcker-Rehage et al., 2010, 2011) tasks. Both increased and decreased activation patterns may turn out to reflect physical activity-induced executive control improvement in older adults. Overall, cardiovascular activity seems to interact with brain activation during performance of executive control tasks, particularly, in frontal and parietal areas.

Research in children confirmed findings from research with older adults. In cross-sectional and longitudinal studies high-fit children (or after exercise intervention) revealed better executive control (Raine, Scudder, Saliba, Kramer, & Hillman, 2015; Chaddock et al., 2012a). Further, higher relational memory (Chaddock et al., 2010a) and learning benefits (Raine et al., 2013) were shown. These behavioral results from high-fit children were accompanied by more effective brain activation, as pronounced in either higher prefrontal cortex activity (Davis et al., 2011; Chaddock et al., 2012a, for the early task blocks) or reduced frontal activity (Chaddock et al., 2012a, for the later task blocks) and reduced parietal activity (Davis et al., 2011; Chaddock et al., 2012a, for the later task blocks), presumably reflecting a reduction of resources required to complete the task. Findings in children suggest that early cardiovascular fitness fosters executive control functioning and (less studied) memory performance and that this better performance may be related to functional and structural benefits, respectively.

In studies focusing on memory performance in adults, higher physical activity levels were paralleled by higher brain activation in the hippocampus and parahippocampal gyrus as well as in the frontal lobe during spatial learning or memory tasks in middle-aged (Holzschneider et al., 2012) and older adults (Smith et al., 2011). As both the frontal lobe and hippocampus are especially vulnerable to age-related functional changes (Grady, Springer, Hongwanishkul, McIntosh, & Winocur, 2006), one might assume that higher cardiovascular fitness or aerobic training contributes to better functioning of these regions. Depending on the sample and the type of task, cardiovascular activity may free up cognitive resources, to increase the engagement of task-relevant regions or to change performance strategies leading either to increased or reduced, but more efficient, activations in task-relevant areas.

Neural connectivity data bear the potential to reveal task-independent measures of brain function. Findings suggest that higher cognitive performance in high-fit older adults or following an extended aerobic intervention might be based on a higher functional connectivity within and between task-relevant brain regions at rest. Voss and colleagues (2010a; 2010b) demonstrated that higher functional connectivity of the so-called default mode network (DMN) was related to better executive control function. Whether other cognitive domains would also benefit from exercise-induced higher functional connectivity is currently not clear. Functional connectivity of the hippocampus with several other brain regions (Burdette et al., 2010) further seems to be enhanced through cardiovascular activity. This might positively influence memory function. To confirm this suggestion, additional research is required.

On the level of brain anatomy, Colcombe et al. (2003) again were the first to examine the association between brain volume and cardiovascular fitness in older adults. They found that age-related decline in brain volume in frontal, parietal, and temporal cortices was attenuated as a function of cardiovascular fitness (Colcombe et al., 2003). So far, brain regions that showed associations with cardiovascular fitness and/or training differ between studies. In older ages, a positive relationship has been found between cardiovascular training and frontal areas (eg, ACC) (Bugg & Head, 2011; Colcombe et al., 2003, 2006; Flöel et al., 2010; Gordon et al., 2008; Ruscheweyh et al., 2011; Weinstein et al., 2012), the temporal lobe (Colcombe et al., 2006; Gordon et al., 2008) or hippocampus (Erickson et al., 2009, 2011; Niemann, Godde, & Voelcker-Rehage, 2014b; Szabo et al., 2011), the parietal lobe (Benedict et al., 2013; Colcombe et al., 2003), and the basal ganglia (Verstynen et al., 2012). However, there were also studies that did not find any relationship between gray matter volume and cardiovascular activity parameter (Rosano et al., 2010; Smith et al., 2011). Also, in children higher levels of cardiovascular fitness or long-term exercise training have been related to larger volumes of the hippocampus (Chaddock et al., 2010a) and the basal ganglia (Chaddock et al., 2010b, 2012b, for an intervention analysis). Cognitive measurements were included in most of the studies and consistently revealed positive associations. However, cognitive domains differ substantially across studies: verbal skills in Gordon et al. (2008) and Benedict et al. (2013), episodic memory in Flöel et al. (2010) and Ruscheweyh et al. (2011), relational memory in Chaddock et al. (2010a), frequency of forgetting in Szabo et al. (2011), executive functions in Weinstein et al. (2012), Verstynen et al. (2012), Chaddock et al. (2010b and 2012a), and spatial memory in Weinstein et al. (2012) and Erickson et al. (2009 and 2011). So far, only one study examined the effect of cardiovascular exercise on brain parameters and cognitive functioning in middle-aged adults (Pereira et al., 2007), with a focus on the dentate gyrus. After a 3-month cardiovascular training, cerebral blood volume in the dentate gyrus of the hippocampus was enhanced and associated with improved cardiovascular fitness, suggesting better vascularization of this tissue. Furthermore, hippocampal blood volume was paralleled by better declarative memory performance of the participants (Pereira et al., 2007).

In comparison to gray matter volume, less research has been done on cardiovascular activity and white matter volume and integrity. Some research on white matter changes revealed a positive association with physical activity (Colcombe et al., 2003, 2006; Ho et al., 2011). However, the majority of studies did not find a relationship between white matter volume and physical activity (Erickson et al., 2010; Flöel et al., 2010; Gordon et al., 2008; Peters et al., 2009, for young adults; Ruscheweyh et al., 2011; Smith et al., 2011, for older adults). An association between white matter volume and cognitive performance has also not been established so far, although a positive association with information-processing speed is highly likely (Jacobs et al., 2011). First studies on white matter integrity in older adults suggested that high aerobic fitness may attenuate age-related decline in myelination of axons in portions of the corpus callosum (Johnson, Kim, Clasey, Bailey, & Gold, 2012), the cingulum (Marks, Katz, Styner, & Smith, 2011), and a frontoparietal brain network related to visuospatial functions, motor control, and coordination (Tseng et al., 2013). Similarly, increases in VO_2 max after a 12-month intervention period were related to increases of fractional anisotropy values in prefrontal and temporal regions (Voss et al., 2013b). However, also contradictory findings exist (Burzynska et al., 2014). In terms of white matter lesions and hyperintensities, more physical activity seems to be associated with less white matter hyperintensities in older adults without advanced diseases (for an exception in men, see Torres, Strack, Fernandez, Tumey & Hitchcock, 2015).

Resistance Training

Although some studies have reported conflicting findings on the role of resistance-exercise training in preventing cognitive decline with age, other studies have demonstrated a beneficial effect of such training on specific cognitive measures. A recent review of studies with healthy older adults revealed overall positive effects of resistance training on cognitive functions including information-processing speed, attention, memory formation, and specific types of executive function (Chang et al., 2012). In comparing resistance-exercise training with other types of exercise, such as flexibility, toning, relaxation, calisthenics, and even endurance exercises (Brown, Liu-Ambrose, Tate, & Lord, 2009; Cancela Carral & Ayan Perez, 2007; Özkaya et al., 2005), some studies showed that resistance training produced equivalent or even higher performance increases in specific cognitive functions. Further, resistance training seems to show clear dose-response effects. Intervention designs with loads of 60–80% 1RM (repetition maximum) with approximately seven movements in two sets separated by 2 min of rest at least twice per week for 2–12 months (usually 6 months), seem best suited to positively affect cognition.

The beneficial effects of resistance training were supported by functional MRI and ERP data indicating changes in (visual) processing strategies (Nagamatsu, Handy, Hsu, Voss, & Liu-Ambrose, 2012) and facilitation of early sensory processing and cognitive functioning in older individuals (Özkaya et al., 2005).

Motor-Coordination Training

Motor coordination measured after an exercise intervention or via motor fitness level is also positively associated with cognitive function. This has been shown for different age groups. In elementary school-aged children, motor fitness levels have been positively related to complex executive control tasks (Luz, Rodrigues, & Cordivil, 2015) and academic achievement (Lopes, Santos, Pereira, & Lopes, 2013). After 3 months (Koutsandréou, Niemann, Wegner, & Budde, 2016) or 6 months (Crova et al., 2014) of motor-demanding and cognitively challenging interventions, executive control performance of 9- to 10-year-old children was improved.

Drawing conclusions from intervention studies (in older adults) is difficult because not only the type of intervention differed (eg, multimodal exercise training including cardiovascular, strength, and motor fitness training, Vaughan et al., 2014; multimodal motor training including coordination, balance, strengthening, agility, and relaxation tasks, Forte et al., 2013; Voelcker-Rehage et al., 2011; flexibility and object manipulation training, Berryman et al., 2014; contemporary dance, Coubard et al., 2011; Kwok et al., 2011), but also cognitive dimensions included in the analyses vary as well as the intervention length (2–12 months). Even in studies using similar interventions and tasks, findings on cognition often could not be replicated (Forte et al., 2013; Klusmann et al., 2010; Vaughan et al., 2014). Nevertheless, positive effects of high motor coordination in older adults were reported on verbal fluency (Vaughan et al., 2014), measurements of fluid intelligence (Raven Standard Progressive Matrices, Kattenstroth, Kolankowska, Kalisch, & Dinse, 2010), information-processing speed (Okely, Booth, & Patterson, 2001; Vaughan et al., 2014; Voelcker-Rehage et al., 2011), Mini Mental State Examination (MMSE; a measure of cognitive impairment, Kwok et al., 2011), executive functions (Berryman et al., 2013; Forte et al., 2013; Okely et al., 2001; Vaughan et al., 2014; Voelcker-Rehage et al., 2011), and cognitive flexibility (Coubard et al., 2011). Some studies, however, failed to report positive effects. For example, Klusmann et al. (2010) could not replicate the findings for verbal fluency and executive control functions after 6 months of a similarly complex physical activity training, but found increases in episodic memory performance (cf. also, Hötting et al., 2012, for effects of a stretching and coordination training on episodic memory in middle-aged adults). There was also no positive influence of motor coordination found on problem solving and inhibition control (Coubard et al., 2011).

Studies on the effects of coordination trainings on neurophysiological measures are rare. An ERP study on task-switching revealed that P3 amplitudes were increased and reaction times were reduced in older adults with a history of regularly participating in Tai Chi as compared to sedentary older adults (Fong et al., 2014). Also, kindergarten children participating in an 8-week coordinative exercise program revealed faster response times as well as shorter P3 latencies and increased P3 amplitudes on a Flanker task at the end of the intervention relative to the beginning (Chang, Tsai, Chen, & Hung, 2013a). We conducted an MRI study on the effects of coordination training and were able to show that motor fitness was related to more efficient cognitive processing, indicated by less cortical activation in brain regions involved in cognitive control, that is, the superior and middle frontal cortex. In addition, motor fitness was related to higher activation of the right inferior frontal–posterior parietal network indicative of improved processing and integration of visuospatial information (Voelcker-Rehage et al., 2010). We further revealed that after a 12-month coordination training (60 min, 3 times per week) brain activation levels during a Flanker task increased particularly in the right inferior frontal gyrus and the superior parietal cortex, which form part of the so-called visuospatial attention network, as well as in the thalamus and caudate body (Voelcker-Rehage et al., 2011). These latter subcortical structures are important for process automation without conscious control. This fits well with other findings showing that high-fit older adults needed less dorsolateral prefrontal (cognitive) resources for movement control than low-fit participants (Godde & Voelcker-Rehage, 2010).

Furthermore, structural brain data indicate that older adults with higher levels of motor fitness or older adults participating in a 12-month coordination training program, revealed larger volumes of the hippocampus (Niemann et al., 2014b; c.f. Fig. 3.2). High motor fitness level as well as motor-coordination training seem to be beneficial to diminish age-related hippocampal volume shrinkage or even to increase hippocampal volume in older adults. Similarly, volume of the basal ganglia (caudate, putamen, and globus pallidus) also benefited from motor fitness and/or coordination training (Niemann, Godde, Staudinger, & Voelcker-Rehage, 2014a). Moreover, basal ganglia volume moderated the relationship between higher motor fitness levels and executive control performance. That is, in participants with low basal ganglia volume, motor fitness was positively correlated with executive control performance. This relationship became negligible when basal ganglia volume was larger. This finding indicates that motor fitness might prevent older adults from showing reduced executive control functioning when basal ganglia volume is low (or vice versa, that there is no additional benefit of motor fitness when basal ganglia size exceeds a certain volume).

To sum up, current research indicates that not only cardiovascular demands contribute to cognitive benefits in older adults, since interventions without any cardiovascular impact also revealed positive effects on the behavioral and neurophysiological level. Therefore, a coordination training including a

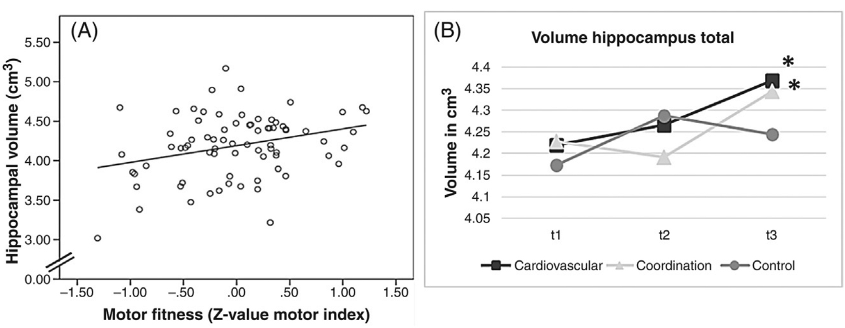

FIGURE 3.2 Cross-sectional and interventional findings of associations of coordinative activity with hippocampal volume of both hemisphere (in cm^3) in healthy older adults aged 62–79 years: (A) Significant relationship of hippocampal volume and motor fitness levels (r= .28); (B) Hippocampal volume at baseline (t1) after 6 (t2) and 12 (t3) months of coordination (and cardiovascular) training. * = p< 0.05. *(Figure adapted from Niemann et al., 2014b.)*

variety of complex movements (for a discussion, see also Voelcker-Rehage & Niemann, 2013) might be essential for cognitive benefits.

Dancing

A first prospective study, by Verghese and colleagues (2003), showed leisure dancing to be associated with a reduced risk of developing dementia. A few years later, however, a cross-sectional study did not confirm this result. Adults aged 80 years, who had engaged in many years of nonprofessional dancing activity, did not demonstrate better cognitive performance in the domains of memory and executive control in comparison to nondancers (Verghese, 2006). Similarly, a pilot study with 13 healthy, older women did not reveal improvements in cognitive performance measured by the MMSE, after a 12-week jazz dance intervention (Alpert et al., 2009). Recent studies, again, showed more positive results. Older adults, with long-term dancing experience, showed better cognitive performance in the domains of fluid intelligence and attention in comparison to age-matched inactive controls (Kattenstroth et al., 2010). Furthermore, the same research group observed increasing performance in an overall index of cognition (comprised of concentration, attention, and nonverbal learning) in older adults participating in a 6-month dancing intervention (Kattenstroth, Kalisch, Holt, Tegenthoff, & Dinse, 2013).

We performed a first neuroimaging study, in which we tested the association of long-term senior dance experience with cognitive performance and gray matter brain volume in older women aged 65–82 years (Niemann, Godde, & Voelcker-Rehage, under review). In this study, we compared nonprofessional senior dancers with a control group consisting of physically active participants without any dance experience. No differences with respect to dance experience were revealed in the four tested cognitive domains (executive control, perceptual speed, episodic memory, long-term memory). Small effects of dance experience were observed in frontal gray matter volume in the right medial frontal gyrus and the left middle frontal gyrus. Volume of the left middle frontal gyrus was positively related to executive control performance, and volume of the hippocampus was positively related to long-term memory performance across the whole sample. Thus, although positive associations of cardiovascular as well as motor-coordination activity on brain structure and function have been previously revealed, data on the effects of dancing activity on the brain are sparse and further research is needed.

Genetic and Physiological Factors to Influence the Acute and Chronic Exercise-Cognition Relationship

Few studies have investigated the link between lifestyle factors such as physical activity, cognitive performance, and genetics. Of particular interest in this context is the catechol-O-methyltransferase (COMT) polymorphisms. The COMT gene has been identified as a candidate gene associated with executive functions (Goldberg & Weinberger, 2004). Numerous human studies showed advantages of met/met allele carriers over val homozygotes in tasks of executive functioning. Stroth and coworkers (2010) revealed that in a sample of healthy adults (17–47 years of age), COMT val homozygotes improved their cognitive performance (Stroop task, dots-mixed task), after 17 weeks of running training, to a greater extent than met allele carriers. Similarly, investigating the effect of a 6-month multicomponent training program (cognitive, aerobic, and activities of daily living) in healthy older adults, Pieramico et al. (2012) revealed the greatest exercise benefits in COMT val/val and val/met allele carriers (and DRD3 ser9gly carriers). We revealed a positive influence of overall fitness, and an interactive effect of fitness and COMT polymorphisms on Flanker accuracy performance (Voelcker-Rehage, Jeltsch, Godde, Becker, & Staudinger, 2015). Val/val carriers revealed the highest positive correlation between fitness and cognition suggesting that particularly val/val allele carriers benefit from exercise by improved cognitive functioning, whereas met/met carriers already perform close to their optimal level.

Endocrinological changes (especially glucocorticoids, eg, cortisol) have also been established as a factor that facilitates the positive effects of acute and/or chronic exercise on cognitive functioning (Lupien, Gillin, & Hauger, 1999; Budde et al., 2010a). Also neurotransmitter (eg, dopamine) and neurotrophic growth factors (eg, brain derived neurotrophic factors, BDNF) are assumed to play a key role in the exercise-cognition relationship. Dopamine has been shown to be affected by exercise in both animals (Hattori, Naoi, & Nishino, 1994; He et al., 2012; Kim et al., 2011) and humans (Kraemer et al., 1999; McMorris et al., 2008; Ruscheweyh et al., 2011; Winter et al., 2007) after both acute and long-term physical activity interventions. The association between physical activity and dopamine concentrations is, however, still controversially discussed; some studies did not find an increase in dopamine levels during (Nybo, Nielsen, Blomstrand, Moller, & Secher, 2003) or after (Wang et al., 2000) exercise.

BDNF as a major growth factor of the brain promotes angiogenesis, neurogenesis, synaptogenesis, gliagenesis, as well as the formation of dendrites and neuron body growth and thus, has an indirect impact on brain structure and cognitive functioning (for a review, see Voss et al., 2013a). Animal research showed that cardiovascular activity seems to enhance the release of BDNF in the hippocampus (Cotman & Berchtold, 2002; Ding, Vaynman, Akhavan, Ying, & Gomez-Pinilla, 2006; Gomez-Pinilla, Vaynman, & Ying, 2008), cortex (Ding, Li, Luan, Ding, Lai, Rafols et al., 2004), and basal ganglia (Ding et al., 2004). In humans, acute and chronic exposure to physical activity was shown to result in increased peripheral levels of BDNF (for a review, see Huang, Larsen, Ried-Larsen, Moller, & Andersen, 2014). Increased BDNF levels in response to cardiovascular activity were accompanied by better memory (Winter et al., 2007; Ruscheweyh et al., 2011), inhibition control (Ferris, Williams, & Shen, 2007), and spatial performance (Erickson et al., 2010). Fitness status was assumed to play a role in BDNF release. For example, in cardiovascular fit young adults, acute BDNF release in response to an acute bout of cardiovascular activity was higher than in less fit adults (Zoladz et al., 2008). In sum, endocrinological and neurochemical growth factors, crucial for brain structure and cognitive performance, are age dependent, but seem to be modifiable by physical activity, which boost the release.

Effects of Physical Activity on Motor Performance and Motor Learning

As compared to cognitive skills, less is known about the relationship between a chronic engagement in physical activity and the performance in motor tasks. No study investigated the effects of chronic physical activity on motor learning processes in humans so far. Existing studies about physical activity and motor performance were conducted with older adults; results are mixed.

Research indicates that older physically fit persons show superior motor performance as compared to their sedentary counterparts for tasks requiring lower limbs, like standing balance, walking speed, or the ability to rise from a chair (Krampe, Smolders, & Doumas, 2014; Pahor et al., 2006). Other studies showed this positive relationship also for the upper limbs in simple motor reaction time tasks (Spirduso, 1980), tasks requiring fine motor control (Bakken et al., 2001) and manual aiming ability (Claudino, Mazo, & Santos, 2013). Data from our own lab supported a positive association between physical fitness and fine motor performance in older adults showing that high-fit older adults performed better in tasks requiring fine motor control (visuomotor force tracking and Purdue Pegboard test) (Hübner, Godde, & Voelcker-Rehage, in preparation) than their less fit counterparts. (cf. Adamo, Alexander, & Brown, 2009; Etnier & Landers, 1998; Krampe et al., 2014 for no effects on fine motor control of the upper limbs).

Up to now, the underlying mechanisms remain unclear to a large extent. Some authors speculated that higher motor and sensory functions, better muscular performance, and conservation of proprioception of the more fit older adults might be responsible for the superior motor performance (Claudino et al., 2013). Animal studies showed that aerobic exercise interventions induced changes in the motor cortex and other areas involved in motor function (cerebellum, basal ganglia, substantia nigra) expressed by enhanced oxidative metabolism (McCloskey, Adamo, & Anderson, 2001; Vissing, Andersen, & Diemer, 1996), hippocampal neurogenesis and synaptic plasticity (van Praag, Shubert, Zhao, & Gage, 2005). These findings indicate that regular exercise does not only modulate brain areas involved in cognitive processing, but also brain regions being active during motor performance. Again, more research is needed to be able to derive well-founded exercise recommendations to improve motor performance or motor learning processes. Findings could have great impact for certain target groups, for example, for rehabilitation of stroke patients.

COMBINATION OF ACUTE AND CHRONIC EXERCISE

Few studies investigated the interplay between the effects of acute and chronic exercise on cognitive functioning. Such a relationship is assumed because physiological changes, which take place while the organism adapts to the demands of an acute bout of exercise, may lead to structural changes in the long run. So far, these studies indicate that individual improvements in physical fitness lead to larger cognitive benefits through acute bouts of exercise (Hopkins et al., 2012). For example, Zervas, Danis and Klissouras (1991) investigated in an acute-chronic-mixed design the performance in a visual discrimination task in preadolescent children. Twenty-five minutes of treadmill running improved cognitive performance and was the highest after 6 months of aerobic training. The fitness effect seems to be especially prominent in highly complex cognitive tasks (Weingarten, 1973). However, so far, intervention lengths were limited (7 and 12 weeks) in studies, only children or young adults have been investigated, and study designs were not well controlled (Gutin, 1966; Weingarten, 1973). We assume that acute exercise effects sum up across an exercise intervention period and lead to pre- to posttest (chronic) changes in cognition and (neuro-) physiological markers.

Roig, Nordbrandt, Geertsen and Nielsen (2013) conclude in their review that fitness level does not interact with acute exercise in tasks requiring short-term memory. In contrast, in tasks requiring long-term memory, acute exercise seems to have a better effect in individuals with an average fitness level as with a low fitness level. Chang et al. (2012) in their review found benefits of high and low fit (but not moderately fit) participants on cognition directly after exercise.

Findings regarding exercise intensity effects are, however, ambiguous as some studies revealed higher cognitive benefits for high-fit or high-active participants in comparison to their less-fit or inactive counterparts (Budde et al., 2012; Pesce, Cereatti, Forte, Crova, & Casella, 2011) and others did not show any differential effects regarding fitness levels (Magnie et al., 2000; Themanson & Hillman, 2006).

To sum up, these results underline the importance to assess physical fitness status and a history of physical activity history (ie, sport participation in the last 12 months) in studies examining effects of acute exercise to control for the interplay of acute and chronic exercise effects.

OUTLOOK

In this chapter we provided an overview about different research facets of the exercise-cognition interaction. It turns out that certain research questions so far have been thoroughly investigated only in certain target groups (eg, chronic exercise effects mainly in older adults and acute exercise effects in younger adults). Further, research methods and paradigms differ immensely between studies. Systematic approaches that bring together the different research areas, methods and results are still missing. Especially the interaction of acute and chronic exercise effects on cognition need to be examined in greater depths, because, as we outlined in this chapter, existing findings seem to be ambiguous. Moreover, studies are needed to investigate whether effects of acute and chronic exercise on behavior and neurophysiological processes are the same in children, as well as younger and older adults. For example, it is unknown whether the exercise effects vary as a function of cognitive processes to a different degree in younger and older adults. Besides younger adults, adolescents, and older adults over the age of 65, another age group that is particularly interesting is that of middle adulthood, spanning the ages 35–65 years. In light of age-related cognitive changes, measures to prevent or to slow down the decline are important to take before first signs of deficits appear. Therefore, the optimal time to take preventive steps is probably the childhood and middle adulthood. As we have shown, physical exercise is a potential mean to modulate cognitive function. A few studies exist that look at the cognition-exercise relationship in middle-aged adults but more research is required to increase our understanding. In the same line of argumentation, more longitudinal studies and long-term follow-up measurements are desirable to further expand our knowledge of how the relationship develops over time. Also, research investigating the relationship between chronic physical activity or acute bouts of exercise and motor performance and motor learning in different age groups is needed. In this field of research, studies measuring neurophysiological processes are missing. Furthermore, only very lab-oriented motor tasks were used so far. Studies testing tasks that are more closely related to daily activities of older adults need to be conducted to better estimate the impact of physical activity and acute exercise on daily functioning and living.

GLOSSARY

Electroencephalography (EEG)

EEG measures the summed synchronous electrical activity of a large number of neurons via electrodes placed on the scalp. The EEG methodology has an excellent temporal resolution and allows for the online measurement of cognitive processing. EEG data are analyzed with two main approaches: continuous EEG data and event-related potentials.

Continuous EEG data that are not time-locked to certain events can be regarded as the linear sum of various oscillatory components. Decomposing the data by, for example, a Fourier transformation reveals typical oscillations in different frequency bands that can be associated with certain cognitive or brain states. *Alpha* oscillations (~8–13 Hz) are associated with a relaxed brain state without active processing of external or internal stimuli. The dominant EEG peak frequency within the individual alpha frequency band is the individual alpha peak frequency (iAPF). The term *event-related desynchronization (ERD)* describes decreases in brain oscillations as a consequence on an external event or stimulus. *Beta* oscillations (~14–30 Hz) are associated with motor behavior and changes in corticospinal output. Other typical oscillations can be observed in the theta (~4–8 Hz) or gamma (>30 Hz) frequency range. The phase consistency of oscillations between pairs of electrodes in each frequency band is called *coherence* and can be interpreted as functional interaction of corresponding brain areas. The power within a certain frequency band is a measure of the strength of the respective oscillations.

Event-related potentials (ERP) are short-lasting positive or negative voltage-changes that are synchronized with certain internal or external events such as stimuli, tasks, or responses. ERPs consist of typical components that are associated with perceptual, cognitive, or motor processes. The following components are of importance in the context of this chapter:

The *P1* and *N1* are the first positive and negative deflections in the ERP peaking around 50–100 ms and 100–150 ms after stimulus onset, respectively. They are associated with early sensory processing but can be modulated by attention. The second positive deflection (*P2*), reaching its peak about 150–200 ms after stimulus onset, reflects sensitivity to specific stimulus features and its occurrence probability. The second negative deflection in the ERP, the *N2*, reaches its maximum amplitude around 200–300 ms after stimulus onset and reflects endogenous cognitive components associated with novelty detection (N2a), executive control (N2b), and classification (N2c). A positive deflection peaking about 300–500 ms after stimulus onset is the *P3*. This component is related to the evaluation and classification of incoming information. *Latency* of the P3 is an index of the timing of respective cognitive processes; *amplitude* has been suggested to indicate processing intensity of the cognitive task at hand.

Other important components are the *readiness potential* (RP) and the *error-related negativity* (ERN or Ne). The RP, also called Bereitschaftspotential (BP), is a negative deflection starting about 1–2 s before the execution of a movement. The RP is further divided into the early and late RP (or early and late BP), reflecting different motor preparation processes. The ERN can be observed about 100 ms following an error was committed in various tasks even without the participant being aware of committing the error.

Structural and Functional Brain Imaging

Magnetic resonance imaging (MRI) is a brain-imaging technique that makes use of the magnetic properties of the atomic nucleus (nuclear magnetic resonance) and has an excellent spatial resolution. It is used for visualizing detailed pictures of the brain structure and to measure the volume of gray (*GM*) or white (*WM*) matter. While neuronal cell bodies, dendrites, and synapses occur as *GM* in the MR image, *WM* refers to the axons of neurons, being responsible for the transfer of information. *Myelin* is a fatty layer surrounding the axons of neurons that enables fast information processing between neurons, and is responsible for the white coloring. *WM integrity* represents a measure of the quality of the WM microstructure, for example, assessed by *fractional anisotropy* (value that refers to the coherence of the orientation of water diffusion).

With increasing age, the volume of the WM decreases and its microstructure and integrity changes leading to axon fiber splitting or swelling. These lesions are called *white matter hyperintensities (WMH)* and are associated with age-related slowing of cognitive, motor, and sensory processes as information transfer is less efficient.

Functional magnetic resonance tomography (fMRI) is a variant of MRI that reveals local brain function by measuring changes of the BOLD (blood oxygenation level dependent)-Signal, which is dependent on the oxygen saturation of the blood. The *default mode network (DMN)* is a network of interacting brain regions that is active when a person is not focused on the outside world, measurable with the fMRI technique.

Functional near-infrared spectroscopy (fNIRS) is another brain-imaging technique that makes use of changes in brain oxygenation during activation. Based on the different light absorption spectra of oxyhemoglobin (oxygenated form of hemoglobin) and deoxyhemoglobin (deoxygenated form of hemoglobin) for near-infrared light that is able to penetrate the skull and brain, activation in specific brain area can be visualized. *Transcranial magnetic stimulation (TMS),* also a noninvasive technique, applies a magnetic field near the sculp. Short electrical impulses are send to brain areas of interest (for example, the primary motor cortex), leading to changes in membrane function. TMS can be used to excite or to inhibit certain brain functions. *Repetitive transcranial magnetic stimulation (rTMS)* is one TMS technique, in which pulses are applied a repetitious manner.

Measuring Executive Functions

Executive functions are a key dimension of cognition and are comprised by components such as selective attention, response inhibition, and working memory. Different tests have been well established to examine individual executive functions:

The *flanker task* (Eriksen & Eriksen, 1974) requires (spatial) selective attention and executive control. In this task, irrelevant stimuli have to be inhibited in order to respond to a relevant target stimulus.

The *Stroop task* (Stroop, 1938) requires selective attention and inhibition control. The participant has to name the color of the ink (eg, blue, red, green) that the name of a color (*"blue," "red," "green"*) is printed in. If ink and color name do not match, reaction times increase because of this interference.

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