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Year: 2021

Version: Published version

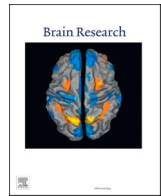
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Please cite the original version:

Hernández, D., Heinilä, E., Muotka, J., Ruotsalainen, I., Lapinkero, H.-M., Syväoja, H., Tammelin, T. H., & Parviainen, T. (2021). Physical activity and aerobic fitness show different associations with brain processes underlying anticipatory selective visuospatial attention in adolescents. *Brain Research*, 1761, Article 147392. <https://doi.org/10.1016/j.brainres.2021.147392>



Physical activity and aerobic fitness show different associations with brain processes underlying anticipatory selective visuospatial attention in adolescents

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ARTICLE INFO

Keywords:

Physical activity
Aerobic fitness
Adolescence
Anticipatory alpha oscillations
Selective attention
Magnetoencephalography

ABSTRACT

Current knowledge about the underlying brain processes of exercise-related benefits on executive functions and the specific contributions of physical activity and aerobic fitness during adolescence is inconclusive. We explored whether and how physical activity and aerobic fitness are associated with the oscillatory dynamics underlying anticipatory spatial attention. We studied whether the link between physical exercise level and cognitive control in adolescents is mediated by task-related oscillatory activity. Magnetoencephalographic alpha oscillations during a modified Posner's cueing paradigm were measured in 59 adolescents (37 females and 22 males, 12–17 years). Accelerometer-measured physical activity and aerobic fitness (20-m shuttle run test) were used to divide the sample into higher- and lower-performing groups. The interhemispheric alpha asymmetry during selective attention was larger in the high than in the low physical activity group, but there was no difference between the high and low aerobic fitness groups. Exploratory mediation analysis suggested that anticipatory interhemispheric asymmetry mediates the association between physical activity status and drift rate in the selective attention task. Higher physical activity was related to increased cue-induced asymmetry, which in turn was associated with less efficient processing of information. Behaviorally, more physically active males showed stronger dependence on the cue, while more fit females showed more efficient processing of information. Our findings suggest that physical activity may be associated with a neural marker of anticipatory attention in adolescents. These findings might help to explain the varying results regarding the association of physical activity and aerobic fitness with attention and inhibition in adolescents.

1. Introduction

Regular physical activity (PA) and aerobic fitness (AF) have been shown to benefit cognitive functions, specifically executive control (Hillman et al., 2008; Smith et al., 2010). These cognitive benefits have been suggested to arise from the influence of PA and/or AF on brain structure and function. Despite an increasing number of studies clarifying the brain correlates of physical activity and fitness, there are still many gaps in the understanding of the specific association between performance measures of the body and the neurocognitive basis of executive functions. At the molecular, cellular, and circuit levels, regular

PA has been suggested to be an important metabolic activator, significantly increasing the levels of neurotrophic factors such as brain-derived neurotrophic factor (BDNF) (Gomez-Pinilla et al., 2008) or vascular-endothelial growth factor (Carro et al., 2001). These changes are further associated with increased neurogenesis (Brown et al., 2003), enhanced synaptic plasticity (O'Callaghan et al., 2007; van Praag et al., 1999), enhanced spine density (Redila and Christie, 2006; Stranahan et al., 2007), and angiogenesis (Carro et al., 2001; van Praag et al., 2005). However, these effects have been almost exclusively shown in mice, and without a direct link to cognitive functions. During recent years, the link between physical performance and the brain has been

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<https://doi.org/10.1016/j.brainres.2021.147392>

Received 3 August 2020; Received in revised form 18 February 2021; Accepted 19 February 2021

Available online 25 February 2021

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increasingly approached also in humans, yet the neural mechanisms underlying the cognitive consequences of higher regular PA and higher AF are still unclear. In the current study, we aim to investigate whether PA or AF associates with modifications in brain functions underlying cognition in adolescents.

Among different cognitive functions, PA and AF have been most often associated with improvements in measures of attention and/or inhibition (de Greeff et al., 2018; Muñoz and Ballesteros, 2018). The evidence is clearer for children (Sylväoja et al., 2014; Crova et al., 2014; van der Niet et al., 2014; Singh et al., 2019) and older adults (Colcombe and Kramer, 2003; Muñoz and Ballesteros, 2018) than for adolescents and young adult populations. This might be related to the developmental changes taking place at this age range especially in cognitive control. Some studies do exist in adolescents, but the results are mixed. Performance in attention tasks is shown to be linked mainly with higher PA (Vanhelst et al., 2016; Booth et al., 2013) and for AF there are both positive (Hogan et al., 2015) and negative findings (Stroth et al., 2009). Tasks requiring inhibition, on the other hand, seem to be associated with higher levels of AF (Huang et al., 2015; Stroth et al., 2009; Westfall et al., 2018; Shigeta et al., 2021), with some exceptions (Tee et al., 2018), but not with PA (Pindus et al., 2015). Thus, although there seems to be general agreement regarding the positive association between physical performance measures and attention/inhibition skills, the more fine-grained interdependencies are not clear. Most of the research so far focus on the outcome measures, (i.e. reaction time or accuracy) and studies attention and inhibition separately. An alternative way would be to focus on the ongoing cognitive process using a task that requires the subject to simultaneously focus on the relevant information while inhibiting the irrelevant information. A kind of task requiring the engagement of both, attention and inhibition could be the one focusing on the anticipatory phases of attention allocation.

Anticipation is a key function of the human brain, which allows an individual to make use of external information to allocate attentional resources in a manner that is relevant for the behavioral goals. It thus reflects a preparatory stage of top-down control of behavior to ease upcoming information processing (Brunia, 1999). Anticipatory selection control in the brain can be shown to operate in two concurrent ways: (1) by selectively pre-activating the brain areas in charge of processing the relevant stimuli and (2) by inhibiting those brain areas intended to process what was determined to be irrelevant. When using a paradigm in which a visual cue implies the forthcoming target to emerge in either hemifield, this two-fold anticipatory process seems to be indexed by interhemispheric modulation (i.e., uneven involvement of the brain hemispheres) of alpha rhythm in the brain (Jensen and Mazaheri, 2010).

Alpha rhythm (at around 10 Hz), a widely studied brain oscillation, has been suggested to be especially important for directing neuronal resources during tasks that require attention to or inhibition of incoming information (Jensen and Mazaheri, 2010; Jensen et al., 2002; Bonnefond and Jensen, 2013; Klimesch, 1999, 2012; Klimesch et al., 2007). Increased alpha activity is considered to reflect system-level inhibition in the brain, while suppression of alpha activity is considered to indicate a release from inhibition or allocation of attention to relevant aspects of a task (Klimesch, 2012). Anticipatory attention is usually studied by using a covert attention task such as the Posner's cueing paradigm. In this task, a cue directs the participant's attention towards the left or right visual hemifield prior to the presentation of a target. The power of alpha activity, measured from the visual areas of the brain immediately after the cue, allows the study of the neural resources allocated to the attended and unattended visual hemifields. A cue-induced decrease in alpha power in the contralateral hemifield (in reference to the cued hemifield) indicates the preparatory engagement of neuronal resources to code information in the attended location. On the other hand, a cue-induced increase of alpha power in the ipsilateral hemisphere implies preparatory inhibition of brain areas involved in coding information of the irrelevant spatial location. This interhemispheric modulation of alpha rhythm during a visuospatial attention task in response to a cue

has been indexed by the modulation index (MI) (Vollebregt et al., 2015, 2016). Magnetoencephalography (MEG) seems to be the most suitable tool to reliably record activity in the brain hemispheres because it offers excellent temporal resolution and high spatial resolution. By focusing on oscillatory alpha activity, MEG can be used to index the allocation of attention and inhibition of irrelevant information during ongoing task performance.

The visuospatial covert attention paradigm has been successfully used to reveal the neural mechanisms underlying anticipatory visual attention in general (Jensen and Mazaheri, 2010; Vollebregt et al., 2015) and changed attentional capacity in cases of attention deficit disorder (Vollebregt et al., 2016). MEG, and especially alpha oscillations, has also shown sensitivity to individual variation with relevance to cognitive performance (Haegens et al., 2014) and thus may show sensitivity also to the variance due to physical performance measures. Similarly, brain oscillations (Chaire et al., 2020; Luque-Casado et al., 2020; Wang et al., 2015), especially alpha rhythm (Chaire et al., 2020), have proven to reflect the influence of PA and AF in the brain. Relevant to the present study, Wang et al. (2015) assessed the relationship between AF and neural oscillations (theta and beta rhythms) during visuospatial attention using the Posner's cueing paradigm. Although they did not explore the effects of PA on anticipatory attention, the authors showed an association between physical performance measures (i.e., AF) and enhanced attentional control in young adults. Thus, the visuospatial covert attention paradigm seems to be a sensitive enough measure to demonstrate changes in the brain's attentional resources related to variance in the level of PA or AF in adolescents.

Adolescence is a particularly interesting period from the perspective of physical activity and aerobic fitness, as the whole body is undergoing significant maturational changes. Importantly, there are multiple factors, both biological and psychological, that are likely to contribute to the specific influence of higher AF (Huang et al., 2015; Hogan et al., 2013, 2015; Marchetti et al., 2015; Stroth et al., 2009; Westfall et al., 2018) or higher level of PA (Booth et al., 2013; Tee et al., 2018; Vanhelst et al., 2016) on cognition during adolescence. During this stage, it is important to be also aware of the possible sex-related differences. Indeed, Colcombe and Kramer's (2003) review of the enhancing effects of AF in older adults found that studies in which more than 50% of participants were women reported greater cognitive benefits of AF than studies enrolling mostly men, indicating that hormonal or other biological sex-related differences may influence the AF-related effects on the brain. Sex-related differences may influence the link between PA or AF and cognition also in other stages of life. This effect could be especially pronounced during adolescence, since it has been suggested to be a sensitive period for pubertal hormone-dependent brain organization (Sisk and Zehr, 2005). For this reason, biological sex is a variable that needs to be controlled for when exploring the link between PA or AF and cognition in adolescents.

To better understand the effect of physical performance-related changes in body metabolism on brain functioning, it is important to consider the specific characteristics of PA and AF. Even though PA and AF are closely related, they are different concepts and are measured distinctively. PA is related to energy expenditure resulting from any body movement (Caspersen et al., 1985), and it is usually measured by quantifying the amount of movement done in a certain period of time. On the other hand, AF is conceived as an achieved condition, and it is usually directly measured by obtaining the maximal oxygen uptake (VO_2 max) during maximal effort tasks. Based on their differences, PA and AF may have also different associations with brain function and structure as well as cognition. Very few studies have investigated the effect of both PA and AF on cognition in the same individuals (but see Haapala et al., 2014; Iuliano et al., 2015; Ruotsalainen et al., 2020a).

Using magnetic resonance imaging (MRI) our group reported associations of AF, but not accelerometer-measured PA, with grey matter volume (Ruotsalainen et al., 2019) and white matter integrity (Ruotsalainen et al., 2020a) in adolescents' brains, indicating that the level of

PA alone is not directly associated with structural modifications in the brain. In contrast, Ruotsalainen et al. (2020b) found that accelerometer-measured PA, but not AF, was related to resting state (BOLD) functional connectivity in adolescents. As PA and AF are influenced by different variables (for example, genes have a clearer influence on AF than on PA [Bouchard et al., 2011; Ross et al., 2019]), we infer that PA and AF might influence brain structure and function in different ways. Therefore, they might have a different impact on cognition: if the same genes influence fitness and some brain structural properties, then fitness is associated with the cognitive functions that are supported by these brain structures. PA, on the other hand, partly reflects fitness-unrelated aspects, which do not need to be associated with the same brain areas. Indeed, PA can influence physiological aspects that are directly linked with body activity (and biological factors caused by this activity, i.e., the accumulated effects of acute ongoing exercise). Also, PA could influence the areas that are directly linked to the activity itself, such as motor areas or visuomotor control. Thus, PA may influence cognition by modulating the dynamics of functional connections rather than structural properties in the brain.

As stated above, the most often reported benefits of PA and AF for cognition are evident in tasks requiring attention and/or inhibition. Behaviorally, some studies report an increase in accuracy scores (Hogan et al., 2013), while others have found reductions in reaction time (RT) (Huang et al., 2015) or both in adolescents (Westfall et al., 2018). A new analysis approach (the “EZ diffusion model”) has been suggested for better quantifying these measures (Wagenmakers et al., 2007). In addition to typical task performance measures (accuracy and RT), the EZ model combines typical behavioral outcomes based on accuracy and RT to measure dissociable underlying processes used to solve the task (drift rate, boundary separation, and non-decision time). “Drift rate” has been defined as an index for the signal-to-noise ratio of the information processing system that can be used to quantify the subject’s ability or the task’s difficulty (Wagenmakers et al., 2007). “Boundary separation” is considered a mechanism of the speed-accuracy trade-off and response strategy. “Non-decision time” refers to the temporal period before a decision, which is usually assumed to be included in the RT measure (Luce, 1986). Earlier studies have related improvements in drift rate and boundary separation to higher AF in adolescents (Westfall et al., 2018), but the brain processes associated with these improvements have not been elucidated.

Altogether, the cellular-level findings in animal studies, along with the evidenced improvement of attention and inhibition throughout the lifespan, suggest that PA and AF influence the underlying mechanisms supporting executive functions in the brain. The micro-level changes (such as neurogenesis, changes in synaptic strength and, intracortical connections) induced by PA and AF directly associate with those brain properties that are suggested to contribute to the electrophysiological activity, such as oscillatory activity (Shors et al., 2012), and hence the cognitive functions that are supported by this oscillatory activity. Alpha oscillations are considered to ‘route’ the information processing in the brain depending on attentional demands. Thus, we hypothesize that the influence of PA and AF on brain functions can be demonstrated in the alpha oscillations underlying anticipatory attention and inhibition in adolescents. More specifically, we assume that the higher levels of PA and AF could be reflected as stronger anticipatory modulation of alpha asymmetry. Based on the reported differences in how PA and AF influence brain structure and function, and their different theoretical and methodological definitions, we further assume they might relate to anticipatory alpha asymmetry in different ways. Thus, we aim to clarify the specific contributions of PA and AF on the underlying brain processes of attention and inhibition during adolescence.

To test our hypotheses, we recorded alpha oscillations using MEG during a Posner cueing paradigm in which the participants had to detect a target from two stimuli located in the right or left hemifields. The location of the target was anticipated by a preceding cue. We focused on the cue-induced modulation of alpha power in the ipsilateral and

contralateral hemispheres. According to the alpha modulation hypothesis (Jensen and Mazaheri, 2010), a lower value of alpha in the visual areas of the contralateral hemisphere, and a higher value of alpha in the visual areas of the ipsilateral hemisphere, in reference to the cue, would indicate a better allocation of resources for attention and inhibition, respectively. Therefore, an increased interhemispheric asymmetry (difference of alpha values between contralateral and ipsilateral hemispheres) would indicate an improvement in the allocation of attentional resources. Based on the task demands, we hypothesized that higher levels of PA or AF would show bigger interhemispheric contrast (stronger modulation) of the alpha band, reflecting more efficient attentional and inhibitory processes in the brain. The behavioral performance in terms of attention and inhibitory control was measured in order to test the exploratory hypothesis that anticipatory alpha oscillations mediate the link between PA or AF and behavioral scores of attention/inhibitory control. The possible influence of sex in the associations of PA or AF with anticipatory selective attention was examined for the behavioral outcomes and controlled for in the brain data analysis.

2. Results

2.1. Demographic information, physical activity and aerobic fitness

Table 1 summarizes the demographic information for the two groups based on PA and AF. Demographic information is also given separately to males and females. Statistically significant differences between PA groups and sexes (independent-samples t-tests) are denoted.

Males showed higher levels of MVPA (moderate to vigorous PA, as measured by the accelerometer on a daily basis) than females (males: 59.60 ± 20.66 min/day; females: 46.98 ± 21.46 min/day) ($t[51] = 2.083$, $p = 0.042$) (see Table 1). Males also showed higher levels of AF (minutes until exhaustion in maximal shuttle run test) (males: $7.53 \pm$

Table 1

Demographic information and statistical differences for the groups based on physical activity (PA), aerobic fitness (AF) and sex.

| | Sex | | PA | | AF | |
|----------------------|----------|----------|----------|----------|----------|----------|
| | Males | Females | High | Modlow | High | Modlow |
| Age (years) | 14.34 | 13.98 ± | 13.66 | 14.23 ± | 14.31 | 13.97 ± |
| ± SD | ± 1.4 | 0.9 (37) | ± 0.7 | 1.2 (36) | ± 1.0 | 1.2 (30) |
| (n) | (22) | | (17) | | (20) | |
| Pubertal stage 1 (n) | 3.43 ± | 3.66 ± | 3.27 ± | 3.56 ± | 3.20 ± | 3.83 ± |
| | 1 (21) | 0.8 (32) | 0.8 (15) | 0.9 (32) | 0.7 (20) | 0.9 (29) |
| Pubertal stage 2 (n) | 3.14 ± | 3.28 ± | 3.00 ± | 3.28 ± | 3.00 ± | 3.41 ± |
| | 1.2 (21) | 0.9 (32) | 0.9 (15) | 1.0 (32) | 1.0 (20) | 1.0 (29) |
| Weight, kg (n) | 55.88 | 54.84 ± | 51.45 | 56.58 ± | 51.09 | 57.36 ± |
| | ± 14.2 | 7.6 (36) | ± 10.8 | 10.2 | ± 9.0 | 10.4 |
| | (22) | | (17) | (35) | (20)* | (30)* |
| Height, cm (n) | 167.54 | 161.15 | 159.76 | 165.17 | 162.94 | 164.37 |
| | ± 12.9 | ± 6.4 | ± 9.2 | ± 8.9 | ± 9.7 | ± 10.1 |
| | (22)* | (36)* | (17)* | (35)* | (20) | (30) |
| Body mass index (n) | 19.60 | 21.11 ± | 19.98 | 20.64 ± | 19.14 | 21.18 ± |
| | ± 2.6 | 2.8 (36) | ± 2.6 | 2.5 (35) | ± 2.0 | 3.0 (30) |
| | (22)* | * | (17) | | (20)* | * |
| MVPA, min/day (n) | 59.60 | 46.98 ± | 78.11 | 38.94 ± | 61.79 | 45.01 ± |
| | ± 20.6 | 21.4 | ± 14.7 | 10.1 | ± 23.8 | 19.1 |
| | (19)* | (34)* | (17)*** | (36)*** | (17)* | (27)* |
| AF, mins (n) | 7.53 ± | 4.69 ± | 7.07 ± | 5.18 ± | 8.07 ± | 4.33 ± |
| | 2.1 (20) | 1.8 (30) | 2.2 (13) | 1.9 (31) | 1.6 (20) | 1.5 (30) |
| | *** | *** | ** | ** | *** | *** |

* p-value under 0.05.

** p-value under 0.01.

*** p-value under 0.001.

SD: standard deviation; MPVA: moderate to vigorous PA; modlow: moderate-to-low.

2.12 min; females: 4.69 ± 1.84 min) ($t[48] = 5.024$, $p < 0.001$) (see Table 1).

PA and AF showed a clear association ($r = 0.524$, $p < 0.001$) in the whole sample (see Fig. 1A and Experimental Procedures in Section 4.2 for details about the subject groups). When females and males were analyzed separately, this association was significant for males ($r = 0.577$, $p = 0.015$) but not for females.

2.2. Associations between physical activity, aerobic fitness and the neural and behavioral correlates of attention/inhibition skills

MEG measurements were performed during the visuospatial covert attention task, in which a cue (a small fish, valid in 75% of the cases) was presented before two possible targets (two sharks on each side of the screen). Participants were instructed to answer as fast as possible which shark (located in the left or right hemifield) opened its mouth more to eat the small fish (see Fig. 2A). The task requirements, and the underlying oscillatory dynamics in the left and right hemispheres (based on extensive literature [Jensen and Mazaheri, 2010; Bonnefond and Jensen, 2013; Vollebregt et al., 2015]), are schematically illustrated in Fig. 2B. From this task, RT, cueing effect for RT, cueing effect for accuracy, and EZ model variables (drift rate, boundary separation, and non-decision time) were included in statistical analysis for behavioral effects. Further, the level of alpha power and its interhemispheric balance were used in the statistical analysis for the neural effects. Finally, the correlation between behavioral and brain measures was also examined.

2.2.1. Physical activity vs. Behavioral performance in visuospatial covert attention task

The visuospatial covert attention task measures did not correlate with PA levels. When this correlation was examined separately for males and females, the cueing effect for RT (reaction time for uncued minus reaction time for cued targets) correlated with PA levels (MVPA, see Experimental Procedures, Section 4.2) in males ($r = 0.485$, $p = 0.035$). This result shows that the higher the PA level, the higher the difference between RTs for uncued minus cued targets (see Fig. 1B). No significant correlations were observed for females.

2.2.1.1. Aerobic fitness vs. Behavioral performance in visuospatial covert attention task. The visuospatial covert attention task measures did not correlate with AF levels. In the separate analysis for males and females, significant correlations were found between drift rate and AF levels for females ($r = 0.580$, $p = 0.001$). This result shows that higher AF was associated with a higher drift rate (see Fig. 1C). No significant correlations between EZ-model variables and AF were found for males.

2.3. Physical activity and aerobic fitness vs. Brain measures

The temporal variation of the spectral power at the alpha band in each hemisphere was measured in cued (i.e. cue to the left hemifield for the left hemisphere target and cue to the right hemifield in the right hemisphere target) and uncued (i.e. cue to the left hemifield for the right hemisphere target and cue to the right hemifield for the left hemisphere target) conditions. To examine the modulation of alpha oscillations in response to the cue, left cued vs. right uncued and left uncued vs. right cued conditions were contrasted. Modulation indexes (MI) for each hemisphere were calculated as the power from left cued trials minus right cued trials normalized by their mean (Vollebregt et al., 2015). Average time–frequency representations (TFRs) over selected occipital MEG sensors in each hemisphere (see Fig. 3B) were obtained. MI for left and right hemispheres were used to test the existence of alpha modulation (i.e. increase vs. decrease in response to the cue) and differences between groups. Three different time-windows were selected *a priori* and used for further analysis (0–400 ms [ms], 401–800 ms and 801–1,200 ms post-cue). To test differences in brain measures (left increase and right decrease of alpha MI in the three time-windows) repeated measures ANOVA (rANOVA) analysis was performed separately for PA and AF groups.

The presence of post-cue alpha modulation was verified. As the MI was calculated by subtracting the right cued from the left cued conditions (divided by their sum), and the alpha increases ipsilaterally to the attended hemifield, MI was expected to be positive in the left hemisphere and negative in the right hemisphere (see Fig. 2B). Fig. 3A illustrates the cue-induced modulation of spectral power in left and right hemispheres (time–frequency representation) for AF groups. In the same way, Fig. 4A show the time–frequency representation obtained for PA groups. Both rANOVAs showed a clear main effect of hemisphere (AF as between subjects factor: hemisphere $F_{(1,48)} = 19.114p < 0.001$; PA as between subjects factor: hemisphere $F_{(1,51)} = 17.246p < 0.001$) in alpha power reflecting the expected pattern between hemispheres (left > right).

When AF was used as between subjects factor no significant interaction or between subjects effect were found for AF. A significant interaction of hemisphere \times time-window was found (hemisphere \times TW $F_{(2,96)} = 8.339p < 0.001$). A main effect of time-window was close to significance (TW: $F_{(1,543, 74,071)} = 3.306p = 0.054$). A follow-up test (separately for each time-window), conducted in order to clarify the more detailed differences, revealed a clear main effect of hemisphere in alpha power in the second (hemisphere: $F_{(1,48)} = 20.962p < 0.001$) and third (hemisphere: $F_{(1,48)} = 17.104p < 0.001$) time – windows reflecting the left > right alpha modulation. The direction of the differences between hemispheres can be seen in Fig. 3C.

When PA was used as a between subjects factor, there was a tendency

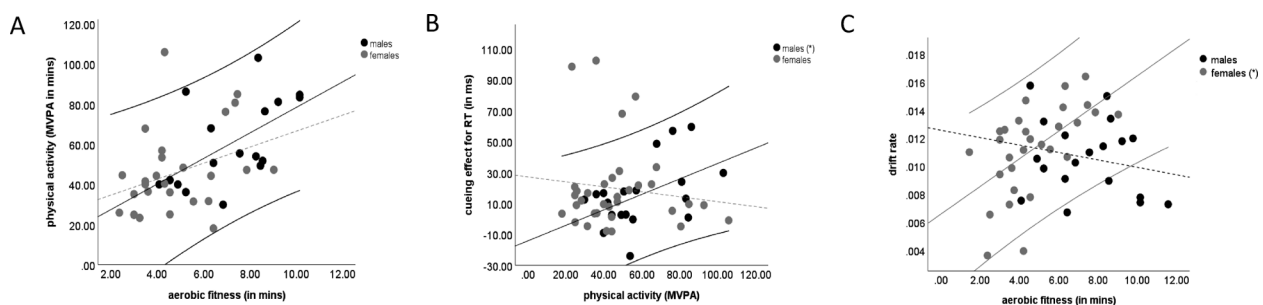


Fig. 1. Associations of studied variables. Black dots represent males and grey dots represent females. The solid central line represents the linear trend line and the two external lines represent the 95% confidence interval for the significant sex group. The dotted central line represents the linear trend line for the non-significant sex group. (A) Aerobic fitness (maximum time during maximal shuttle run test, min) plotted against physical activity (MVPA, moderate to vigorous physical activity, min/day) for males and females. Solid trend line and confidence interval for males, dotted trend line for females. (B) Cueing effect for reaction times from visuospatial covert attention task plotted against physical activity for males and females. Solid trend line and confidence interval for males, dotted trend line for females. (C) Drift rate from visuospatial covert attention task plotted against aerobic fitness for males and females. Solid trend line and confidence interval for females, dotted trend line for males.

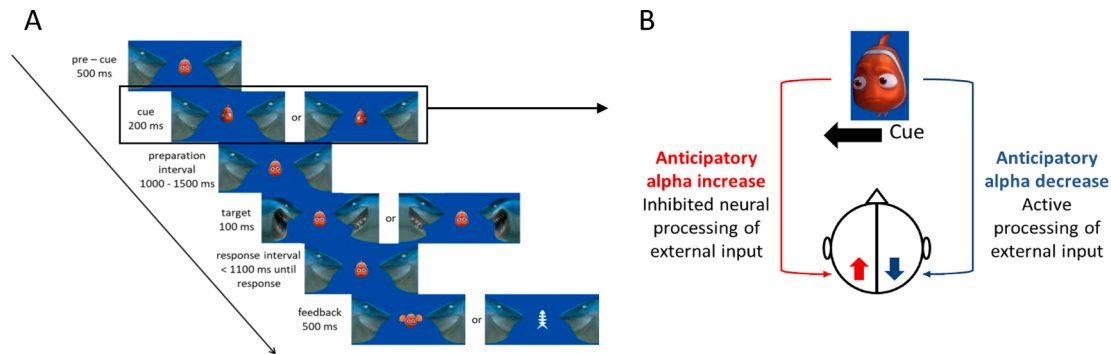


Fig. 2. Schematic representation of Posner's modified visuospatial covert attention task. (A) The progress of the task: a visual cue (fish looking either left or right) was followed by a target (one shark opens its mouth more than the other). Participants should detect the target as soon as possible by pressing the left or right button. (B) Illustration of the alpha modulation hypothesis (Jensen and Mazaheri, 2010) and the expected change in alpha power during the visuospatial covert attention task in the two hemispheres.

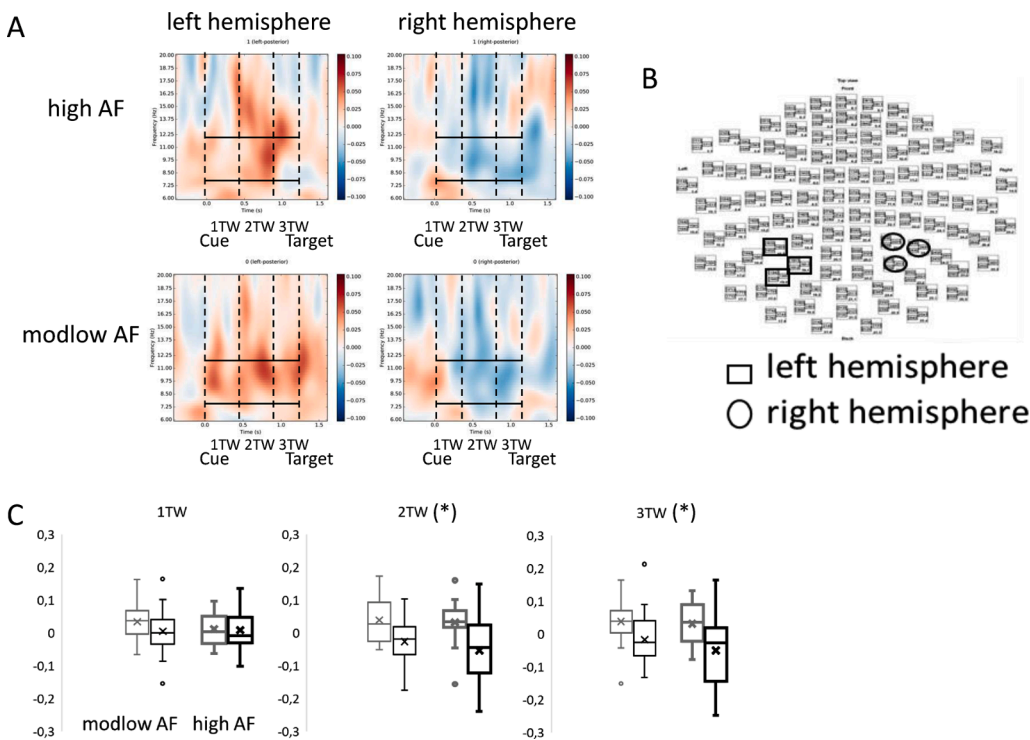


Fig. 3. Modulation of alpha power in response to the spatial cue for AF groups. (A) Time-frequency representations of the alpha power modulation index in the left and right hemispheres for moderate to low (modlow) and high aerobic fitness (AF) groups. Dotted lines delimit the three *a priori* selected time-windows. The first dotted line corresponds with the onset of the cue and the last dotted line corresponds with the onset of the target. Solid horizontal lines delimit the alpha rhythm frequency range (8–12 Hz). (B) Location of selected channels for calculating the alpha modulation index in the left and right hemispheres (square for the left hemisphere and circle for the right hemisphere). (C) Boxplot representation of left (in grey) and right (in black) hemispheres in each time-windows for modlow (light color) and high (dark color) AF groups.

towards significant main effect for group (TW: $F_{(1, 51)} = 3.544p = 0.065$). Moreover, also the effect of time-window (TW: $F_{(1.727, 88.099)} = 2.983p = 0.063$) and hemisphere \times time-window interaction (hemisphere \times TW: $F_{(1.728, 88.152)} = 2.474p = 0.098$) showed small p-values, however not reaching the 0.05 level of significance. To perform similar analysis as for AF groups, and to test our hypotheses on group differences, we further tested the effect of hemisphere and group in each time-window. The follow up test revealed a main effect of hemisphere in the three TWs (1TW: $F_{(1, 51)} = 4.831p = 0.033$; 2TW: $F_{(1, 51)} = 14.838p < 0.001$; 3TW: $F_{(1, 51)} = 19.580p < 0.001$) and a hemisphere \times PA group interaction for the third TW (hemisphere \times TW: $F_{(1, 51)} = 4.268p = 0.044$). Also, a main effect of PA group in the second time-window ($F_{(1,51)} = 4.468p = 0.039$) was found, probably reflecting the way alpha MI is calculated. The direction of the differences between hemispheres can be seen in Fig. 4B.

2.4. Associations between MEG measures and cognition

To test the correlation between the brain activation and behavioral performance, interhemispheric asymmetry (the difference between left – right hemisphere alpha MIs) was calculated as a single variable indexing the observed difference between hemispheres.

The interhemispheric asymmetry during the third time-window showed a significant correlation with drift rate. A bigger interhemispheric asymmetry during the third time-window was associated with lower drift rate values ($r = -0.359, p = 0.006$) (see Fig. 5B). No significant correlations were identified between the interhemispheric asymmetry during the third time-window and other behavioral measures from the visuospatial attention task.

2.5. Brain oscillatory dynamics as mediators between physical activity or aerobic fitness and cognition

The possible mediator role of brain oscillatory measures in the

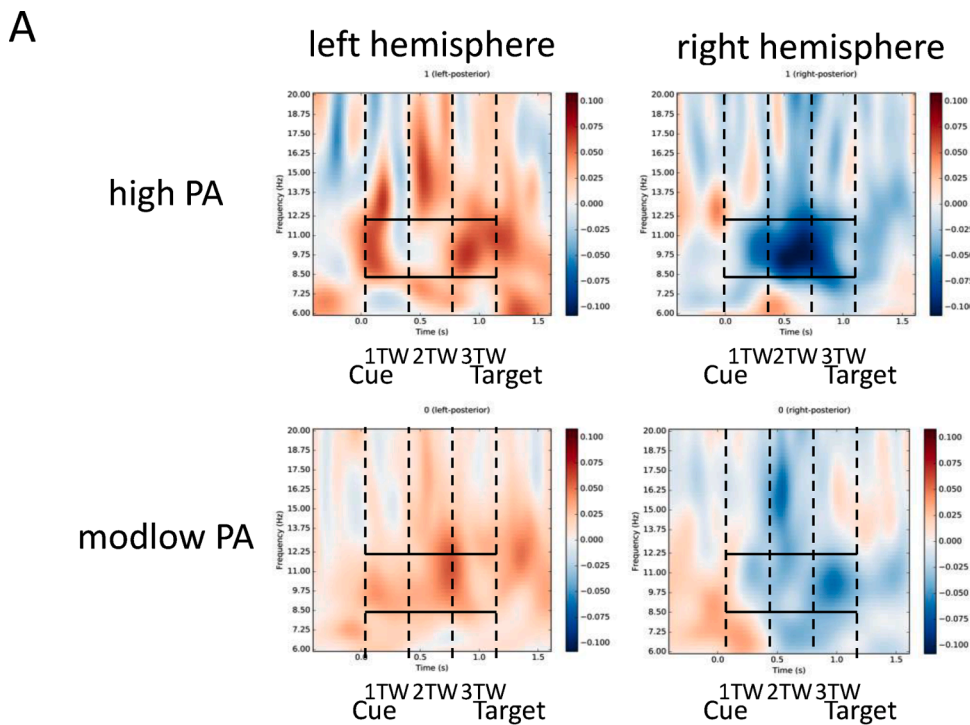


Fig. 4. Modulation of alpha power in response to the spatial cue. (A) Time-frequency representations of the alpha power modulation index in the left and right hemispheres for moderate-to-low (modlow) and high physical activity (PA) groups. Dotted lines delimit the three *a priori* selected time-windows. The first dotted line corresponds with the onset of the cue and the last dotted line corresponds with the onset of the target. Solid horizontal lines delimit the alpha rhythm frequency range (8–12 Hz). (B) Boxplot representation of left (in grey) and right (in black) hemispheres in each time-windows for modlow (light color) and high (dark color) PA groups.

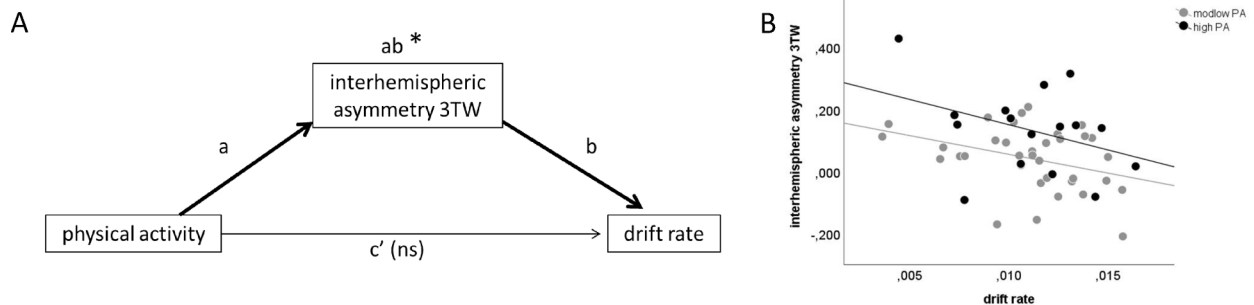
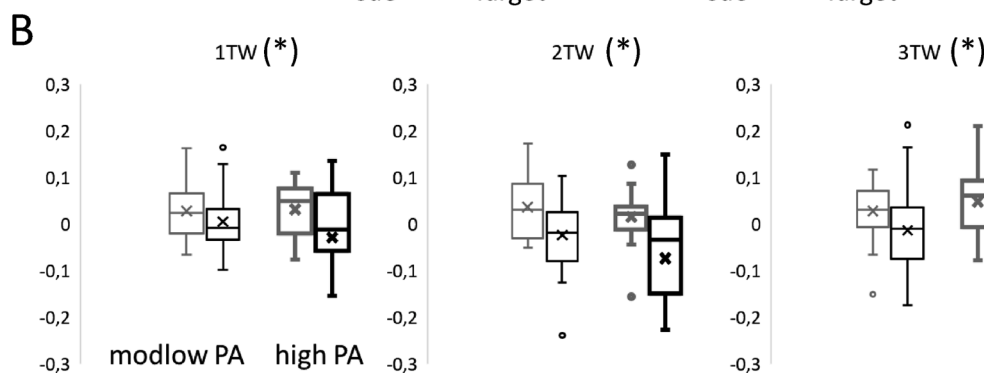


Fig. 5. Schematic illustration of the mediation model. (A) Mediation path examined about the role of interhemispheric asymmetry of alpha modulation index during the third time-window in mediating the relationship between physical activity and drift rate from the visuospatial covert attention task. Darker arrows indicate a significant path (only an indirect effect). (B) Interhemispheric asymmetry during the third time-window plotted against drift rate for both physical activity groups. Black dots and trend line correspond to high physical activity group and grey color dots and trend line correspond to moderate-to-low (modlow) physical activity group.

relationship between PA or AF and cognition was tested. A mediator analysis was used to test the underlying assumption that task-related modulation of oscillatory power mediates the influence of PA or AF on performance in visuospatial covert attention task. First, significant correlations between brain measures, PA or AF groups and cognitive variables were tested. Of the brain measures, only the interhemispheric

asymmetry of alpha power during the third time-window fulfilled this assumption correlating with PA groups (but not AF groups) and cognitive variables (only drift rate). The resultant combination was tested with a mediator model using MPlus software by means of a bootstrap of 1,000 samples. Mediation was tested by determining whether the confidence interval for the indirect effect contained zero (Fritz and

MacKinnon, 2007). The intervals not including zero were considered significant.

The mediation model was built with PA groups as the independent variable, drift rate as the dependent variable and interhemispheric asymmetry during the third time-window as the mediator. Indirect effect was significant (ab estimate = -0.107 , bias-corrected bootstrap confidence interval = $[-0.306; 0.000]$) but direct and total effects were not (direct: c' estimate = 0.104 , $p = 0.458$; total: c estimate = -0.003 , $p = 0.983$) (see Fig. 5A). In this model, the relationship between independent (PA groups) and dependent (drift rate) variables was not significant, but this relationship was increased in magnitude when late interhemispheric asymmetry was included as a mediator. As the mediated effect and the direct effect have opposite signs, the model indicates substantial mediation (MacKinnon, 2008). The results of this model thus suggest that the late interhemispheric asymmetry of alpha power mediates the association between PA levels and drift rate in the visuospatial covert attention task across the whole sample.

To determine if sex influenced the above mediation effect, a moderation in the mediator effect analysis was performed. The results showed no significant difference in indirect effects between males and females (d4 estimate = -0.103 , $p = 0.798$, bias-corrected bootstrap confidence interval = $[-1.144; 0.503]$). The results of this model suggest that sex does not moderate the indirect or total effects of late interhemispheric asymmetry of alpha power in the association between PA levels and drift rate.

3. Discussion

This study evaluated the influence of PA and AF on brain oscillatory measures underlying anticipatory attention allocation within the same sample of adolescents. As expected, even though the levels of PA and AF were strongly correlated, they showed specific associations with cognitive performance and underlying brain measures. Adolescents, especially males, with higher levels of PA showed stronger utilization of the cue in anticipating their response, reflected as a bigger cueing effect (RT difference between uncued vs. cued targets) in reaction time. In line with these behavioral findings, the group with higher PA level showed stronger cue-induced interhemispheric alpha asymmetry during the stage of attention allocation in a modified Posner's cueing task, in which attention (vs. inhibition) is selectively directed to one of the visual hemifields. The exploratory mediation analysis suggested that this interhemispheric alpha asymmetry mediated the association between PA status and drift rate, a measure of information processing speed, calculated as an individual performance measure in the Posner's cueing task. Larger cue-induced asymmetry was associated with slower overall information processing at the behavioral level, in an analysis integrating valid and invalid spatial cues. Although males and females showed a differential association between PA and AF and cognition, this mediator effect was not influenced by sex.

Males with a higher level of PA indicated stronger cue-based anticipation, as the bigger difference in reaction times between cued and uncued trials, suggesting a greater reliance on the cue. It is important to note that this bigger difference could be determined from a gain of valid cueing or by a cost of invalid cueing. As paying attention to the cue is what makes the targets valid or invalid, both, a gain of valid cueing and cost of invalid cueing, could be considered as cueing effect. The result of a stronger reliance on the cue for higher physically active males is partly in line with an earlier study showing a complex association between attentional control and PA measures especially in males (Booth et al., 2013). By measuring selective attention, sustained attention, and attentional control/switch, Booth and colleagues found that higher total volume of PA (mostly including light intensity activity) predicted poorer performance on the attention tasks, while higher MVPA was associated with better executive function performance in adolescent males. In contrast, Vanhelst et al. (2016) reported a positive effect of PA on attention capacity in adolescents independent of sex. Differences

between our results and earlier findings might be related to the way the attentional tests were administered (computerized vs. paper and pencil), and to the way cueing was used in the experiments. In our study, we used a rather high ratio of cued/uncued trials (75/25%) which may emphasize attentional shifting over efficient attention control for optimal performance. It seems important to acknowledge the specific task requirements to make correct interpretations of the behavioral benefits by PA. In sum, there is some evidence for an association between higher levels of PA and more dependence on the cue in adolescents, more clearly in males than in females. The possible sex difference indicated by our findings needs to be confirmed by further studies, as we had a fairly small number of participants (especially when both sex and physical activity groups were separately analyzed).

Interestingly, we demonstrated a modest but significant difference at the brain level, related to the cue-based allocation of attentional resources. The significant hemisphere \times PA group interaction indicated a larger difference between the ipsilateral increase and contralateral decrease of alpha oscillations in the two hemispheres in the high PA group. This effect appeared at around 800 ms after the cue onset, right before the target. This means that for adolescents with a higher level of PA, the cue-based engagement of visual attentional resources (anticipatory inhibition/preparation of the brain processes corresponding to the uncued/cued hemifield, respectively) is stronger than for individuals with lower levels of PA. This result can be interpreted according to Banich (1998), who suggested that, depending on task demands, the interaction between the brain hemispheres, rather than the specific processes accomplished by each hemisphere separately, can influence selective attentional functioning. Therefore, PA seems to be related to a stronger reliance on cues for engaging anticipatory attentional control, reflected in both behavioral measures (reaction time difference between uncued vs. cued targets) and brain measures (anticipatory interhemispheric asymmetry of alpha oscillations).

The effect of PA was not observed in the overall performance in the selective attention task. It was seen instead in the strategy of performing the task, perhaps reflecting prioritization of anticipatory focusing of attentional resources over adaptive shifting of attention. Indeed, the overall behavioral outcome did not differ, but only the reliance on the cue. In fact, as evidenced by the subsequent mediation analysis, the strong interhemispheric asymmetry was linked with less efficient attentional processing, as measured by the drift rate variable (reflecting the speed of information processing), when a single measure of drift rate was calculated, integrating cued and uncued targets. Our results would thus suggest that rather than focusing on the absolute benefit of PA on cognitive functions, it would be useful to examine the influence of PA on the more specific mechanisms of information processing in the brain. Indeed, it might be that by specifically influencing part of the neuro-cognitive resources underlying attentional control, PA may appear beneficial for executive functions in some tasks but not in others. Thus, differential effects across tasks could depend on the specific neuro-cognitive requirements of a given task. This interpretation of our data would help to explain the discrepant findings concerning the effects of PA on executive functions in youth (Alvarez-Bueno et al., 2017; Esteban-Cornejo et al., 2015).

What could then be the underlying mechanisms by which PA contributes to the neural bases of attention? Our experimental manipulation focused on the attentional control that requires communication between the left and right visual areas. The dynamic interaction between hemispheres, modulating the processing capacity of the brain, is proposed to occur via the main pathway connecting the cerebral hemispheres, the corpus callosum (Banich, 1998; Qin et al., 2016). A recent study by our group (Ruotsalainen et al., 2020a) investigated the link between both PA and AF with the white matter connections in adolescents using MRI and fractional anisotropy (assessing microstructural changes in the brain's white matter). The main results in this study showed that only the level of AF (and not PA) was related to white matter properties. However, it was also described that the level of fractional anisotropy in the body of

the corpus callosum could moderate the relationship between PA and working memory. Specifically, high levels of PA were positively related to working memory only when the fractional anisotropy level was low (which could signify e.g. earlier stages of corpus callosum maturation). The authors suggest that specific tracts of white matter (such as corpus callosum) could moderate the relationship between both PA and AF with cognition in adolescents. This reasoning is in line with the general notion that the responsiveness of the brain networks to external influences (including physical activity), i.e. brain plasticity, is not stable but varies across development.

Interestingly, it has been suggested by some studies, that the changes in white matter fractional anisotropy are associated with variations in alpha oscillatory activity in corresponding areas (Jann et al., 2012; Valdés-Hernández et al., 2010). It may thus be, that white matter properties, representing the structural skeleton for neuronal communication, bring about the physical activity (and fitness) -related influences into oscillatory dynamics and attention allocation. When both of these measures show also developmental differences, it would be critical to acknowledge the maturational state (and consequently, the level of plasticity) of the brain to explain the possible effects of PA and AF over cognitive performance. Further research is warranted to clarify the role of interhemispheric interaction via the corpus callosum in the influence of PA and AF on executive functions (such as attentional control/inhibition and working memory).

Our exploratory mediation analysis indicated that the interaction (or, more specifically, the degree of imbalance) between the hemispheres (interhemispheric asymmetry) during attention allocation seemed to mediate the relationship between physical activity levels and performance in a visuospatial selective attention task. PA increased the imbalance between the ipsi- and contralateral hemispheres according to the selective attention task requirements. However, this increment in interhemispheric asymmetry did not improve the efficiency in the selective attention task (as measured by drift rate). This unexpected result could be partly explained by a strategy of choice emphasizing the processing of the cue. Adolescents with higher PA could be prioritizing the anticipation for upcoming information, as was hinted also by the stronger behavioral cueing effect. Similar results were obtained in a longitudinal study measuring the association of preadolescent children's motor competencies with working memory maintenance and neurophysiological measures of task preparation (Ludyga et al., 2020). Ludyga et al., (2020) described a more effective utilization of the cue-relevant information by an increase in the cue-P300 amplitude during the task preparation stage in a Stenberg paradigm (used to assess working memory capacity) in children with higher motor competencies, thus in line with our findings. The authors suggest that children with high motor competencies exhibited a more proactive control strategy allowing active maintenance of task goals.

It seems that the differences in strategy between children with low and high accelerometer-measured motor competencies can also be observed in adolescents when solving a selective attention task. However, this strategy could have a cognitive cost leading to a worse global efficiency in the selective attention task, especially when the proportion of uncued targets in the task is rather high. The cost-benefit effect of relying on the cue could also arise due to shared neural resources between selective attention and working memory (For a review see Gazaley and Nobre, 2012). PA has been associated with increased working memory capacity in children and adults (Alvarez-Bueno et al., 2017; Kamijo et al., 2011; Ludyga et al., 2020). In a task requiring both, working memory (holding the side of the target in memory) and possible attentional switching, the strategy relying on working memory may limit the resources for adaptive attentional switching (Luna et al., 2020).

In line with earlier studies in youth, PA and AF were found to be strongly correlated (Butte et al., 2007; Gutin et al., 2005; Ruotsalainen et al., 2019). Nevertheless, they showed different associations with executive control and its underlying brain processes. While AF was shown to be associated with brain structural measures more strongly than PA

(Ruotsalainen et al., 2019, 2020b), the opposite was true for functional measures, i.e. brain oscillatory dynamics underlying anticipatory attention allocation: We did not find any relationship between AF and alpha oscillations. This result aligns with earlier findings obtained with a very similar paradigm to ours. Wang et al., (2015) performed a similar study in young adults measuring oscillatory brain activity during the performance in Posner's visuospatial covert attention paradigm. Even though they aimed to measure a broader band of brain rhythms including theta and beta oscillations in addition to alpha oscillations (and, topographically, they focused on broader scalp areas: midline frontal to posterior regions), they also found that fitness levels did not modulate alpha recruitment in response to a cue. Thus, we replicated this Wang et al. (2015) result, and expand it to concern also earlier life stages, namely adolescence.

Although brain functional measures did not associate with AF, there was an indication of a correlation between behavioral measures and AF. Higher AF was related to higher drift rate values in the visuospatial attention task, but only in females. Drift rate was calculated as part of the EZ diffusion model for two-choice RT tasks (Wagenmakers et al., 2007) and was based on the variance of reaction times for correct decisions and the proportion of correct decisions. The drift rate has been interpreted as an index of processing speed in decision tasks (Wagenmakers et al., 2007). Previous studies have also reported the association between fitness and behavioral performance in attention/inhibition in adolescents (Cadenas-Sanchez et al., 2017; Huang et al., 2015; Marchetti et al., 2015; Westfall et al., 2018). Therefore, although the anticipatory gating of relevant information, reflected as asymmetric alpha oscillations in visual areas, was not specifically influenced by AF, AF seems to be related to selective attention/inhibition processing.

The tendency to observe PA vs. AF -related influences in males vs. females, respectively, cannot be fully scrutinized based on our moderate sample size but evokes interesting questions about the role of sex differences. In our data, the AF level in females seemed to be associated with more efficient attentional/inhibitory processing (drift rate) in the visuospatial attention task. On the other hand, PA level in males seemed to be associated with the clearer benefit of cued over uncued targets (presumably reflecting a choice of strategy). The latter result concerning sex-specific benefits of PA was already discussed above and shown to receive some support from earlier findings (Booth et al., 2013). The selective advantage of AF for females' cognition/executive functions has also been reported before for older adult populations (Baker et al., 2010; Barha et al., 2017; Colcombe and Kramer, 2003; van Uffelen et al., 2008). Our minor finding support and expands those previous studies by showing a sex-dependent positive effect of AF over selective attention/inhibition also earlier in life. There are some potential underlying explanations for the observed female-specific advantage of fitness for executive functions. Based on a study exploring the association between circulating BDNF levels and cognitive functioning, it has been hypothesized that the brain-derived neurotrophic factor (BDNF) is more closely related to cognition in women compared to men (Komulainen et al., 2008). Moreover, some studies have suggested that increased feminine hormone, estradiol, might be related to greater BDNF expression in the cortex and hippocampus of females of different species (Scharfman et al., 2003; Singh et al., 1995; Sohrabji et al., 1995). While BDNF is one of the mechanisms by which physical performance is thought to contribute to cognition, these differences may underlie also the differential effects between the sexes. However, more studies are needed to investigate the differences in PA and AF in the two sexes and the possible mediator role of sex hormones in the relationship between AF-related increments of BDNF and cognition.

It is important to note that we cannot rule out the effect of peer group influence, personality, and preferences in free-time activities, that are likely to influence PA more than AF (Palmer-Keenan and Bair, 2019; Sevil et al., 2018), which thus impacts the interpretation of our results, and especially the possible sex differences. In line with earlier studies (Booth et al., 2013; Tomkinson et al., 2018; Woll et al., 2011), PA levels

were higher in males than in females. It may be that higher levels of activity in boys at this age also reflect engagement to regular, goal-directed training, which could be generalized as higher competitiveness also in other contexts. This could influence the choice of strategy in the visuospatial attention task. In the same way, underlying genetic factors could influence the association between AF and attentional processing in females.

Our results also raise the probable developmental perspective in the study of the underlying brain mechanisms in the association between PA or AF and attention/inhibition. Benefits from PA have been reported mostly for young adults (Hillman et al., 2006; Kamijo et al., 2011; Kamijo and Takeda, 2009). Evidence of benefits from PA on attention/inhibition is weaker in other age groups. However, AF seems to benefit selective attention and inhibition, especially during childhood (Chaddock et al., 2011; Pontifex et al., 2011; Voss et al., 2011) and older adulthood (Colcombe et al., 2004; Prakash et al., 2011). Perhaps this age-dependent variation in observed interlinks between physical performance measures (AF vs. PA) and neurocognitive functions reflects also the overall changes in the strength of genetic contribution, more strongly reflected in the AF, on these functions. Altogether, the current evidence suggests a U-shaped relationship between PA and selective attention/inhibition across the lifespan. Further work is required to establish whether this is the case or whether this reflects only an insufficient number of studies tackling regular PA engagement across the lifespan.

A major limitation of this study resides in its small sample size, which limits the strength of our interpretations. Another limitation lies in the cross-sectional nature of this study, which prevents us from making causal inferences from the associations found for PA or AF. The results of our mediator analysis provide valuable insights for understanding brain processes that might mediate the effects of PA on cognition, although they should be interpreted with caution. The absence of a direct effect in our mediation model (direct influence of PA over drift rate) could be a result of the reduced sample size. It may thus be that there was sufficient power to detect the indirect effect, but insufficient power to detect the direct and total effects. Longitudinal studies would be needed for a better understanding of the neural level mediators of the cognitive benefits of PA and AF during different phases of life. Finally, this study measured only PA and AF effects over selective attention and inhibitory control processes in the visual modality. Testing these effects in different modalities or cross-modal interactions should also be considered in future research.

In conclusion, our results showed that higher levels of PA, but not AF, were related to improved anticipatory brain processes underlying allocation of attention in the adolescent brain. However, the anticipatory interhemispheric asymmetry was related to reduced overall performance in the visuospatial attention task, thus suggesting a choice of strategy prioritizing the cue processing. Behaviorally, female and male adolescents showed dissociable effects of PA and AF on anticipatory selective attention/inhibitory control.

4. Experimental procedures

4.1. Participants

Sixty-three adolescents were recruited to participate from among the participants of a larger study related to the Finnish Schools on the Move Program (Joensuu et al., 2018; Syväoja et al., 2019) measuring the behavioral effects of PA and AF on cognition. The potential subjects were informed about the study and voluntarily manifested their interest to participate. All subjects were native Finnish speakers and came from the Central Finland area ($n = 54$) or the South Finland area ($n = 9$). Sixty participants were classified as right-handed and three as left-handed by the Edinburgh Handedness Inventory. From the initial 63 participants, four were excluded from further analysis due to low quality of MEG data ($n = 2$) or very few responses in the uncued condition during the

visuospatial covert attention task ($n = 2$). Finally, the analysis was done with a total of 59 participants (22 males and 37 females) with age ranges from 12.8 to 17.0 years old (14.11 ± 1.07 years).

All participants were volunteers, and they as well as their legal guardians signed informed consent before the beginning of the study in agreement with prior approval of the Central Finland Healthcare District Ethical Committee. Participation in this study was compensated with a €30 gift card. The sample did not include participants with neurological disorders, major medical conditions or those using medication that influences the central nervous system. All participants had normal or corrected to normal vision.

Self-reports about the participants' stages of puberty with the Tanner Scale (Marshall and Tanner, 1969, 1970) were used to measure the pubertal development in our sample. All the participants reported being between categories 2 and 5 for pubertal stage 1 and between 1 and 5 for pubertal stage 2. For demographic information and statistical differences for the groups based on AF, PA or sex, see Table 1.

4.2. Measures of physical activity and aerobic fitness

AF was estimated with the shuttle run test (Leger et al., 1988; Joensuu et al., 2018), a measure widely used to estimate a person's maximum oxygen uptake ($\text{VO}_{2\text{max}}$). Participants were instructed to run between two lines with a separation of 20 m. Speed should have accelerated every time they heard an audio signal. The time participants spent before failing to reach the end lines in two consecutive tones indicated their level of AF. The speed in the first and second levels was 8.0 and 9.0 km/h, respectively. Afterward, speed increased by 0.5 km/h per level. The duration of each level was one minute. The number of minutes that each participant lasted until exhaustion and abandoning the test (normalized by gender and age) was used to measure the participant's AF level. To differentiate them by their level of AF into high or moderate-to-low (modlow) AF groups, the distribution of minutes until exhaustion was divided into three equal parts. Participants in the highest tertile (cutoff point tagging 66% of the distribution) were considered as being part of the high AF group. In the same way, participants in the two lowest tertiles were allocated to the modlow AF group.

PA was measured with accelerometers, specifically triaxial Acti-Graph (Pensacola, FL, USA) GT3X + and wGT3X + monitors, which the participants wore during seven consecutive days (Joensuu et al., 2018). They were instructed to wear it on their right hip during waking hours except for water-related activities. A valid measurement day consisted of at least 10 h of data. Data were collected in raw 30 Hz acceleration, standardly filtered and converted into 15 s epoch counts. Periods of at least 30 min of consecutive zero counts were considered as non-wear time. A customized Visual Basic macro for Excel software was used for data reduction. A cut-off point of ≥ 2296 cpm (Evenson et al., 2008) was used to define moderate to vigorous intensity PA (MVPA, min/day). MVPA was calculated as a weighted mean value of MVPA per day ($[\text{average MVPA min/day of weekdays} \times 5 + \text{average MVPA min/day of weekend} \times 2] / 7$). To differentiate participants by their PA level into the high or modlow PA groups, the distribution of MVPA (min/day) was divided into three equal parts. Participants in the highest tertile (cutoff point tagging 66% of the distribution) were placed into the high PA group. In the same way, participants in the two lowest tertiles were allocated to the modlow PA group.

PA was measured in a total of 53 participants and AF was measured in a total of 50 participants. School absence on the day of the test was the reason for missing AF values (2 males and 7 females), while an insufficient number of valid measurement days (two weekdays and one weekend day) was the reason for missing data of regular PA measurements (3 males and 3 females). All subjects had at least one measure of PA or AF.

4.3. Stimuli and task

We used a visuospatial covert attention paradigm from Vollebregt et al. (2015) based on a modified Posner's cueing paradigm (Posner, 1980). The task of the participants was to save a fish from being eaten by a shark. A schematic representation of the sequence of phases displayed in the task is shown in Fig. 2A. The first phase was the pre-cue period (500 ms), when the subjects were presented with a fish in the middle of the screen as a fixation point and two sharks on both sides of the screen. Next, a cue was presented during 200 ms consisting of the fish's eyes looking to the left or the right shark. The cue indicated the side of the screen where the target would appear. The target (both sharks opened their mouths but one more than the other) was presented after 100 ms. The probability of validly cued targets (the gaze of the fish was directed towards the same side as the targeted shark) was 75%. Afterward, participants had a preparation interval varying in time (1,000–1,500 ms) to avoid the subject's prediction of the target's occurrence. The duration of the response interval following the target presentation was determined by the subject's response with a maximum time of 1100 ms. Subjects had to report (by using their index finger in a MEG-compatible response pad) the side corresponding to the shark that opened its mouth more. Afterward, the feedback (a happy fish for correct responses or a fishbone for errors) was presented. During the whole task, subjects were instructed to continuously watch the fish's eyes (fixation point). Instructions with standardized guidelines were given to the subjects in advance, and before starting the measurements, the instructions were repeated in a short video (4 s of duration). To ensure that the participants learned the instructions correctly, a practice session was performed with 100 trials and the same amount of right and left targets. During the practice, the task was the same, only the probability of validly cued targets was modified (80%) to reinforce learning the cue. Subjects were reminded about fixating on the small fish's eyes at the beginning of the task and in every break between blocks.

The visuospatial covert attention task was programmed and controlled using Presentation software (Neurobehavioral Systems, Albany, CA) and consisted of four blocks of 100 trials each. Each block contained 75 cued targets and 25 uncued ones. Between blocks, subjects could rest and after some minutes they decided when to start the following block. Left and right cues had the same probability of occurrence. The total duration of the task was approximately 20 min.

4.4. MEG recordings and analysis

The brain activity related to the visuospatial covert attention paradigm was recorded using an Elekta Neuromag Triux system (Elekta Neuromag, Helsinki, Finland) for the subjects living in Central Finland. The recordings for the subjects from Southern Finland were performed in Aalto Brain Centre's MEG core using Elekta Neuromag™ (Elekta Neuromag, Helsinki, Finland). The MEG devices in the two institutes are essentially the same. During the subject's preparation, five head-position indicator coils were attached to their heads (three in the front and two behind both ears). Coil locations were determined using a 3-D digitizer in reference to three anatomical landmarks (nasion and pre-auricular points). At the beginning of the recording, their position with respect to the helmet was measured and continuously tracked during the whole measurement (Uutela et al., 2001) to correct for head movement during the analysis stage. With the use of the electrooculogram (EOG), vertical (two electrodes located at the external canthi of both eyes) and horizontal (two electrodes above and below the right eye) eye movements were monitored. During the measurements, the subjects were seated comfortably inside a magnetically shielded room and were instructed to avoid movements of the head and the eyes. Two response pads (left and right) were positioned on a table attached to the chair and located over the subject's legs. The task was projected on a panel located 1 m from the subject's eyes.

The MEG signals were band-pass filtered at 0.03–330 Hz and

sampled at 1000 Hz. The raw data were pre-processed using Maxfilter™ 2.2 software (Elekta Neuromag, Helsinki, Finland). A signal space separation method (SSS) (Taulu et al., 2003), removing external interference emerging during the measurement, was used in most of the subject's recordings. SSS was replaced by the spatiotemporal signal space separation method (tSSS) (Taulu and Simola, 2006) (also included in Maxfilter 2.2 software) for the analysis of data from participants wearing braces or other internal magnetic sources. Head movements occurring during the measurement were also corrected by using Maxfilter 2.2 software. The rest of the analysis was performed with MNE-Python software (Gramfort et al., 2014). The analysis was performed with the brain activity recorded from the gradiometers. The time–frequency representations (TFRs) were calculated in a frequency range of 2–30 Hz and for a time period ranging from –0.2 to 1.4 s in reference to the onset of the cue. The frequency resolution used was 2 Hz. A Morlet wavelet transformation (Morlet et al., 1982) was used for this purpose with the number of cycles equal to half of each frequency value. For each channel, a modulation index (MI) was calculated with the following equation:

$$MI = (\text{freq_left cued trials} - \text{freq_right cued trials}) / \frac{1}{2} * (\text{freq_left cued trials} + \text{freq_right cued trials})$$

The resulting MIs were used to evaluate the visuospatial covert attention task-based modulation in the alpha band (8–12 Hz). Whole head TFRs were averaged together for the whole sample of 59 participants. Averages of three MEG channels in occipital regions where alpha increased (left) and alpha decreased (right) could be clearly identified were selected. The location of the left (contralateral) and right (ipsilateral) selections of MEG channels for the occipital region used for further analysis is shown in Fig. 3B. The difference between the alpha MI from the left minus right hemispheres was used to calculate the inter-hemispheric asymmetry of alpha MI during the task. Because there are not references from previous studies to infer where (in time) the PA or AF-related effects could appear, we chose to use an exploratory approach. The whole time-window available (0–1200 ms) of alpha MI in the left and right hemispheres and interhemispheric asymmetry, was divided in three equal and smaller time-windows (0–400 ms, 401–800 ms, 801–1,200 ms).

MEG and behavioral data were analyzed in a blinded manner towards the group assignment to obtain an unbiased assessment of neurophysiological or cognitive outcomes.

4.5. Behavioral performance analysis

During the MEG measurement, behavioral responses from the visuospatial covert attention task were collected and analyzed. Incorrect responses (<2.5% of the data) and reaction times below or above 2.5 standard deviations from the mean in each condition for each participant (<2.5% of the data) were considered as outliers and excluded from further analysis. Reaction times under 250 ms were considered too short to reflect selective attention processing and were removed from the analysis. There was no difference in the number of cued and uncued targets from the visuospatial covert attention task used for further analysis for the whole sample divided by sex, the two groups based on AF and for the two groups based on PA.

Average reaction times for cued and uncued targets were calculated separately for each subject. A cueing effect index for RT was calculated as the difference between the reaction times for uncued minus cued targets. Accuracy was calculated as the percentage of correct responses. The cueing effect index for accuracy was calculated as the difference between the number of correct responses for cued minus uncued targets. Accordingly, average reaction times, accuracy for cued and uncued targets and the cueing effect indexes were used in further analysis.

In addition to typical task performance measures (accuracy and RT), the EZ model was used to analyze the results from the visuospatial covert attention task. Three new variables (drift rate, boundary separation and non-decision time) were calculated for each participant according to

Wagenmakers et al. (2007). Drift rate, boundary separation, and non-decision time are determined from three parameters: the mean RT for correct responses (MRT), the variance of RT for correct responses (VRT), and the proportion of correct responses (Pc), as in the EZ model (for more details and R code see Wagenmakers et al. 2007).

4.6. Statistical analysis

Statistical analysis was performed with IBM SPSS Statistics for Windows, Version 24.0 (Armonk, NY: IBM Corp.). Variables resulting from behavioral measures were assessed for normality. Only variables showing normal distribution were included in the statistical analysis. Resulting variables from the visuospatial covert attention task used for further analysis were: RT for cued and uncued targets, cueing effect for RT, drift rate, boundary separation and non-decision time. All brain measures were included in future analyses.

We conducted two rANOVAs on the MI of alpha power, one for each between-subjects factor (PA and AF groups). Within-subjects factors were hemisphere (left, right) and time-windows (1st, 2nd, 3rd). In the first version of the models used, sex and puberty (1 and 2) were included as covariates. However, the model showed that none of the covariates were significant predictors. Because of this, biological sex and puberty as covariates were removed as covariates from the final models. Subsequent follow-up tests with rANOVA (separately for each time-window), were conducted for AF and PA groups as between-subjects factors to clarify the more detailed differences revealed by the primary analysis of variance tests.

Bivariate Pearson correlation coefficients were used to describe the associations between relevant brain data (interhemispheric asymmetry of alpha MI during the third time-window), the cognitive measure (visuospatial covert attention task) and PA or AF variables (MVPA and minutes until exhaustion in the shuttle run test).

Because sex is a variable that needs to be controlled for when exploring the link between PA or AF and cognition in adolescents, the existence of a sex effect in the behavioral performance was tested. Unfortunately, we could not do the same with the brain data because of the low signal to noise ratio, which could compromise the reliability of the potential results.

To test our hypothesis on whether oscillatory dynamics at the alpha band mediates the effect of PA or AF on cognition, a mediator analysis was performed by using MPlus software version 8.0 (Muthén and Muthén, 1998–2017). Before the analysis, we tested whether the assumptions for using the mediator model (normality and significant correlations between the three variables included in each model [independent variable, dependent variable, and moderator]) were met. Combinations with significant correlations of the mediator with independent and dependent variables were also included in the analysis. All possible models where alpha modulatory activity could mediate cognition improvements due to PA or AF levels were tested. The resultant combination was tested with a mediator model using MPlus software using a bootstrap of 1000 samples. Full information of maximum likelihood (FIML), which accounts for missing values at random (MAR) and includes all available data, was used.

In the mediation analysis, the bootstrap confidence interval was used, as it makes no assumption about the shape of the sampling distribution of the indirect effect (*ab*; Hayes and Rockwood, 2017). In bootstrapping, the indirect effect is estimated by randomly resampling cases from the dataset and estimating the model and resulting indirect effect in the bootstrap sample (Hayes and Rockwood, 2017; Preacher and Hayes, 2004). An empirical representation of the sampling distribution of the indirect effect is built by repeating this process 1,000 times. By using various percentiles of the bootstrap distribution, a confidence interval for the *ab* is constructed. Mediation is tested by determining whether the 95% confidence interval contains zero (Fritz and Mackinnon, 2007). If the interval is above or below zero, this supports mediation, and if the interval includes zero, it does not provide evidence

of mediation. As recommended by Mackinnon (2008), the bias-corrected and accelerated bootstrap confidence intervals for the indirect effect were estimated using 1,000 bootstrap samples.

CRedit authorship contribution statement

Doris Hernández: Investigation, Formal analysis, Writing - original draft, Visualization. **Erkka Heinilä:** Software, Formal analysis. **Joona Muotka:** Formal analysis. **Ilona Ruotsalainen:** Project administration, Investigation, Writing - review & editing. **Hanna-Maija Lapinkero:** Project administration, Investigation. **Heidi Syväoja:** Funding acquisition, Investigation, Writing - review & editing. **Tuija H. Tammelin:** Funding acquisition, Investigation, Writing - review & editing. **Tiina Parviainen:** Funding acquisition, Conceptualization, Supervision, Methodology, Formal analysis, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was supported by the Academy of Finland [grant numbers 273971, 274086 and 311877]. We would like to thank Ole Jensen for sharing the visuospatial covert attention task and his guidance in brain data analysis. For their valuable comments on this manuscript, we would like to thank Ole Jensen, Georgia Gerike and Krista Lehtomäki. We also thank Janne Rajaniemi for his valuable help in the data collection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.brainres.2021.147392>.

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