

COGNITIVE NEUROSCIENCE

Physical and motor fitness are both related to cognition in old age



Claudia Voelcker-Rehage, Ben Godde and Ursula M. Staudinger

Jacobs Center on Lifelong Learning and Institutional Development, Jacobs University Bremen, Campus Ring 1, 28759 Bremen, Germany

Keywords: aging, attention, cognition, exercise, fMRI, human, motor

Abstract

The benefits of fitness for cognitive performance in healthy older adults have repeatedly been demonstrated. Animal studies, however, have revealed differential relationships between physical and motor fitness and brain metabolism. We therefore investigated whether for older humans different dimensions of fitness are differentially associated with cognitive performance and brain activation patterns. Seventy-two participants (mean age 68.99 years, SD = 3.66; 52 females) completed four psychometric tests reflecting two primary abilities of higher cognitive functioning (executive control, perceptual speed) and a battery of fitness tests comprising two fitness dimensions (physical and motor fitness). We found that not only physical fitness indexed by cardiovascular fitness and muscular strength, but also motor fitness including movement speed, balance, motor coordination and flexibility showed a strong association with cognitive functioning. Additionally, functional brain imaging data revealed that physical and motor fitness were differentially related to cognitive processes. Results are discussed with regard to the compensation hypothesis and potential consequences for intervention work.

Introduction

The benefits of high levels of fitness for the preservation and reactivation of cognitive functioning in old age have been repeatedly examined since the 1970s (e.g. Dustman *et al.*, 1994; Etnier *et al.*, 1997; Colcombe & Kramer, 2003; Kramer & Erickson, 2007). For example, cardiovascular fitness has been found to correlate with performance in tests of cognitive flexibility, fluid intelligence or automatic processing (for a review see Dustman *et al.*, 1994). Fitness, however, is a multi-faceted concept that not only includes physical (i.e. cardiovascular fitness and muscular strength) but also motor fitness indexed by components such as flexibility, speed, balance and fine coordination. Accordingly, animal studies have revealed differential relationships of physical and motor fitness with brain metabolism (e.g. Black *et al.*, 1990; Anderson *et al.*, 1994). We therefore investigated whether also for older humans different dimensions of fitness (i.e. physical, motor) were differentially associated with cognitive performance as indexed by executive control and perceptual speed. Moreover, we were interested in whether brain activation patterns were differentially associated with different dimensions of fitness and how these differential patterns were related to cognitive performance.

Cardiovascular fitness, as one aspect of physical fitness, is known to be associated with better executive control processes such as the allocation of attentional resources, elicited conflict evaluation or faster

stimulus encoding (Hillman *et al.*, 2006, 2008). A meta-analysis revealed that this effect was even stronger when cardiovascular fitness was combined with muscular strength (Colcombe & Kramer, 2003). The impact of cardiovascular fitness on perceptual and simple speed tasks, however, was quite small.

To date, little empirical evidence is available about the association between motor fitness and executive control or perceptual speed tasks. Motor fitness requires perceptual and higher-level cognitive processes, such as attention, that are essential for mapping sensation to action and ensuring anticipatory and adaptive aspects of postural control or motor coordination. Thus, motor fitness is probably related to cognitive tasks that demand, besides attention, the ability to handle visual and spatial information (Smith & Baltes, 1999).

In animal studies, neurophysiological activity patterns have also been found to differ between physical and motor fitness (e.g. Black *et al.*, 1990; Anderson *et al.*, 1994). Therefore, in the present study we assumed that both physical and motor fitness would result in more effective use of resources as indicated by less occipital and frontal activations (cf. Colcombe *et al.*, 2004). We also expected that both dimensions of fitness affected cortical areas related to executive control functions such as the anterior cingulate or the middle and inferior frontal gyrus. In particular, however, motor fitness was assumed to be selectively associated with activity patterns in the parietal areas involved in visuo-spatial integration and action initiation.

We analysed the association between physical and motor fitness on the one hand and cognitive functioning on the other using behavioral tests and functional magnetic resonance imaging (fMRI).

Correspondence: Dr C. Voelcker-Rehage, as above.
E-mail: c.voelcker-rehage@jacobs-university.de

Received 18 March 2009, revised 14 September 2009, accepted 6 October 2009

Materials and methods

Participants

Ninety-two older adults were recruited from a member register of a German health insurance company (DAK). Participants were excluded from the study if they had a history of cardiovascular disease, any neurological disorder (e.g. self-report of neurological diseases such as brain tumor, Parkinson's disease, stroke), any other motor or cognitive restriction [a score of less than 27 in the Mini Mental Status Examination (MMSE)] or metal implants. All subjects participated voluntarily in the study and provided written informed consent to the procedures of the study, which was approved by the ethic's committee of the German Psychological Society. The study conforms to the Code of Ethics of the World Medical Association (Declaration of Helsinki). We excluded four participants from data analysis due to incomplete MRI data, and 15 participants due to incomplete motor data. One participant was excluded due to cognitive impairment (MMSE < 27).

The remaining 72 participants had a mean age of 68.99 years (SD = 3.66; range 62–79 years; 52 females) and were tested for normal vision (Freiburg Visual Acuity Test; Bach, 2007) and hearing (simultaneous auditory thresholds at multiple frequencies for both ears; presentation software: Neurobehavioral Systems, Albany, Canada; Yund, 2003).

Cognitive tests

A subset of four experimental cognitive tests from the Berlin Cognitive Battery (Li *et al.*, 2004) was applied reflecting two primary intellectual abilities: executive control and perceptual speed.

Perceptual speed

Perceptual speed was measured by the Identical Picture Test (Ekstrom *et al.*, 1976) and a Visual Search Task (Hommel *et al.*, 2004). The stimuli used in the Visual Search Task were filled and unfilled squares and circles (Hommel *et al.*, 2004). In feature search, participants were asked to search for a filled circle (target) among two, eight or 14 empty circles (distractors). In the conjunction search, participants were asked to search for a filled circle (target) among two, eight or 14 unfilled circles and filled squares (distractors). Each participant performed four blocks of 48 trials each in a randomized order with the possible combinations of three display sizes (two, eight or 14 items), two conditions (target present or absent) and eight target locations (four inner and four outer quadrants, which was relevant in target-present conditions only). Participants indicated the presence of the target by pressing a key (right) as quickly and accurately as possible, and they indicated the absence of a target by pressing the left key. Participants completed one practice block prior to testing to ensure that they understood the directions for the task.

In the Identical Picture Task participants viewed a target figure and decided which of five test figures was identical with it by pointing to the figure. Participants were asked to rate as many figures as possible within 90 s (maximum number of items was 46).

Executive control

As indicators for executive control, response competition was measured by a modified version of the Flanker Task with three response conditions (Li *et al.*, 2004). Working memory was measured by a letter n-Back Task with three difficulties (0-, 1-, 2-back) (Dobbs & Rule, 1989; Voelcker-Rehage *et al.*, 2006). In the Flanker Task, participants were asked to identify a colored target in the center (red or green) surrounded by four distractors by pressing a button. In the

congruent condition, the color of the distractors was the same as the color of the target, whereas in the incongruent condition, the color of the distractors was identical to the color of the stimulus that required the competing response. In the neutral condition, the color of the distractors (blue) differed both from the color of the target and from the color of the stimulus that required the competing response. In the control condition, to separate the pure motor response from executive control processes, white targets with white distractors were used and participants were asked to press any button. Participants underwent eight 30-s blocks of Flanker items presented in randomized order. All items within each test block were of the same type (congruent, incongruent, neutral, control). Participants performed one practice block prior to testing to ensure that they understood the directions for the task. The Flanker Task was performed within the MRI scanner. This task was chosen for fMRI because earlier findings (meta-analysis and empirical studies) reported effects of physical fitness in particular on executive functions (e.g. Colcombe & Kramer, 2003; Colcombe *et al.*, 2004; Hillman *et al.*, 2008).

The n-Back Task required participants to repeat the *n*th item back in a sequentially presented list of items (Dobbs & Rule, 1989; Li & Sikström, 2002). The difficulty of the task is increased when participants are required to remember items further back in the list. In this study the number of intervening letters varied from zero to two. The letters were presented at a rate of about one item every 1.5 s. Participants performed five 30-s trials at each n-back condition (0, 1- and 2-back). Participants were given one to three practice trials prior to testing to ensure that they understood the directions for the task.

Motor tests

Fitness was assessed by using a heterogeneous battery of ten tests representing two fitness dimensions, i.e. physical and motor fitness. Tests of motor fitness comprised shoulder flexibility (Rikli & Jones, 1999) (as an indicator of flexibility), hand tapping (Oja & Tuxworth, 1995), feet tapping (Voelcker-Rehage & Wiertz, 2003) and an agility test (Adrian, 1981) (as indicators of movement speed), a backwards beam walk (Kiphard & Schilling, 1974) and a one-leg-stand with eyes open and closed (Ek Dahl *et al.*, 1989) (as indicators of balance), and the Purdue Pegboard test (Tiffin & Asher, 1948) (as an indicator of fine coordination).

Physical fitness was assessed by measuring grip force (Igbokwe, 1992) (as an indicator of muscular strength) and by spiroergometry (ZAN300, a measurement system of oxygen consumption and for indirect calorimetric assessment) as an indicator of cardiovascular fitness. During spiroergometry participants completed a submaximal graded exercise test (a modified Porszasz protocol; Porszasz *et al.*, 2003) on a Lode Valiant motor-driven treadmill with electrocardiography activity monitored by a ten-lead fully digital stress system (Kiss, GE Healthcare, Munich, Germany). Oxygen uptake volume (VO₂) was measured breath-by-breath and in data analysis the mean VO₂ of the highest complete performance level achieved by the participant was used. The test was terminated due to volitional exhaustion or (at the latest) by reaching a respiratory exchange ratio of 1. Protocols that were terminated because maximum age-predicted heart rate was reached or because other risk factors (e.g. blood pressure above 230/115 mmHg) occurred before volitional fatigue or the respiratory quotient reached 1 were not used for analysis.

Design

Each participant completed the motor and cognitive tests in two individualized laboratory sessions of approximately 2 h each. Both

sessions took place within 1 week. On day 3, participants performed the Flanker Task within the MRI scanner.

Data analysis of behavioral and fMRI data

Behavioral data

Performance of the Flanker (within the MRI scanner) and the Visual Search Tasks were measured by speed (reaction time) and accuracy (percentage of correct answers). In addition, standardized performance indices (IQ-score) were calculated from reaction time and response accuracy as follows (Gualtieri & Johnson, 2008): $\text{IQ-score} = \text{IQ} / \text{mean reaction time (RT)} / \text{IQ of \% of correct responses}$, where IQ (RT) and IQ (% correct) were standardized; they have a mean of 100 and a standard deviation of 15. A lower IQ-score represents faster, more accurate performance on the test.

Performance on the n-Back Task was expressed as the percentage of correctly repeated letters (mean value of each n-back condition) and performance on the Identical Picture Test as the number of correct answers within 90 s. Higher scores indicated better performance.

Group differences in cognitive functioning become more visible in complex than in simple tasks (e.g. Voelcker-Rehage *et al.*, 2006). Thus, for statistical analysis we used the most complex flanker, visual search and n-back conditions, i.e. the performance scores for the incongruent condition of the Flanker Task and the conjunction search condition with 14 distractors of the Visual Search Task. n-back performance was measured as the percentage of correctly repeated letters in the 2-back condition.

A principal components analysis using the Eigenvalue criterion > 1 with oblimin rotation confirmed the two theoretically assumed fitness dimensions, reflecting physical fitness (strength and cardiovascular fitness) and motor fitness (flexibility, movement speed, balance and fine coordination). These two factors explained 60.01% of the variance. All items had their highest loadings (between 0.52 and 0.88) on the factor predicted on theoretical grounds.

Neuroimaging protocol

Differences in brain processing during the Flanker Task as a function of participants' fitness were measured using blood oxygenation level-dependent (BOLD) MRI at a 3-T MRI scanner. The Flanker Task was performed in randomized block design as described above [two blocks per condition, 30 s per block, alternating task conditions (congruent, incongruent, neutral, control) with a 30-s fixation task as baseline condition]. For functional scans, we employed a T2-weighted fast echo-planar imaging (EPI) sequence (TR = 2560 ms, TE = 58 ms, 200 volumes per run with 44 slices per volume, in plane resolution $3 \times 3 \text{ mm}^2$, slice thickness 3 mm). Functional runs (one run per subject) were co-registered to a high-resolution T1-weighted anatomical scan (MPRAGE sequence, $1 \times 1 \times 1 \text{ mm}^3$ isotropic resolution, TR = 2300 ms, 160 slices). Using Brain Voyager (Brain Innovation B.V., Maastricht, the Netherlands), fMRI data were corrected for motion artifacts and linear trends, smoothed in the temporal (2.8 s) and spatial (6 mm) domain, and normalized to Talairach space.

Statistical analyses of behavioral and fMRI data

Behavioral data

In a first analytical step, we investigated the effect of the two fitness dimensions and their interaction on cognitive functioning. Communality analysis was used to identify which fitness dimension or which interaction was mainly responsible for the relationship between fitness

and cognitive performance. Results were controlled for age, sex, education, subjective health and estrogen replacement therapy. Second, to follow up on the significant interactions between motor and physical fitness, univariate analyses of variance were used to test for differences between high and low motor and physically fit participants. Therefore, participants were divided into four groups; participants with low motor and low physical fitness (M-P-), high motor and low physical fitness (M+P-), low motor and high physical fitness (M-P+), and high motor and high physical fitness (M+P+). Analyses were conducted separately for the four cognitive tests. *Post-hoc* least-significant difference (LSD) tests were used to determine effects between the single groups.

fMRI data

In a first analysis, conducted separately for physical and motor fitness, participants were divided into two groups – low-fit and high-fit – based on the median split of the respective fitness index. No significant interactions between different flanker conditions and fitness groups were found. Thus, for testing the hypotheses of the present study, data collected in the neutral, congruent and incongruent conditions were pooled to create a more reliable performance estimate.

Statistical analysis was performed using GLM and second level ANOVA of the resulting beta-values. Separately for both fitness dimensions, effects of the Flanker Task and fitness status were analysed using random effects ANOVA with one within factor [task: Flanker Task (all three conditions) vs. fixation] and one between factor (fitness status: high vs. low fitness level). For between-group contrasts *P*-values were corrected for multiple comparisons by false discovery rate (FDR, $P < 0.05$) and cluster threshold estimation ($k > 80$) (Forman *et al.*, 1995; Goebel *et al.*, 2006). Clusters surviving these thresholds were defined as regions of interest (ROIs) and anatomically identified by the Talairach coordinates of their activation peaks.

In the second analytical step, we tested for differences in activation strength between the fitness groups for the incongruent condition vs. fixation for those ROIs which have been previously identified to be dependent on fitness status. For this, we extracted for each individual the beta estimates for the incongruent condition and forwarded them to a multivariate ANOVA with two fixed factors (the two fitness dimensions with levels high and low).

Subsequently, more detailed analyses were conducted for those ROIs which revealed significant effects for fitness dimension or significant interaction effects for the incongruent condition. By analogy to the behavioral analysis, an ANOVA with four fitness groups (M-P-, M+P-, M-P+, M+P+) as fixed factors was calculated. For significant group effects, *post-hoc* LSD tests were performed.

Results

Behavioral data

To investigate the relative contribution of physical and motor fitness as well as their potential interaction, four multiple regression analyses with the two main effects (physical fitness, motor fitness) and their interaction predicting performance on each of the four cognitive tasks in turn were conducted. The entry of the cross-product physical \times motor fitness contributed significantly only to predicting performance in the Flanker and the Visual Search Task.

For the Flanker Task, communality analysis revealed that 44.7% of the total variance was explained, of which physical fitness uniquely explained 6.0%, motor fitness 14.8% and the significant interaction covered 8.0% unique variance (shared variance = 15.9%; $F_{3,68} = 18.30$, $P < 0.001$). For the n-Back Task, the total variance

explained (18.6%) was composed of physical fitness (5.9% unique variance) and motor fitness (10.8% unique variance) (shared variance = 2.1%; controlled for sex; $F_{3,67} = 6.95$, $P < 0.001$). Thus, again both physical and motor fitness contributed significantly to the prediction.

In contrast, for both perceptual speed tests only indicators of motor fitness had significant predictive power (for standardized beta values cf. Table 1). For the Visual Search Task, motor fitness uniquely explained 12.5% (controlled for education; $F_{3,66} = 3.59$, $P = 0.018$) and for the Identical Picture Task 20.4% (controlled for education; $F_{3,66} = 7.12$, $P < 0.001$). In addition, for the Visual Search Task the interaction between physical and motor fitness was significant and uniquely explained 5.8% of the total variance (19.8%; shared variance 1.4%, controlled for education; $F_{4,65} = 4.01$, $P = 0.006$). [Note. When analysed separately for speed and accuracy, results remained unchanged. In the Flanker Task physical and motor fitness explained 14% and 31% of the total variance for speed and accuracy, respectively. For the Visual Search Task only motor fitness was a significant predictor. This was true for both speed (11%) and accuracy (6%).]

Figure 1 illustrates these results by plotting the mean performance in the four cognitive tests split by fitness level. Reflecting the potential interaction between physical and motor fitness, participants were divided into four fitness groups as described above (M–P–, M+P–, M–P+, M+P+). Figure 1 shows that performance on the Flanker and n-Back Tasks were both influenced by the levels of physical and motor fitness. Performance in the Identical Picture Test, however, was solely influenced by motor fitness. Results for the Visual Search Task were somewhat inconsistent. Neither the sole influence of motor fitness nor the effect of the cross product motor \times physical fitness could be clearly shown (cf. Fig. 1c).

Univariate analyses of variance, with fitness group as independent variable, confirmed a significant group effect for the executive control tasks (Flanker Task: $F_{3,68} = 6.08$, $P = 0.001$, $\eta^2 = 0.212$, n-Back Task: $F_{3,67} = 2.42$, $P = 0.074$, $\eta^2 = 0.098$) and for one of the perceptual speed tasks (Identical Picture Task: $F_{3,68} = 3.48$, $P = 0.021$, $\eta^2 = 0.133$). This was not the case for the Visual Search Task ($F_{3,68} = 1.33$, $P = 0.271$). *Post-hoc* LSD tests for the Flanker Task revealed significant group differences between M–P– participants and the three other groups (all $P < 0.01$). The same was true for the n-Back Task ($P < 0.10$), confirming the importance of fitness for cognitive functioning in the area of executive control. For the Identical Picture Task, performance of the low-fit group (M–P–) differed from that of the M+P– and M+P+ groups ($P < 0.050$). Furthermore, the M+P– group showed higher performance as compared with the M–P+ group ($P < 0.010$) (cf. Fig. 1d). These results stress the role of motor fitness for performance in the

TABLE 1. Summary of multiple regression analyses predicting performance in four cognitive tasks based on levels of physical and motor fitness, and the physical \times motor fitness interaction (P \times M)

	Flanker		n-Back		Visual search		Identical pictures	
	B	β	B	β	B	β	B	β
Physical	–0.10	–0.27**	2.41	0.47*	–0.02	–0.04	–0.53	–0.10
Motor	–0.22	–0.40***	2.73	0.35**	–0.31	–0.37**	3.33	0.42***
P \times M	0.19	0.32**	–0.06	–0.01	–0.25	–0.28*	–1.26	–0.15

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. B and β : understanderized and standardized regression coefficients, respectively. For the Flanker and Visual Search Task, lower values represent faster, more accurate performance (indicated by negative B and β values).

Identical Picture Task. Together, these results confirmed that physical fitness was mainly related to executive control tasks, whereas motor fitness showed a significant association with both the executive control and the perceptual speed tasks.

Neuroimaging data

Generally, task-related activations (Flanker Task vs. fixation, regardless of task condition) were found bilaterally in the mediofrontal gyrus (Brodmann Areas BA 9, 46), superior frontal gyrus (BA 6), inferior frontal gyrus (BA 44), pre- and postcentral gyrus (BA 4, 1, 2, 3a, 3b), supramarginal gyrus (BA 40), superior parietal gyrus (BA 5, 7), anterior cingulate gyrus (BA 24, 32), anterior insula (BA 13), cerebellum and thalamus ($F_{4,280} > 8.71$, $P < 0.05$, Bonferroni corrected; data not shown).

Using median splits we then defined groups of low- and high-fit participants independently for physical and motor fitness and created brain activation maps contrasting high- vs. low-fit participants for these two fitness dimensions (cf. Fig. 2). As expected, for both fitness dimensions high-fit participants demonstrated less activation in the superior and middle frontal gyrus (BA 6, 8; left BA 9, 46), the superior temporal gyrus (BA 39) and the occipital cortex (Cuneus, BA 18), indicating less effort in cognitive control and visual perception (cf. Fig. 2 and Supporting information, Table S1). In addition, there were separate effects for physical fitness and motor fitness on brain activation, as well as regions with opposite effects of these fitness dimensions. Areas affected only by physical fitness were the left middle temporal gyrus (BA 21/22) and the left parahippocampal gyrus (BA 34), which both revealed higher activations for physically fit participants. Less activation compared with low-fit participants was found in the right supramarginal gyrus (BA 40). In the motor fitness dimension, high-fit compared with low-fit participants showed reduced activity in the precentral gyrus (BA 4, right), the right precuneus (BA 31), the right superior temporal gyrus (BA 41), the left supra marginal gyrus (BA 40) and the left anterior cingulate (BA 32). Stronger activation for high- vs. low motor-fit participants was found in the parietal cortex (BA 7, bilaterally). Differential effects of physical and motor fitness were found in the superior, middle and inferior frontal gyrus (BA 10, right BA 46 and 47) and the right middle temporal gyrus (BA 21/22). All areas revealed increased activation for the physically high-fit but decreased activation for the motor high-fit participants. In contrast, in the left supramarginal gyrus (BA 40) activation strength was higher for high vs. low motor-fit participants with the opposite effect for physical fitness.

In a next step we further inspected these ROIs to identify those regions which were particularly affected by fitness status during processing of the incongruent condition. Extracted beta estimates from all ROIs (peak voxel) for the incongruent conditions were forwarded to a multivariate ANOVA with two fixed factors (the two fitness dimensions with levels high and low). As summarized in Table 2, the left superior (BA 9) and middle (BA 46) frontal gyrus, in particular, revealed less activation in high- vs. low-fit participants for both fitness dimensions. Areas affected by only physical fitness were the right premotor cortex (BA 6) with reduced activation and the right middle temporal gyrus (BA 21/22) with increased activation for high-fit participants. Specific effects of motor fitness were found for the left and right parietal cortex (BA 7, increased activation) and the right superior temporal gyrus (BA 41, decreased activation for high-fit subjects). Interaction effects of physical and motor fitness were found in the precentral gyrus (left premotor cortex, BA 6, and right motor cortex, BA 4) and the left anterior cingulate cortex (BA 32).

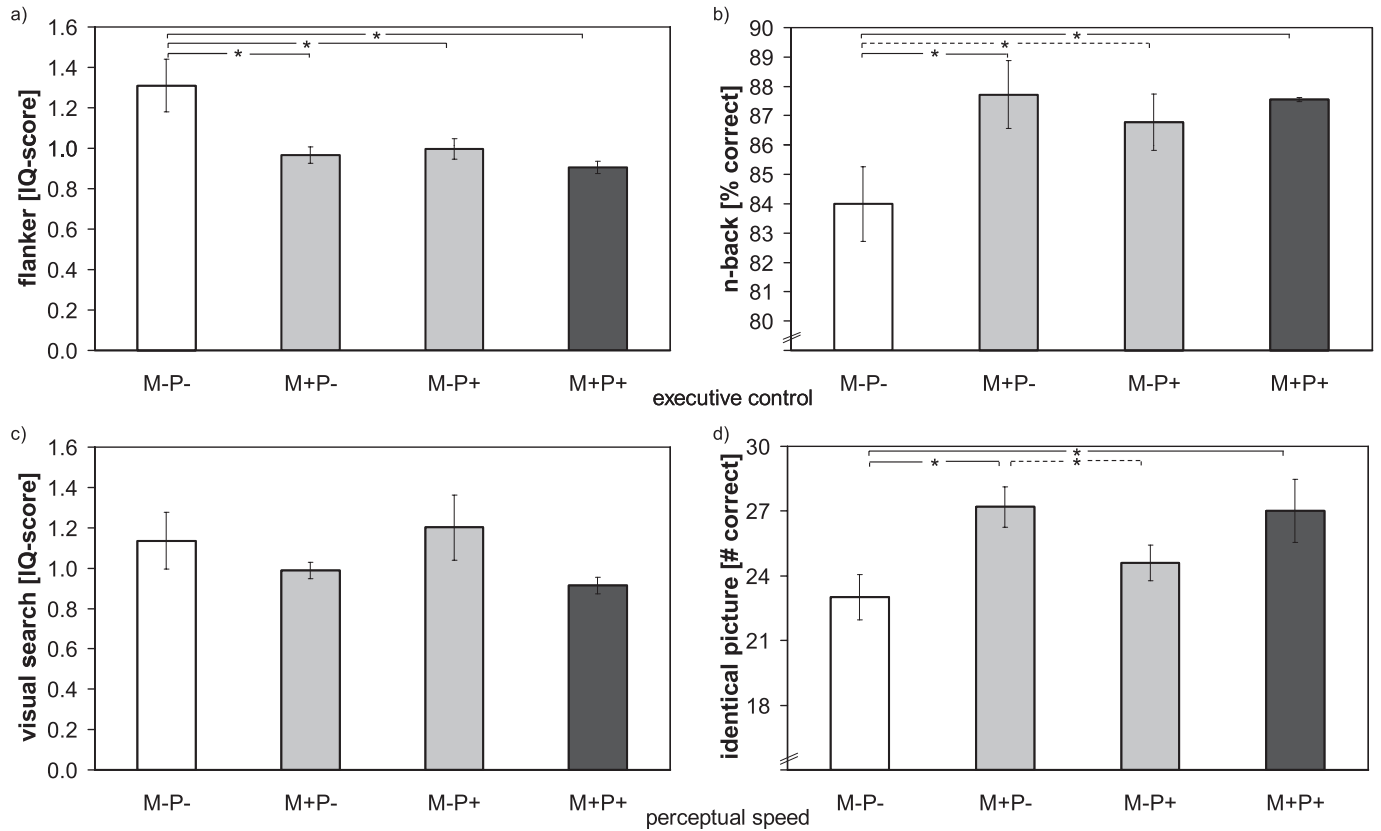


FIG. 1. Performance (mean and SE) for the four cognitive tests, split by fitness status: low motor and low physical fitness (M-P-), high motor and low physical fitness (M+P-), low motor and high physical fitness (M-P+), and high motor and high physical fitness (M+P+). (a) Results of the Flanker Task, (b) results of the n-Back Task, (c) results of the Visual Search Task, and (d) results of the Identical Picture Task. *Filled (dotted) lines with asterisks indicate (marginally) significant group differences with $P < 0.05$ ($P < 0.1$), *post-hoc* LSD test. Note: for the flanker and visual search tasks a lower performance index represents faster, more accurate performance on the tests.

To follow up and illustrate the identified main and interaction effects, in analogy to the behavioral analysis, participants were divided into four fitness groups (M-P-, M-P+, M+P-, M+P+). Figure 3 illustrates the effect of the different fitness levels on activation in the specified ROIs (cf. Table 2) during the incongruent condition. Shown are the mean beta estimates for the four groups of participants: (a) with a low fitness level on both dimensions (M-P-), (b) with high motor but low physical fitness (M+P-), (c) with low motor but high physical fitness (M-P+) and (d) with high levels in both dimensions (M+P+). In particular in the left frontal cortical areas M+P+ is associated with the lowest activation levels (BA 9, BA 6, BA 46) even though high fitness in one dimension (M+P- or M-P+) can have similar but less pronounced effects in BA 9 and 46, whereas M-P+ has a similar effect in BA 6. Similarly, reduced activation is found for the M+P+ and M+P- groups in the motor cortex (BA 4). Significantly reduced activation in the left anterior cingulate cortex (BA 32), indicative of less effort exerted in the inhibition of distracting information, however, requires high fitness levels on both dimensions. In contrast, the right middle temporal cortex (BA 21/22) shows a different pattern. In this region high physically-fit participants show strongly enhanced activation during the incongruent condition but only if accompanied by low motor fitness (M-P+). If motor fitness is high, this effect disappeared, revealing that physical and motor fitness might impact not only similar cortical areas but also competing cortical networks. The finding that the parietal cortex (BA 7) is particularly activated in high motor- but not physically-fit participants (M+P- and M+P+; cf. Table 2) supports this view.

Discussion

Both behavioral and imaging data revealed differential associations between physical and motor fitness and cognitive performance as well as related brain processes. On the behavioral level, as hypothesized, physical fitness was mainly related to executive control processes (measured with the Flanker and n-Back Task), whereas motor fitness showed a significant association with both the executive control and the perceptual speed tasks (measured with the Identical Picture and Visual Search Task). Thus, together, our behavioral results support the idea that fitness is differentially associated with indicators of fluid intelligence (Elsayed *et al.*, 1980; Dustman *et al.*, 1994) such as perceptual speed and executive control (Lindenberger & Baltes, 1997).

Until now, studies that investigated the correlation between physical fitness and human brain functions have focussed on one facet of physical fitness, namely cardiovascular fitness (Colcombe *et al.*, 2004). These authors found that high aerobically fit individuals showed a reduced distraction effect in cognitive performance and a pattern of fMRI activation similar to that displayed by younger controls while working on a Flanker Task. Similarly, Hillman *et al.* (2006) showed in a cross-sectional study with participants aged 15–71 years that physical activity (sweat index) was associated with faster reaction times in the congruent and incongruent conditions of a Flanker Task and that, particularly in older adults, more physical activity was also associated with higher accuracy during the incongruent condition of this task. Our results confirmed these earlier results, supporting the association of physical fitness with executive

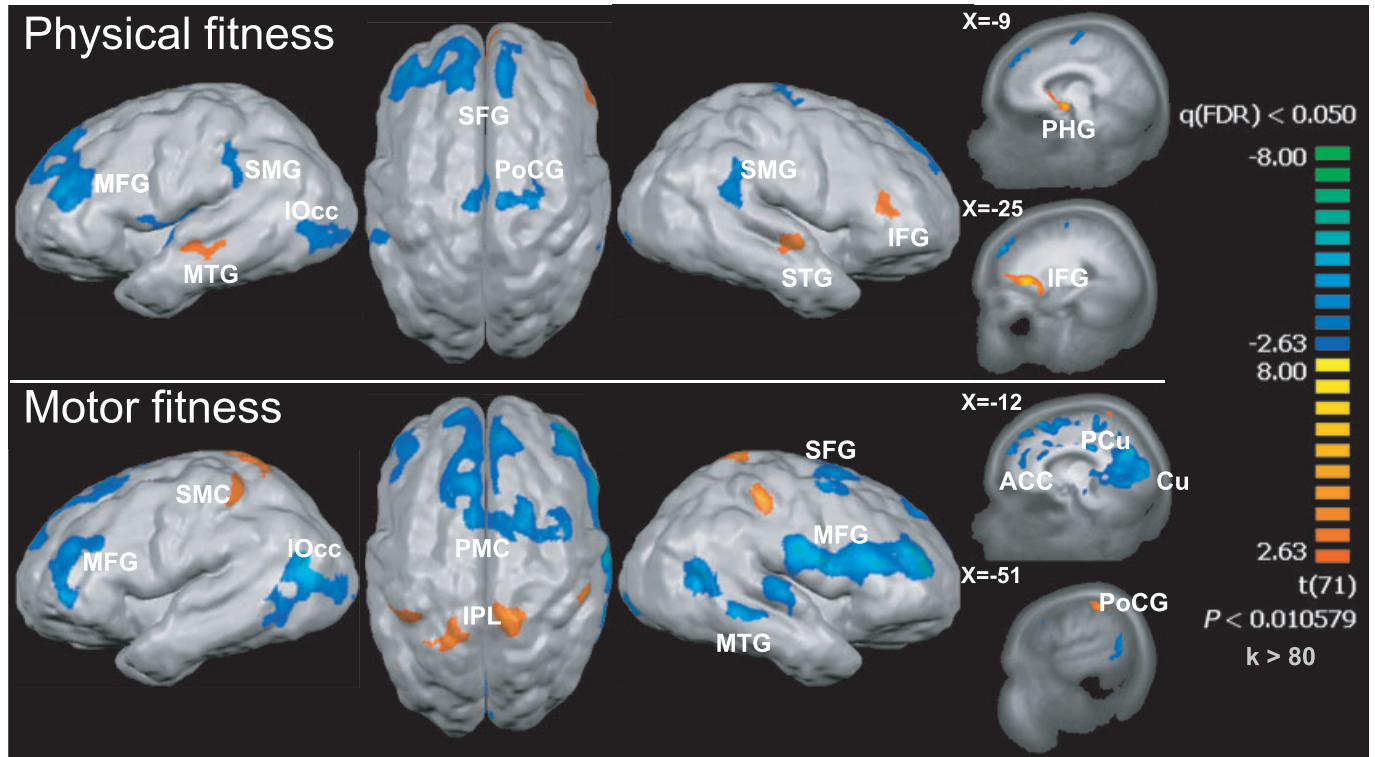


FIG. 2. Effect of fitness status on activation strength during the Flanker Task (relative to fixation). *t*-values for the contrasts high fit > low fit are overlaid onto the average cortical surface separately for physical fitness (upper panel) and motor fitness (lower panel). Positive *t*-values (orange to yellow) indicate higher activation for high-fit participants, negative *t*-values (blue to green) indicate higher activation for low-fit participants. STG; superior temporal gyrus; MTG, middle temporal gyrus; SFG, superior frontal gyrus; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; PoCG, postcentral gyrus; SMG, supramarginal gyrus; PMC, premotor cortex; IPL, inferior parietal lobe; IOcc, lateral occipital lobe; PHG, parahippocampal gyrus; PCu, precuneus; Cu, cuneus; ACC, anterior cingulate cortex.

TABLE 2. Regions of interest with a significant effect of fitness level on activation during the incongruent condition of the Flanker Task relative to fixation

	L/R	Talairach coordinates			Effect	F(P)	F(M)	F(M × P)
		x	y	z				
Similar effects for both types of fitness								
Superior frontal gyrus (BA9)	L	-27	53	34	M↓,P↓	4.703*	4.334*	0.023
Middle frontal gyrus (BA46)	L	-42	47	23	M↓,P↓	4.040*	5.564*	0.763
Effects for physical fitness only								
Precentral gyrus (BA6)	R	12	-16	67	P↓	5.217*	0.031	1.034
Middle temporal gyrus (BA21/22)	R	57	-10	-5	P↑	4.467*	0.339	1.463
Effects for motor fitness only								
Postcentral gyrus (BA7)	L	-17	-49	69	M↑	0.852	4.702*	0.016
Postcentral gyrus (BA7)	R	12	-47	70	M↑	0.133	3.729*	0.048
Superior temporal gyrus (BA41)	R	57	-19	7	M↓	0.078	6.383*	2.119
Opposed effects for physical and motor fitness								
Precentral gyrus (BA6)	L	-2	-7	58	M × P	10.53**	0.152	5.493*
Precentral gyrus (BA4)	R	57	-7	25	M × P	0.886	4.937*	2.904 ⁺
Anterior cingulate cortex (BA32)	L	-5	20	25	M × P	1.524	3.768 ⁺	3.599 ⁺

Given are Talairach coordinates for the cluster peaks and maximal *F*-values for physical (P) and motor (M) fitness as well as for the interaction between physical and motor fitness (M × P). The effect of high relative to low fitness levels on activation strength is indicated with M↑/↓ (P↑/↓), i.e. higher/lower activation for motor (physical)-fit participants during the incongruent condition. L/R, left/right hemisphere. M × P indicates interaction effect. Asterisks indicate significant effects: **P* < 0.05, ***P* < 0.01, ⁺*P* < 0.1, marginally significant effect.

functioning and brain aging. Moving beyond this, however, we were also able to show that motor fitness seems to play a pivotal role for cognition and brain functioning in old age, and that physical and motor fitness differentially relate to cognitive processes.

These associations between cognitive functioning and motor fitness are very much in line with earlier work on the association of sensory (including proprioception) and cognitive functioning in old age (e.g. Lindenberger *et al.*, 2000). Furthermore, our findings are in line with

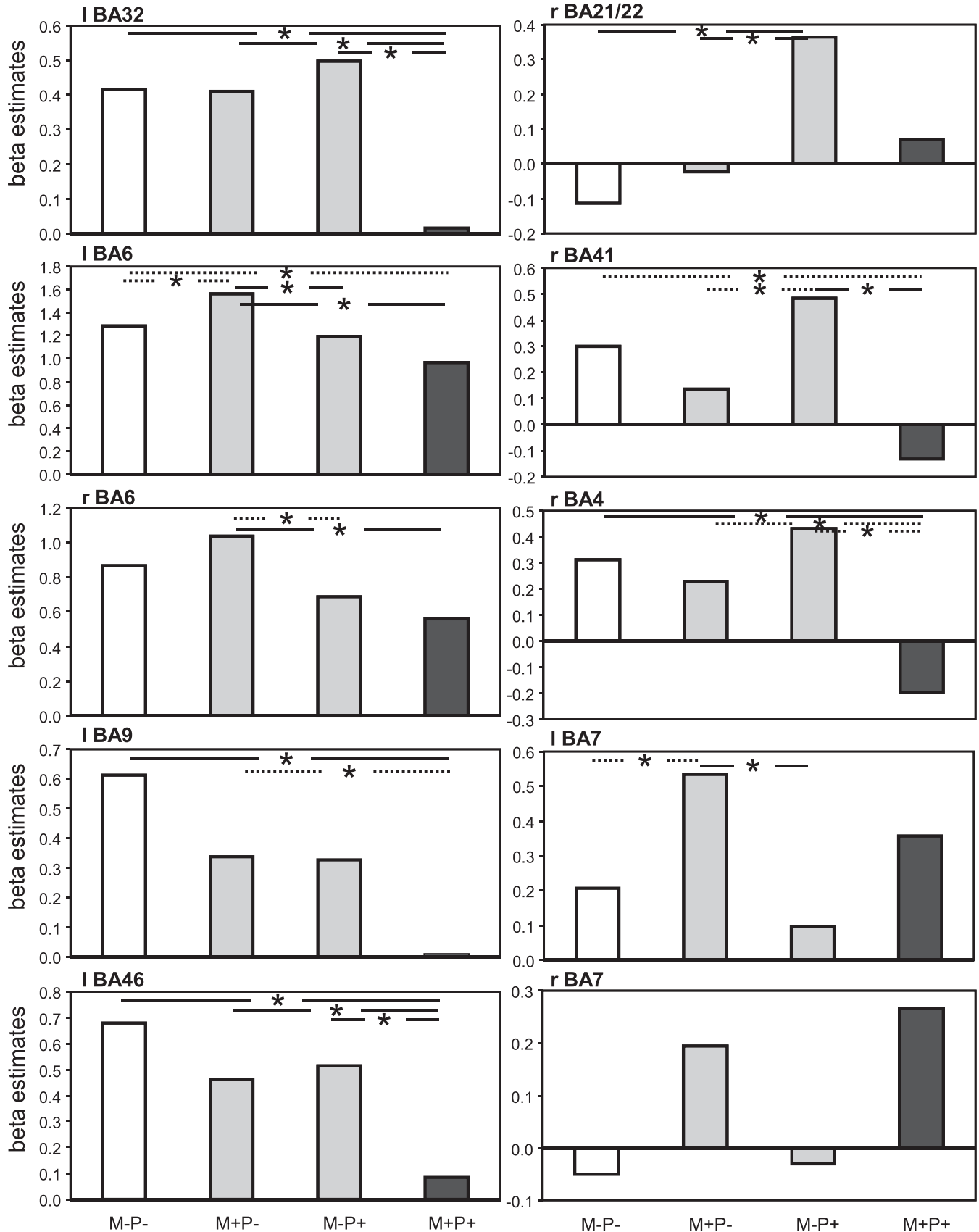


FIG. 3. Effect of fitness status on activation strength (beta estimates) during the incongruent condition (relative to fixation) for selected regions of interest split by fitness status: low motor and low physical fitness (M-P-), high motor and low physical fitness (M+P-), low motor and high physical fitness (M-P+), and high motor and high physical fitness (M+P+). *Filled (dotted lines) with asterisks indicate (marginally) significant group differences with $P < 0.05$ ($P < 0.1$).

earlier studies with adolescents. In one study, for instance, motor coordination and motor speed, in particular, revealed the strongest associations with cognitive performance (Planinsec, 2002). Also, first intervention studies showed that a 6-week bimanual coordination program improved the reading comprehension skills in grade 5 students compared with controls (Uhrich & Swalm, 2007), and that 10 min of acute coordinative exercise improved subsequent cognitive performance in adolescents (Budde *et al.*, 2008).

When turning to earlier neuroimaging work, Casey *et al.* (2000) have found four distinct neural subsystems being differentially involved in the performance of the Flanker Task. The anterior system, involving the anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (DLPFC), a selective attention system involving the right superior frontal gyrus (BA 8), superior parietal cortex (BA 7) and portions of the right cerebellum, a system including the caudate nucleus and insula (sensitivity to violations of expectancies or sudden changes), and finally a system involving inferior parietal (BA 40) and temporal regions (BA 41/42) (decreased activation during incompatible trials). The anterior system and the selective attention system have been shown to be affected by physical fitness (Colcombe *et al.*, 2004). Less activity in the anterior cingulate was accompanied by higher activation in the right superior and middle frontal cortex.

We confirmed here activation in most of these areas, i.e. in ACC and DLPFC, the superior frontal and parietal cortex as well as in the inferior parietal and the temporal cortex. Also, the present study extended and differentiated these findings by focusing on activation patterns depending on the level of motor and physical fitness. And indeed, we found different activation patterns with regard to the four fitness groups. Whereas some areas were activated in both the highly physical- and motor-fit groups, respectively, other areas were only activated for either the highly physical- or motor-fit groups (cf. Table 2).

Our imaging data for the Flanker Task indicated that independent of the fitness dimension, high-fit participants needed less resources for visual processing (less occipital activation) and cognitive control (reduced activations in several superior and middle frontal areas such as BA 6, 8, 9 and 46), possibly related to the availability of more resources for executive-control processes. Recent aging research has revealed stronger and more widespread and bilateral frontal activations in old as compared with young adults indicative of compensatory processes during aging (for reviews, cf. Greenwood, 2007 or Reuter-Lorenz & Cappell, 2008). Our data suggest that both types of fitness have positive effects on brain processing during the cognitive task so that less compensation seems to be necessary.

However, our data also indicate that this less widespread frontal activation in high-fit participants is associated with positive fitness effects on different cortical networks: physically fit persons (as compared with low-fit individuals) revealed higher levels of activation in very specific regions involved in executive functions and processing (BA 10, 21/22, 46, 47). Specifically, high physical fitness was positively related to activation of the right inferior frontal gyrus and the superior temporal gyrus. The former has been shown to be important for interference control during the Flanker Task (Colcombe *et al.*, 2004) whereas the latter is essentially involved in visuo-spatial awareness as indicated by lesion studies (Karnath *et al.*, 2001). Furthermore, physical fitness was accompanied by higher activation in the parahippocampal and middle and superior temporal gyrus and lower activation in the supramarginal gyrus (BA 40). Physical fitness probably counteracts aging effects in the frontal and temporal areas resulting in the activation of this network at the expense of sensorimotor cortical areas.

Contrasting results were found for the high motor-fit groups with lower activation in BA 10, 21/22, 46 and 47. Motor fitness requires perceptual and higher-level cognitive processes, such as attention, that are essential for mapping sensation to action and ensuring anticipatory and adaptive aspects of postural control or motor coordination. We assumed that motor fitness, in particular, influenced activity patterns in the fronto-parietal network involved in visuo-spatial integration and action initiation. This was confirmed by stronger activations in parietal areas involved in visuo-motor coordination and visuo-spatial processing (i.e. BA 7, 31 and 40) in motor-fit participants. Thus, high motor fitness seems to be associated with the exertion of less effort to inhibit distracting information, more automated motor responses, and more effective processing and integration of visuo-spatial information. This was also indicated by less activation in the left ACC (BA 32) as found for high vs. low motor-fit participants. Interaction effects between both fitness dimensions in the left prefrontal cortex (BA6) and the right temporal gyrus (BA21/22) provide further evidence that physical and motor fitness might have impact not only on similar cortical areas but also on competing cortical networks. An active fronto-parietal network for visuo-spatial integration and action initiation as found for high motor-fit individuals seems to attenuate the facilitative effect of high physical fitness on temporal brain regions. With less motor fitness, however, the right temporal cortex (BA21/22) gains increasing importance for visuo-spatial awareness in physically fit participants. The finding that the parietal cortex (BA 7) as part of the fronto-parietal network is particularly activated in high motor but not physically fit participants supports this view.

Experimental and clinical evidence has also pointed to the importance of the frontal lobes, especially the prefrontal areas, for the mediation of motor coordination (a part of motor fitness) (Hernandez *et al.*, 2002) on the one hand and cognitive functions such as executive control (Miller & Cohen, 2001) on the other hand. A higher level of motor fitness seems to provide for more functional networks related to executive- and visual-spatial processing, which in turn seem to be associated with improved performance in the Flanker Task.

Reduced activity in the ACC has also been found in earlier studies (e.g. Colcombe *et al.*, 2004; and cf. Hillman *et al.*, 2008, for a review) and has been interpreted as an increased ability of the frontal attentional network to bias task-relevant activation in the posterior cortex. In these studies the reduced activity was associated with higher physical fitness, whereas in our study this effect was found to be mainly related to higher motor fitness and significant reduction of ACC activation in the incongruent condition required high fitness levels in both fitness dimensions. As the level of motor fitness was neither assessed nor controlled in the earlier studies, the two findings cannot easily be related to each other. Thus, in future studies, it may be useful always to assess both types of fitness.

The differential relationship of physical and motor fitness with cognitive processes as shown by our fMRI data are interpreted such that different brain processes are facilitated by different types of fitness. Animal experiments have shown that rats regularly running on a treadmill (cardiovascular training) had an increase in the density of capillaries (Black *et al.*, 1990) and shorter diffusion distance from blood vessels in the molecular layer of the paramedian lobule (Isaacs *et al.*, 1992) without an increase in the synaptic numbers. Rats that participated in motor-skill learning tasks (e.g. traverse an elevated obstacle course requiring substantial motor coordination to complete; comparable with motor fitness), however, showed a greater number of synapses per neuron without an increase in the density of capillaries. Rats that were taught complex motor skills substantially increased the volume of the molecular layer per

Purkinje neuron and sufficiently increased the number of blood vessels to maintain the diffusion distance. Furthermore, they had significantly more parallel fiber to Purkinje cell synapses than walking and inactive animals (e.g. Isaacs *et al.*, 1992; Kleim *et al.*, 1998). This evidence from the animal model seems to suggest that different types of fitness cause different anatomical and probably functional changes and thus are very much in line with the findings of the present study.

In summary, our data indicate that physical fitness and also motor fitness such as movement speed, balance, fine coordination and flexibility are positively and differentially associated with cognitive performance and brain activation patterns. Activation patterns associated with motor and physical fitness seem to point to a very close connection as well as interdependency between different cortical networks. It seems that for higher levels of cognitive performance high as compared with low physically fit older adults more specifically and focally activate areas related to executive control and that highly motor-fit as compared with lowly motor-fit participants more strongly activate areas involved in visuo-spatial processing. Both strategies seem to result in more efficient use of the available resources. Increased frontal activation is often interpreted as a compensatory mechanism necessary to overcome age-related changes. For both dimensions of fitness, the improved recruitment of task-specific areas accompanies less compensatory over-activation, for instance, in superior and middle frontal areas (Reuter-Lorenz & Cappell, 2008). Such reduced activity together with better performance might point to the fact that fewer resources are necessary to perform the task, i.e. the brains of the fit participants might look younger.

One limitation of our cross-sectional study is the inability to distinguish independent effects of learning on brain structure from diverse environmental and/or genetic influences (Draganski & May, 2007). A further limitation is that only one task was performed within the MRI machine. We used an inhibitory task (Flanker Task) as our main behavioral outcome measure because deterioration in inhibitory processes is thought to play a central role in age-related losses in many cognitive functions. Age-related declines in inhibition are implicated in declines in memory (e.g. Hasher & Zacks, 1988), task shifting (Kramer *et al.*, 1999; Kray *et al.*, 2002) and increased semantic interference (Panek *et al.*, 1984). Inhibitory processes are also largely thought to be instantiated in the prefrontal cortices, which, in light of their disproportionate deterioration in aged individuals, have figured prominently in research on cognitive aging and its interactions with physical fitness (e.g. Kramer *et al.*, 1994).

It has been shown that the so-called incongruency effect is much stronger when incongruent trials follow congruent trials ('Gratton effect', Gratton *et al.*, 1992). This, however, would require an event-related design. We used a block design instead to provide, first, enough statistical power to compare brain activation during the Flanker Task to rest and, second, to protect our older participants from long scanning sessions. The missing Gratton effect might be a reason why we found only weak effects for the incongruent as compared with the congruent or neutral condition in our study.

Nevertheless, our study for the first time confirmed that physical and also motor fitness are related to cognitive functioning in older adults – on a behavioral and on a neurophysiological level. Thus, a one-sided focus on the association between cardiovascular fitness and cognition as frequently observed in the literature might run the risk of neglecting important interacting effects on healthy cognitive aging. As a next step, a longitudinal study is needed to test the specific cognitive and neurophysiological effects of a motor-fitness training program as compared with a classical cardiovascular training.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Regions of interest with a significant effect of fitness level on activation during the Flanker Task relative to fixation.

Please note: As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset by Wiley-Blackwell. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Acknowledgements

This study was supported by the Robert Bosch Foundation (12.5.1366.0005.0) and the German health insurance company DAK.

Abbreviations

(f)MRI, (functional) magnetic resonance imaging; ACC, anterior cingulate cortex; BA, Brodmann Area; BOLD, blood oxygenation level dependent; DLPFC, dorsolateral prefrontal cortex; EPI, echoplanar imaging; FDR, false discovery rate; GLM, general linear model; LSD, least square difference; MMSE, mini mental status examination; ROI, region of interest; T1/T2, longitudinal/transverse relaxation; TE, echo time; TR, repetition time; VO2, oxygen uptake volume.

References

- Adrian, M.J. (1981) Flexibility in the aging adult. In Smith, E.L. & Serfass, R.C. (eds), *Exercises and Aging: The Scientific Basis*. Enslow Publishers, Hillside, NJ, pp. 45–58.
- Anderson, B.J., Alcantara, A.A., Isaacs, K.R., Black, J.E. & Greenough, W.T. (1994) Glial hypertrophy is associated with synaptogenesis following motor-skill learning, but not with angiogenesis following exercise. *Glia*, **11**, 73–80.
- Bach, M. (2007) The Freiburg visual acuity test – variability unchanged by post-hoc re-analysis. *Graefes Arch. Clin. Exp. Ophthalmol.*, **245**, 965–971.
- Black, J.E., Isaacs, K.R., Anderson, B.J., Alcantara, A.A. & Greenough, W.T. (1990) Learning causes synaptogenesis, whereas motor activity causes angiogenesis, in cerebellar cortex of adult rats. *Proc. Natl Acad. Sci. USA*, **87**, 5568–5572.
- Budde, H., Voelcker-Rehage, C., Pietrassyk-Kendziorra, S., Ribeiro, P. & Tidow, G. (2008) Acute coordinative exercise improves attentional performance in adolescents. *Neurosci. Lett.*, **441**, 219–223.
- Casey, B.J., Thomas, K.M., Welsh, T.F., Badgaiyan, R.D., Eccard, C.H., Jennings, J.R. & Crone, E.A. (2000) Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proc. Natl Acad. Sci. USA*, **97**, 8728–8733.
- Colcombe, S.J. & Kramer, A.F. (2003) Fitness effects on the cognitive function of older adults: a meta-analytic study. *Psychol. Sci.*, **14**, 125–130.
- Colcombe, S.J., Kramer, A.F., Erickson, K.I., Scaif, P., McAuley, E., Cohen, N.J., Webb, A., Jerome, G.J., Marquez, D.X. & Elavsky, S. (2004) Cardiovascular fitness, cortical plasticity, and aging. *Proc. Natl Acad. Sci. USA*, **101**, 3316–3321.
- Dobbs, A.R. & Rule, B.G. (1989) Adult age differences in working memory. *Psychol. Aging*, **4**, 500–503.
- Draganski, B. & May, A. (2007) Training-induced structural changes in the adult human brain. *Behav. Brain Res.*, **192**, 137–142.
- Dustman, R.E., Emmerson, R. & Shearer, D. (1994) Physical activity, age, and cognitive-neurophysiological function. *J. Aging Phys. Act.*, **2**, 143–181.
- Ekdahl, C., Jarnlo, G.B. & Andersson, S.I. (1989) Standing balance in healthy subjects. *Scand. J. Rehabil. Med.*, **21**, 187–195.
- Ekstrom, R.B., French, J.W., Harman, H. & Derman, D. (1976) *Kit of Factor-Referenced Cognitive Tests*. Educational Testing Service (rev. ed.), Princeton, NJ.
- Elsayed, M., Ismail, A.H. & Young, R.J. (1980) Intellectual differences of adult men related to age and physical fitness before and after an exercise program. *J. Gerontol.*, **35**, 383–387.

- Etnier, J.L., Salazar, W., Landers, D.M., Petruzzello, S.J., Han, M. & Nowell, P. (1997) The influence of physical fitness and exercise upon cognitive functioning: a meta-analysis. *J. Sport Exerc. Psychol.*, **19**, 249–277.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A. & Noll, D.C. (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn. Reson. Med.*, **33**, 636–647.
- Goebel, R., Esposito, F. & Formisano, E. (2006) Analysis of functional image analysis contest (FIAC) data with Brainvoyager QX: from single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. *Hum. Brain Mapp.*, **27**, 392–401.
- Gratton, G., Coles, M.G. & Donchin, E. (1992) Optimizing the use of information – strategic control of activation of responses. *J. Exp. Psychol. Gen.*, **121**, 480–506.
- Greenwood, P.M. (2007) Functional plasticity in cognitive aging: review and hypothesis. *Neuropsychology*, **21**, 657–673.
- Gualtieri, C.T. & Johnson, L.G. (2008) A computerized test battery sensitive to mild and severe brain injury. *Medscape J. Med.*, **10**, 90.
- Hasher, L. & Zacks, R.T. (1988) Working memory, comprehension, and aging: a review and a new view. *Psychol. Learn. Motiv.*, **22**, 193–225.
- Hernandez, M.T., Sauerwein, H.C., Jambaque, I., De Guise, E., Lussier, F., Lortie, A., Dulac, O. & Lassonde, M. (2002) Deficits in executive functions and motor coordination in children with frontal lobe epilepsy. *Neuropsychologia*, **40**, 384–400.
- Hillman, C.H., Motl, R.W., Pontifex, M.B., Posthuma, D., Stubbe, J.H., Boomsma, D.I. & de Geus, E.J.C. (2006) Physical activity and cognitive function in a cross-section of younger and older community-dwelling individuals. *Health Psychol.*, **25**, 678–687.
- Hillman, C.H., Erickson, K.I. & Kramer, A.F. (2008) Be smart, exercise your heart: exercise effects on brain and cognition. *Nat. Rev. Neurosci.*, **9**, 58–65.
- Hommel, B., Li, K.Z.H. & Li, S.C. (2004) Visual search across the life span. *Dev. Psychol.*, **40**, 545–558.
- Igbokwe, N.U. (1992) Hand grip dynamometer and arm muscle size in teenage boys and girls. *J. Phys. Educ. Sport Sci.*, **4**, 15–19.
- Isaacs, K.R., Anderson, B.J., Alcantara, A.A., Black, J.E. & Greenough, W.T. (1992) Exercise and the brain: angiogenesis in the adult rat cerebellum after vigorous physical activity and motor skill learning. *J. Cereb. Blood Flow Metab.*, **12**, 110–119.
- Karnath, H.-O., Ferber, S. & Himmelbach, M. (2001) Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, **411**, 950–953.
- Kiphard, E.J. & Schilling, F. (1974) *Körperkoordinationstest für Kinder [Body Coordination Test for Children]*. Beltz, Weinheim.
- Kleim, J.A., Swain, R.A., Armstrong, K.A., Napper, R.M.A., Jones, T.A. & Greenough, W.T. (1998) Selective synaptic plasticity within the cerebellar cortex following complex motor skill learning. *Neurobiol. Learn. Mem.*, **69**, 274–289.
- Kramer, A.F. & Erickson, K.I. (2007) Capitalizing on cortical plasticity: influence of physical activity on cognition and brain function. *Trends Cogn. Sci.*, **11**, 342–348.
- Kramer, A.F., Humphrey, D., Larish, J., Logan, G. & Strayer, D. (1994) Aging and inhibition: beyond a unitary view of inhibitory processing in attention. *Psychol. Aging*, **9**, 491–512.
- Kramer, A.F., Hahn, S. & Gopher, D. (1999) Coordinative executive processes during task switching. *Acta Psychol.*, **101**, 339–378.
- Kray, J., Li, K.Z.H. & Lindenberger, U. (2002) Age-related changes in task-switching components: the role of task uncertainty. *Brain Cogn.*, **49**, 363–381.
- Li, S.C. & Sikström, S. (2002) Integrative neurocomputational perspectives on cognitive aging, neuromodulation, and representation. *Neurosci. Biobehav. Rev.*, **26**, 795–808.
- Li, S.C., Lindenberger, U., Hommel, B., Aschersleben, G., Prinz, W. & Baltes, P.B. (2004) Transformations in the couplings among intellectual abilities and constituent cognitive processes across the lifespan. *Psychol. Sci.*, **15**, 155–163.
- Lindenberger, U. & Baltes, P.B. (1997) Intellectual functioning in old and very old age: cross-sectional results from the Berlin aging study. *Psychol. Aging*, **12**, 410–432.
- Lindenberger, U., Baltes, P.B. & Marsiske, M. (2000) Memorizing while walking: increase in dual-task costs from young adulthood to old age. *Psychol. Aging*, **15**, 417–436.
- Miller, E.K. & Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.*, **24**, 167–202.
- Oja, P. & Tuxworth, B. (1995) *Eurofit for Adults – Assessment of Health-Related Fitness*. Council of Europe Publishing, Tampere.
- Panek, P., Rush, M. & Slade, L. (1984) Locus of age-Stroop interference relationship. *J. Genet. Psychol.*, **145**, 209–216.
- Planinsec, J. (2002) Relations between the motor and cognitive dimensions of preschool girls and boys. *Percept. Mot. Skills*, **94**, 415–423.
- Porszasz, J., Casaburi, R., Somfay, A., Woodhouse, L.J. & Whipp, B.J. (2003) A treadmill ramp protocol using simultaneous changes in speed and grade. *Med. Sci. Sports Exerc.*, **35**, 1596–1603.
- Reuter-Lorenz, P.A. & Cappell, K.A. (2008) Neurocognitive aging and the compensation hypothesis. *Curr. Dir. Psychol. Sci.*, **17**, 177–182.
- Rikli, R.E. & Jones, C.J. (1999) Development and validation of a functional fitness test for community-residing older adults. *J. Aging Phys. Act.*, **7**, 129–161.
- Smith, J. & Baltes, P.B. (1999) Trends and profiles of psychological functioning in very old age. In Baltes, P.B. & Mayer, K.U. (eds), *The Berlin Aging Study*. Cambridge University Press, New York, pp. 197–226.
- Tiffin, J. & Asher, E.J. (1948) The Purdue Pegboard: norms and studies of reliability and validity. *J. Appl. Physiol.*, **32**, 234–247.
- Uhrich, T.A. & Swalm, R.L. (2007) A pilot study of a possible effect from a motor task on reading performance. *Percept. Mot. Skills*, **104**, 1035–1041.
- Voelcker-Rehage, C. & Wiertz, O. (2003) *Die Lernfähigkeit sportmotorischer Fertigkeiten im Lichte der Entwicklungspsychologie der Lebensspanne [Motor Skill Learning in Focus of Lifespan Developmental Psychology]*. Universität Bielefeld, Germany.
- Voelcker-Rehage, C., Stronge, A.J. & Alberts, J.L. (2006) Age-related differences in working memory and force control under dual-task conditions. *Aging Neuropsychol. Cogn.*, **13**, 366–384.
- Yund, E.W. (2003) Simultaneous auditory thresholds at multiple frequencies and for both ears. *Arch. Neurobehav. Exp. Stimuli*, **69**, http://www.neurobs.com/ex_files/expt_view?id=69.