ACADEMIC LITERATURE REVIEW

An examination of the mechanisms underlying the effects of physical activity on brain and cognition

A review with implications for research

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Abstract Physical activity positively influences brain health and cognitive functioning in older adults. Several physiological and psychological mechanisms have been identified to underlie such a relationship. Cardiovascular fitness is accompanied with changes in mechanisms such as cerebral blood flow, neurotrophic factors, neurotransmitter systems and neural architecture that have themselves been associated with cognitive performance. Factors associated with exercise such as arousal, mood and self-perception of competence seem also to influence cognitive performance. Other explanation for the benefits of exercise in cognition, results from the fact that the performance of motor skills involve an important cognitive component (e.g., executive functions and information processing speed). Evidence of brain plasticity and behavior has been provided from studies where animals are exposed to enriched or complex environments. Exposure to such paradigms in which physical activity plays an important role has been found to influence various aspects of brain function and structure. Studies using neuroimaging techniques have established a link between the acquisition of different motor skills and the occurrence of neuroplasticity in human adults. This literature review indicates that the type of exercise and its specific perceptual and cognitive characteristics may influence cognitive performance. However, most of the research has been focused on self-paced movements or automatized skills and few intervention studies have examined the results of merging exercise and cognitive training in a single program. An important scientific challenge for the coming years is to design exercise programs capable of mobilizing several type of mechanisms underlying the effects of physical activity on brain and cognition.

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Introduction

Physical activity has the potential to intervene positively in several perceptual, cognitive, and physical abilities as well as health factors. The benefits of physical activity seem to have a singular expression among the older population because it is well known that aging is associated with noticeable functional changes that can impact activities of daily living. Research on the effects of physical activity in cardiovascular function, muscular function, body composition and health conditions (e.g., hypertension and diabetes) is abundant, and its positive influences are now well established [22]. At the same time, a growing body of work has been dedicated to the study of the relationship between physical activity and cognition. This emergent line of investigation has reported promising findings, particularly in the older population. There is now strong evidence, including from several longitudinal studies, that physical activity and exercise have a significant impact on several psychological parameters [22]. Research has generally shown that older adults who are more physically active exhibit better cognitive performance than do older adults who are less physically active [10,35,42,119]. Meta-analytic reviews show that the effect size of exercise in cognition frequently ranges from small to moderate [24,44]. These benefits of exercise

include, but are not limited to the following: greater efficiency in information processing [44,73], enhancement of attention capacity [59,108], better performance on tasks that demand visual–spatial processing [116], benefits for executive-control processes [24] and greater psychomotor speed [119].

Studies in animals and humans have investigated the physiological, neurobiological and psychological bases that account for the positive associations between physical activity and cognition. At the physiological and neurobiological levels of analysis, mechanisms that have been proposed to justify the exercise–cognition relationship include cortical structure (neurogenesis and synaptogenesis), cerebral metabolism, neurotransmitters, neurotrophic factors, oxygen availability, glucose regulation, and oxidative stress [27,43]. At the cognitive and behavioral levels of analysis, important roles has been attributed to executive control processes [24], to attentional resources [104] or to effects on mediating variables known to affect cognition, like arousal, self-efficacy, mood or depression [90,125].

In this article, we first focus on the factors that support a positive relationship between physical activity and cognition. Physiological and psychological mechanisms and behavioral interventions are reviewed from animal and human studies. Subsequently, we analyse the implications of the reviewed literature for the research about the effects of exercise on the brain and cognition. Special emphasis is given in the last section to the potential effects of different types of exercise. Throughout the article physical activity refers to body movement produced by the contraction of skeletal muscles that results in energy expenditure above resting levels [18]. Exercise refers to a subset of physical activity that is planned, structured, and repetitive and has as a final or an intermediate objective the improvement or maintenance of one or more components of physical fitness [18]. Physical fitness is a set of attributes that are either health-related (e.g., cardiovascular fitness) or skill-related (e.g., reaction time).

Aerobic fitness and cognition

Probably, the *cardiovascular fitness hypothesis* has been the most recognized hypothesis for explaining the positive association between physical activity and cognition. It suggests that the gains in cardiovascular (aerobic) fitness achieved through regular participation in physical activity mediate cognitive performance benefits [21,45,127]. The enhancement of aerobic fitness is thought to be accompanied with changes in the underlying mechanisms such as cerebral blood flow [38,122], brain-derived neurotrophic factor (BDNF) [132,139] and cerebral structure [25,26] that have themselves been associated with cognitive performance.

The magnitude of the training effect on older adults' cardiovascular condition differs among studies, and it has been suggested that the amount of physical improvement engendered is related to the degree of change in mental abilities. It has been pointed out [9,125] that studies showing positive effects of exercise in cognition have tended to demonstrate large changes in individual pre- to post-intervention scores for aerobic fitness. Findings from several cross-sectional and other observational studies also showed that aerobically fit adults performed better on cognitive tests than did less fit adults [20,39,60,127].

Nevertheless, some studies have failed to obtain evidence for the relationship between aerobic training and cognitive function. Panton et al. [101] assigned older adults (70–79 years) to aerobic training, strength training and control conditions. Neither form of exercise was related to subjects' reaction times or movement speed. Furthermore, an important meta-analysis [24] found no relationship between the magnitude of improvements in VO_{2max} and the effect of exercise interventions on neurocognitive function. Correspondingly, in the study by Etnier et al. [45], a meta-regression analysis did not support the *cardiovascular fitness hypothesis*.

Cerebral circulation hypothesis

Because oxygen and glucose are not stored in the brain, the vascular system must quickly respond to environmental demands on the central nervous system (CNS) by resupplying activated brain areas with these substances [34]. Despite representing only 2 % of the total body weight, the brain uses 20–25 % of the total body oxygen and 25 % of the total body glucose to meet the brain's energy needs and for metabolism and turnover of neurotransmitters [47]. Given this fact, the *cerebral circulation hypothesis* suggest that chronic exercise results in an enhancement of oxygen and glucose transportation to the brain, which results in better cognitive performance because of the increased resources available to the cerebral environment [21,45]. This is particularly important for older adults because there is strong evidence that age is inversely related to efficient delivery of blood to the CNS [118,123]. Among the various mechanisms that have been pointed to as being responsible for the age-related decrement in blood flow are an increase in whole-blood viscosity and plasma viscosity, loss of elasticity and progressive fibrosis of cerebral vasculature [1,93].

Marks et al. [83] demonstrated that cerebral blood flow and cognitive function is maintained in aerobically active older adults; McFarland [88] showed that cognitive decline observed in older adults was similar to impairments seen in younger individuals under conditions of hypoxia. It was reported [106] that older adults who are physically active

or are still engaged in physically demanding work sustained more constant cerebral blood flow levels than those that who were classified as physically inactive; furthermore, active individuals and workers also scored better on cognitive testing compared to the inactive ones. Others have concluded that individuals who retired and led a sedentary lifestyle were at an increased risk of cerebrovascular disease with associated cognitive impairment [106]. Finally, some studies showed small but significant improvements in cognitive performance (e.g., memory and reaction time) following supplemental administration of oxygen [95,112] or glucose [81,82].

Neurotrophic stimulation hypothesis

There are various studies of animal models that have shown that PA induces BDNF and other growth factors consistent with improved neuronal activity, synaptic structure, and neuronal plasticity [34,135]. Findings in human samples showed that a single bout of exercise can increase plasma BDNF concentration [135]; a 5-week endurance training also led to an increase in both basal as well as the end-exercise BDNF [140]. Specifically, BDNF supports the health and functioning of glutaminergic neurons, stimulates neurogenesis and improves learning and mental performance [27].

Neurotrophins are expressed throughout the brain, and some of the highest levels have been found in the hippocampus, an area of the brain important in learning and memory [27,96]. In addition to increasing the expression of neurotrophins in the brain, exercise increases levels of other types of trophic factors derived from endocrine tissues. Investigation in animal models demonstrated that insulin-like growth factor-I (IGF-I) levels increase in both the periphery and in the brain after exercise [17]. IGF-I might be an upstream mediator of BDNF gene regulation, neurogenesis and the ability of exercise to protect the brain from injury [17,27].

It seems that exercise mobilizes gene expression profiles that would be predicted to benefit brain plasticity processes [27]. The effects of genes encoding neurotrophins and other proteins predict that exercise could regulate downstream anatomical changes that support brain plasticity [27]. The idea that neurogenesis also occur in the adult brain [2] was first received with scepticism by the scientific community. At present, it is well established that the mammalian adult brain can produce new neurons [53,128,129]. At least one study [41] demonstrated that the human hippocampus also retains its ability to generate neurons throughout life. The dentate gyrus, a hippocampal sub-region associated with memory and learning, is the primary region where the neurogenesis phenomenon takes place [63,75]. Recent studies have suggested that neurogenesis can also be found in neocortical association areas such as the prefrontal and posterior parietal cortices of nonhuman primates [54,55].

Physical activity is one of the factors that positively affect adult neurogenesis [75,129]. Colcombe et al. [26] showed that significant increases in brain volume, in both grey and white matter regions, were found as a function of fitness training for subjects who participated in an aerobic fitness training but not for subjects who participated in a stretching and toning (nonaerobic) control group. Recently, it was reported that aerobic exercise training is effective at reversing hippocampal volume loss in late adulthood, which is accompanied by improved memory function [40].

Neurotransmitter systems

The degeneration of neurotransmitter systems, primarily the dopaminergic system, may contribute to age-related gross and fine motor declines as well as to higher cognitive deficits [115]. Age-related working memory impairment was related to reduced prefrontal cortex dopaminergic transmission caused by decreased dopamine synthesis in the prefrontal termination region [94].

Directly testing of neurotransmitters changes in humans is not possible. As a result, animal studies have been carried out to support the claim that exercise induces changes in brain concentrations. Researchers have focused their efforts on the study of noradrenaline and dopamine. There is some evidence of increased dopamine concentrations during and following acute exercise and as a result of chronic exercise. Research on acute exercise has demonstrated increases particularly in the brainstem and hypothalamus [92]. There seems to be a "threshold speed" above which neurotransmitter release begins [58,92]. Chronic exercise shows region-specific effects with increases in the hypothalamus and midbrain concentrations but decreases in the prefrontal cortex, hippocampus and striatum [91].

In general, studies have shown either a decrease or no significant effect of chronic exercise on noradrenaline concentrations in the whole brain, although there are some regional variations (especially in the hypothalamus) [91,92]. There is, however, unequivocal evidence for increased catecholamine turnover in the brain during exercise [89]. Increased concentrations of catecholamine metabolites (the by-products of catecholamine synthesis and usage) have been found in the brain during and following acute exercise. As such, it is reasonable to state that exercise induces increased catecholaminergic activity in the brain during activity [89].

Taken together, animal studies have provided evidence that the central dopaminergic, noradrenergic, and serotonergic activity, release, and metabolism are influenced by

exercise [90]. The results seem to be more consistent for neurotransmitter response during exercise than for long-term adaptations. Nevertheless, the studies in this research area are scarce and have been marked by technological limitations (e.g., measurements in the synapses are not yet possible). An important question to be answered is how changes in the synthesis and metabolism of neurotransmitters as a result of exercise can influence cognition. One of the possible answers is that it might follow an indirect pathway: neurotransmitter changes may underlie most of the impact of exercise in reducing depressive symptoms both in healthy and clinical populations [33]. Hence, associations between depression and cognitive decline have been observed in several studies of older adults [50,109].

Cognitive energetics, arousal and self-efficacy

It has been hypothesized that declines in mental and physical health, regardless of age, result from insufficient physical and mental challenge and that controlled and repeated challenge, either physical or mental, builds up the resources and the "mental toughening" needed to meet environment demands and cope with stress [29,30]. According to Dienstbier [29], data from both non-human and human studies shows that better performances across a variety of tasks appear to be associated with increased catecholamine levels (adrenaline, noradrenaline, and dopamine) and quicker return to baseline rates following stressful manipulations.

Extending this perspective, Tomporowski [125] considers that older adults' responses to challenging tasks are predicted to lead to both short-term and long-term physiological benefits as the increase in the levels of arousal and energy set the stage for individuals to meet and overcome task demands. An individual's newly acquired history of success, in turn, motivates him or her to continue to engage in challenging activities. The continued performance of challenging activities by older adults would be expected to lead to practice and its associated maintenance of skilled behavior [125]. Within this framework, the level of difficulty of the activities that integrate the intervention programs for older adults is an important issue [51]. Training tasks (both physical and cognitive) that are much too difficult or much too easy will lead to lower levels of arousal and motivation and thus substantially reduced learning. The learning rate would be at a maximum when the task is challenging yet still doable [56] as it is evidenced in the well-known Yerkes–Dodson law [138], which predicts that learning is an inverted U-shaped function of arousal level.

Frequently, older adults develop low perceptions of their control and competence, with negative consequences on their motivation [86,125]. Thus, the benefits of physical and mental training might reside more in changed beliefs

than in cognitive abilities per se [19]. One important aspect of the perceived control over one's life is the construct of self-efficacy. Self-efficacy is concerned with the individual's beliefs in his or her capabilities to execute necessary courses of action to satisfy situational demands [6]. According to McAuley and Elavsky [86], mastery experiences (performance accomplishments) are the most potent source of self-efficacy beliefs, often providing objective evidence relative to what constitutes a success or a failure. Self-beliefs of efficacy can enhance or impair performance through their effects on the cognitive, affective, or motivational intervening processes; more efficacious individuals approach more challenging and varied tasks [7]. It has been shown that self-efficacy is a significant predictor of exercise adherence [87,98] and that it can be also a consequence of exercise participation [86]. The role of self-efficacy for exercise participation (adherence, maintenance and effort expended) could indirectly influence cognitive function, given the known effects of physical activity on cognition. Also, it has been hypothesized that efficacy may play a mediating role in the relationship between physical activity and fitness and cognitive function inasmuch as fitter, more active, and more efficacious older adults are likely to demonstrate less anxiety in challenging cognitive situations, thereby performing better than their less active, less fit, and less efficacious counterparts [86]. Further investigation is needed to better understand the role that exercise self-efficacy plays in the exercise–cognitive function relationship.

Cognitive complexity and cognitive training

Some types of exercise require demanding information processing, and it is reasonable to consider that their practice over time is also a form of cognitive training. Accordingly, it has been hypothesized that the cognitive complexity level of work and leisure-time activities could affect older people's intellectual functioning [113]. It is widely believed that keeping mentally active will prevent age-related mental decline [111]; from a neurobiological perspective, this notion states that the use of neurons and neuronal networks prolongs the efficiency of CNS activity during life [117,121]. Some longitudinal studies have provided support to the "use it or lose it" hypothesis. Zunzunegui et al. [141] reported that few social ties, poor integration, and social disengagement are risk factors for cognitive decline among community-dwelling older persons. Others have found that higher frequencies of participating in activities like reading, playing chess, and completing crosswords were related to slower declines in perceptual speed [52]. Even in old age, working out on a regiment of substantively complex tasks appears to build the capacity to deal with the intellectual challenges that complex environments provide [113].

There is also a growing body of evidence of positive effects of programmed cognitive training at a behavioral and functional level. In a frequently cited work, Ball et al. [4] enrolled 2,800 subjects in training programs and reported benefits on the specific abilities trained (speed of processing, memory and reasoning). Results from other study [126] provide evidence that even brief periods of increased cognitive training (10–12 weeks) can improve older adults' problem solving and flexible thinking. When the additional effort required by more cognitive effort tasks is rewarded (e.g., by the beneficial effect associated with learning a new skill) it is possible that people become more motivated to further develop these capacities.

In a controlled clinical trial, older adults randomized to cognitive speed-of-processing training experienced improvements in a visual attention test (useful field of view test, UFOV®) [3] which were maintained over a 5-year period relative to controls [134]. Results by Edwards et al. [36] indicate that the cognitive speed-of-processing training not only improves processing speed, as indicated by performance on the UFOV®, but also transfers to certain everyday functions, as indicated by improved performance on timed instrumental activities of daily living (e.g., quickly finding a telephone number). Furthermore, it was shown that the enhancement of processing speed is protective against declines in health-related quality of life across 5 years [136,137] and against mobility declines among older drivers [37].

Environmental enrichment

Environmental enrichment is an experimental model in which animals are housed in conditions that potentiate social interactions and sensory and motor stimulation [107,114]. The "use it or lose it" hypothesis is also supported by this research paradigm, which provides evidence that stimulating and challenging habitats are beneficial to the cognitive functioning of laboratory animals [14,66,132]. Thus, as a result of living in an enriched environment, the brains of animals undergo molecular and morphological changes leading to improvements in learning and memory. Mediating mechanisms engendered by enriched environments and training in behavioral tasks includes increased dendritic branching and synaptogenesis, changes in supportive glial cells, addition to the brain's capillary network, the development of new neurons, and a cascade of molecular and neurochemical changes [70].

Some authors support the hypothesis that environmental enrichment and exercise affects brain neuronal circuitry in similar ways, including the regulation of growth factors, neurogenesis and structural changes, which regulate behavioral plasticity [11,27,130]. Others consider that environmental enrichment and exercise affect different phases of the neurogenic process in distinct ways: the former seems to increase the likelihood of the survival of new cells, whereas the latter increases the level of proliferation of progenitor cells [80]. Nevertheless, clear conclusions on this issue are difficult to make because in some studies more opportunities for physical activity are also included as part of the environmental enrichment [64].

The type of exercise is another important issue that has been debated in environmental enrichment paradigms. Some research found that exercise characterized by unskilled motor movements increased capillary density without a significant change in synapse number, whereas motor skill learning induced synaptogenesis in higher-order brain regions involved in motor learning with no change in capillary density [14,66,67]. Klintsova et al. [68] reported that while motor skill training (obstacle course) enhanced performance on a number of subsequent behavioral tasks such as parallel bars, rope climbing, and rotarod, motor activity alone such as walking in a closed alley had little effect on performance. Other studies, however, have found a positive association between running and neurogenesis in young and old animals, which translated into improvements in behavioral tasks [129,131]. There seems to exist also a potential relationship between social interaction and exercise on brain function and cognition. Thus, a recent study showed that the effects of exercise on hippocampal neurogenesis were substantially delayed and reduced for a group of socially isolated rodents compared with animals that were housed in a group setting [120]. Future studies should examine this issue in humans.

Environmental enrichment research has been mostly done on rodents, but similar effects have been documented in primates [69]. Direct research in humans has been limited because it requires histological study of the brain. However, a study that involved the autopsy of human brains [62] was consistent with the environmental enrichment research results in animals and suggested that dendritic systems in humans function as a sensitive indicator of an individual's (a)vocational activities (education had a consistent and substantial effect such that dendritic measures increased as educational levels increased). Taken together, findings related in this type of research provide a biological explanation for the positive effects produced by physical and mental activity on different cognitive functions in older adults and also for the reduction in the risk of developing neurodegenerative disorders [23,114].

Transfer of learning

Transfer of learning is another factor that should be considered in the analysis of the association between the regular practice of exercise and the individual's functional capacity.

In the context of motor learning, Magill [79] defines the transfer of learning as the influence of previous experiences in a new context or on learning a new skill. In the tradition of the "identical elements theory" of Thorndike and Woodworth [124], Magill considers two hypotheses to explain why transfer of learning occurs. The *skills components hypothesis* assumes that the transfer of learning occurs because the components of the skills (e.g., its kinematics characteristics) and/or the context in which the skills are performed are similar. The *similarity of the cognitive processes hypothesis* posits that transfer occurs primarily because of similarities between the amount and types of cognitive processes (e.g., engaging in problem-solving activity, rapid decision-making, attention control, or the dual-task functioning) required by the two skills or two performance situations.

In the domain of sports psychology, some studies have demonstrated that skill changes associated with sports practice are transferable to specific cognitive abilities The results of a recent meta-analysis [133] that examined the relationship between expertise in sports and measures of cognition gave some support to the *similarity of the cognitive processes hypothesis*. It was found that interceptive sport types (e.g., squash, tennis) had largest effects on measures of processing speed and attention (e.g., divided attention) than closed, self-paced sports (e.g., golf and swimming). A recent study showed a beneficial effect of playing tennis on the collision avoidance skill of 70- to 80-year-old tennis players [78]. Also, it was shown that older adults with expertise in orienteering activities seem to develop attentional skills that withstand the age-related changes of some aspects of visual attention [103].

In the driving-related literature, two recent experimental studies [84,85] used an exercise program for older drivers supported in the hypothesis that positive transfer of learning occurs primarily because of similarities between the amount and types of cognitive processes required by the performance situations. For instance, it was hypothesized that incorporating tasks in the exercise program that intend to enhance speed of behavior could have a higher impact on the individual's capacity to respond quickly to environmental stimuli during actual driving. The authors reported that improvements resulting from the exercise intervention took place on several measures of visual attention, behavioral speed, and multitask processing; this was a very positive outcome given that motor learning frequently show a great specificity with little generalization to related tasks or new environments [56].

Research has also shown that transfer of learning can occur on dual-task conditions using a variable priority training technique [71,72]. In this procedure, participants are required to vary their response priorities between the two tasks, whereas in the more typical fixed priority condition, attention was given equally to the tasks. The greater improvement obtained under the variable priority condition suggests that learning to modulate attention may be crucial in the acquisition of task coordination skills.

Starting from these promising findings, it is necessary to continue to investigate which cognitive abilities subserved by the CNS are malleable in response to the participation in exercise and to what extent they are transferable for activities of daily living. The mode of exercise is an important issue in this field, as it is possible that different exercise types impose characteristically different sets of mental demands upon the practitioner, targeting different perceptive and cognitive abilities and giving distinctive contributions for the functional capacity of older adults.

Implications for research on the effects of exercise on the brain and cognition

In the next paragraphs, the implications of the reviewed literature for the orientation of future research on the area are discussed.

Much research has been focused on the effects of aerobic fitness on measures of cognitive function. Thus, the enhancement of aerobic fitness (*the cardiovascular fitness hypothesis*) is very often considered as responsible for the enhancement of cognitive functioning that accompanies the practice of PA due to its influence in underlying mechanisms such as cerebral blood flow, BDNF and cerebral structure [26,127]. This paradigm of investigation is likely to change in the next years, especially because important meta-analytic studies have failed to obtain strong evidence for the relation between aerobic fitness and cognitive function [24,45], indicating that the underlying mediators of this relationship have yet to be fully identified [45].

Studies that have compared the individual and combined effects of physical and mental exercise interventions reported cognitive benefits to be larger with the combined cognitive and physical training paradigms [46,99]. Efforts should be taken to extend this line of investigation and to examine if the effects of exercise that merge physical and cognitive stimulation might transfer to other tasks of daily living in older adults. As we have seen before, some studies have already provided a positive answer to this question, namely in the context of driving [84,85]. It is desirable that more research be conducted to examine the general effects of exercise interventions planned to stress not only physiological systems, but also perceptive and cognitive mechanisms. For example, it has been proposed that exercise that results in gains in cardiorespiratory fitness leads to benefits in tasks with a substantial frontal-lobe-dependent executive control component [24,74]. These are the cerebral areas that exhibit the largest age-related declines and are also the ones

that show the largest exercise or fitness-related improvements. Tasks that are included in the executive functioning umbrella include those involving the use of information retained in working memory, simultaneous execution of multiple tasks, task switching, and inhibition of an ongoing or prepotent response. Considering these characteristics, the greatest gains in executive functioning might be achieved if the exercise training stimulates aerobic capacity (and by this means promoting physiological adaptations such as higher blood perfusion and neurotransmitters turnover) and also incorporate behavioral tasks that directly stimulate executive control components (e.g., planning, inhibition and task switching).

Research has been trying to determine whether some particular causes could have broad effects on many aspects of cognitive functioning. This is an appealing idea, as the identification of such causes might support the design of interventions that translate into a broader range of positive consequences in the individual's functional capacity. One hypothesis that has been proposed is that all components of information processing decline at approximately the same rate, independently of task complexity and task types [12] leading to the conceptualization of a model that held that age differences in the performance of cognitive tasks can be explained by age differences in the speed of processing [110]. In this view, it is reasonable to consider that the improvement of information processing speed has the potential to impact the general cognitive ability in older adults, leading to positive effects on their functional status, independence and quality of life [36,100]. This was already shown in the cognitive training literature [5], and recent studies have also reported positive effects of exercise programs on the information processing speed of older adults [84,85]. Future research using longitudinal designs is needed to examine which exercise characteristics could improve information processing speed in older adults and if this hypothetical improvement has a large impact on the individual's functional abilities.

An interesting event associated with aging is increased cautiousness or a shift in the speed–accuracy trade-off [57]. This change probably contributes to the well-established age-related tendency for slowness of perceptual, motor, and cognitive processes [13,28,97]. In chronometric studies, models of the speed–accuracy trade-off indicate that there will be large costs in reaction time for small gains in accuracy at high levels of performance. Thus, relatively small differences between younger and older adults in their response criteria could produce substantial differences in reaction time [57]. Perhaps, if one could change this extra-cautiousness behavior of older people (typically, they emphasize accuracy rather than speed), their performance differences compared with younger adults could be reduced. Previous work has shown that this is possible: after speed-

behavior training in a memory search task, equivalent accuracies were achieved for young and old adults and the response time differences between the groups present at baseline were substantially reduced [8]. In this experiment, subjects were trained with a deadline procedure in which they were required to constantly increase the speed with which they performed the task. Thus, these data suggest a more substantial improvement in performance related to speed of responding for the old than for the younger adults when exposed to appropriate training. The same kind of strategy should be tested using exercise programs, which regularly include motor activities dependent on reaction and execution times. Marmeleira et al. [85] provided evidence that exercise could be a good strategy to change the conservative relationship between speed and accuracy that is typical in older adults. In their experimental study, the need to quickly choose between different motor responses according to the stimuli presented was recurrently trained during the exercise sessions. At the end of the intervention, significant differences between the group of older adults that participate in the exercise program and the control group were found in a choice reaction time task, while accuracy stayed very close to the baseline values for both groups.

The type of exercise is a factor that should be examined more closely given its potential to induce specific effects in the brain and in perceptual and cognitive abilities. The investigation on the relationship between physical activity and cognition in older adults has mainly examined the effects of self-paced movements or automatized skills (e.g., walking), and frequently the type of activity is considered mainly on its effects on aerobic fitness. However, based on the literature reviewed, it seems reasonable to hypothesize that exercises which exert large cognitive demands (e.g., involving learning processes, executive control, information processing speed) could have a higher impact on cognition. For instance, could an activity like dance exert a differential influence in neuroplasticity in comparison with walking? Can the learning of new motor skills or the retraining and improvement of older ones induce positive changes in the brain and in cognition? This kind of questions are pertinent if one considers the idea that nothing speeds brain atrophy more than being immobilized in the same environment and that the monotony undermines our dopamine and attentional systems crucial to maintaining brain plasticity [31]. As observed previously in this article, it is well documented that an enriched environment and cognitive training can lead to improved learning and memory as well as structural and morphological changes in the brain [105]. Experimental animal studies have shown that exercise associated with planning and execution of complex movements is related to changes in brain structure [61]. Some studies with animals demonstrated that exercise characterized by unskilled motor movements can increase

capillary density without a significant change in synapse number, whereas motor skill learning induce synaptogenesis in higher-order brain regions involved in motor learning with no change in capillary density [14,15,67].

In recent years, with the advent of sophisticated neuroimaging techniques, several studies were able to establish a link between the acquisition of different skills and the occurrence of neuroplasticity in human adults. For example, grey matter volume differences were reported for motor, auditory, and visual–spatial brain regions when comparing professional musicians (keyboard players) with a matched group of amateur musicians and non-musicians [49]. In an elegant study, it was shown that the posterior hippocampi of people with extensive navigation experience (taxi drivers) were significantly larger relative to those of control subjects [80]. In another frequently cited study, it was demonstrated that young adults who have learned to juggle, show a transient and selective structural change in brain areas that are associated with the processing and storage of complex visual motion [32]. The findings from this last study were reproduced in older adults [16]. Further research in humans is needed to understand the influence of neuromotor exercise training in brain health and cognition, which incorporates motor skills such as balance, coordination, agility, and proprioceptive training [48]. Moreover, some forms of neuromotor exercise also contain an important aerobic component, which is also a factor considered to influence brain health and cognitive functioning.

Research has already started to reveal that different types of exercise have specific repercussions on the brain and cognition. A comparison between a group of internationally competitive judo players and a group of healthy controls showed a significantly higher grey matter tissue density in the brain areas of judo players [61]. Another study [102] reported that blood volume in the dentate gyrus (the only hippocampal sub-region that supports adult neurogenesis) of adults, assessed by magnetic resonance imaging as an in vivo marker of neurogenesis, increased significantly over a 3-month period of aerobic exercise. Moreover, this increase in dentate gyrus blood volume was significantly correlated with gains in maximal aerobic capacity, and an improvement in short-term memory. These results were corroborated in a recent study that concluded that aerobic exercise training (walking program) is effective at reversing hippocampal volume loss in late adulthood, which is accompanied by improved memory function [40]. Important findings have been also reported in the research about alternative forms of exercise that intend to simultaneously target mind and body (e.g., tai-chi and yoga). Kerr et al. [65] suggested that tai-chi may elicit long-term plasticity in primary sensory cortical maps, while others have demonstrated improvements in both physical and psychological domains [76,77]. Mind–body exercise also has a meditative aspect, which has been proven very effective in lowering stress and is likely to preserve memory and the hippocampal neurons [31].

Given all the evidence, future work should explore a line of investigation where the focus of attention is on the potential for different exercise programs to mobilize/stimulate a broad range of abilities (i.e., physical, perceptual and cognitive) and, therefore, to produce higher benefits on functional capacity, chronic disease risk, and quality of life of older adults.

Summary

The brain is remarkably plastic at functional and anatomical levels in response to experience, and evidence has accumulated that physical activity preserves brain health and cognition. Animal and human studies support that several physiological and psychological mechanisms underlie the relationship between physical activity and cognitive functioning.

Cardiovascular fitness has been considered as a major factor responsible for the positive influence of physical activity in brain and cognition. Important mechanisms such as cerebral oxygen and glucose availability, BDNF, neurotransmitters and cerebral structure have been hypothesized to accompany changes in cardiovascular fitness. Nevertheless, some studies have failed to obtain strong evidence for the relation between aerobic fitness and cognitive function.

Some types of cognitive training for older adults have shown benefits that were sustained for relatively long periods of time. Also, the regular participation in complex occupational activities seems to benefit older people's intellectual functioning. Considering that cognition plays an important function in performing motor skills, it is reasonable to consider that cognitive training also results from the regular practice of exercise. This seems especially true for those types of exercise that rely on high cognitive effort. Important evidence of the influence of physical activity in brain plasticity and behavior has been provided also from studies where animals are exposed to enriched or complex environments. Exposure to such environments in which physical activity plays an important role has been found to influence various aspects of brain function, neurochemistry, and neural architecture.

The available scientific evidence supports the hypothesis that maintaining an intellectually stimulating and physically active lifestyle promotes successful cognitive aging. Until now, the great majority of studies have focus their analysis on single factors thought to influence cognitive function in older adults. The few human intervention studies that have examined the combined influence of multiple lifestyle factors (e.g., merging exercise and cognitive training) provided evidences of the potential of such an approach. This view is

related with another important issue: the role of different types of exercise in cognitive functioning and overall functional capacity of older adults. Using sophisticated neuro-imaging techniques, several studies were able to establish a link between the acquisition of different motor skills or the practice of specific types of exercise and the occurrence of neuroplasticity in human adults.

Mode of exercise and its specific perceptual and cognitive characteristics/demands may influence the learning and mental performance obtained. However, the investigation on the relationship between physical activity and cognition in older adults has mainly examined the effects of self-paced movements or automatized skills. The body of work examining the effects of specific types of exercise/sports on the functional capability of older adults should be expanded in the future. Hence, an important scientific challenge is to design exercise programs capable of mobilizing several type of mechanisms underlying the effects of physical activity on brain and cognition.

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