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Intelligence is differentially related to neural effort in the task-positive and the task-negative brain network

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ABSTRACT

Previous studies on individual differences in intelligence and brain activation during cognitive processing focused on brain regions where activation increases with task demands (task-positive network, TPN). Our study additionally considers brain regions where activation decreases with task demands (task-negative network, TNN) and compares effects of intelligence on neural effort in the TPN and the TNN. In a sample of 52 healthy subjects, functional magnetic resonance imaging was used to determine changes in neural effort associated with the processing of a working memory task. The task comprised three conditions of increasing difficulty: (a) maintenance, (b) manipulation, and (c) updating of a four-letter memory set. Neural effort was defined as signal increase in the TPN and signal decrease in the TNN, respectively. In both functional networks, TPN and TNN, neural effort increased with task difficulty. However, intelligence, as assessed with Raven's Matrices, was differentially associated with neural effort in the TPN and TNN. In the TPN, we observed a positive association, while we observed a negative association in the TNN. In terms of neural efficiency (i.e., task performance in relation to neural effort expended on task processing), more intelligent subjects (as compared to less intelligent subjects) displayed lower neural efficiency in the TPN, while they displayed higher neural efficiency in the TNN. The results illustrate the importance of differentiating between TPN and TNN when interpreting correlations between intelligence and fMRI measures of brain activation. Importantly, this implies the risk of misinterpreting whole brain correlations when ignoring the functional differences between TPN and TNN.

1. Introduction

Stable individual differences in fluid intelligence have been an important topic of psychological research since decades. It is generally believed that stable differences in cognitive ability between people can, at least partly, be explained by differences in brain structure and function. Different approaches have been used to investigate the neural underpinnings of intelligence, including the study of total brain size (for a review and meta-analysis, see McDaniel, 2005), the regional morphology of specific brain sites (e.g., Haier, Jung, Yeo, Head, & Alkire, 2004), and brain activation during cognitive demands as assessed by PET, EEG, and fMRI (e.g., Gray, Chabris, & Braver, 2003; Haier, Siegel, Nuechterlein, & Hazlett, 1988; Neubauer, Freudenthaler, & Pfurtscheller, 1995). These studies on structural and functional neural correlates of intelligence converged on the notion that a network of brain regions, consisting of frontal and parietal areas, is associated with individual differences in intelligence (see the Parieto-Frontal Integration Theory; Jung & Haier, 2007). Notably, this parieto-frontal network, defined on the basis of Brodman areas (BA) in the P-FIT model, largely

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overlaps with a set of regions that typically show an *increase in activation* under cognitive demand. These regions are also subsumed under the term *cognitive-control network* (Cole & Schneider, 2007) or *task-positive network* (Fox et al., 2005). The task-positive network (TPN; Fox et al., 2005) consists of regions in the lateral prefrontal cortex (compare: BAs 6, 9, 10, 45, 46, 47 in the P-FIT model), the supplementary motor area (SMA) and dorsal anterior cingulate cortex (ACC; compare: BA 32 in the P-FIT model), the intraparietal sulcus (IPS) and the adjacent inferior parietal lobe (compare: BAs 7, 39, 40 in the P-FIT model), the insula, and middle temporal cortex (compare: BAs 21, 37 in the P-FIT model).

A different line of research using graph analyses to study characteristics of functional brain network topology as reflected in resting state brain activity (Song et al., 2009; van den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009), suggested a role for another functional brain network in intelligent behaviour, the so-called *default mode* or *task-negative network* (TNN; Shulman et al., 1997; Raichle et al., 2001; Buckner, Andrews-Hanna, & Schacter, 2008; Fox et al., 2005). The task negative network (TNN) consists of a distributed set of brain regions including medial prefrontal, posterior cingulate, superior frontal, inferior and medial temporal as well as medial and lateral parietal cortices. It shows a *decrease in the fMRI BOLD signal* when cognitive demands increase that is attributable to an actual reduction in neural activity - rather than to physiological effects like changes in respiration rate, atypical blood responses, or a reallocation of blood flow to adjacent active brain regions (Lin, Hasson, Jovicich, & Robinson, 2011). The graph theory analyses suggested that within the TNN, high-intelligent individuals show particularly high global communication efficiency, which has been argued to support superior cognitive performance (Song et al., 2009; van den Heuvel et al., 2009).

However, while the cited studies suggest a role of TNN functional connectivity during rest for intelligence, it is at present unclear whether the extent of task-induced TNN activation change is also related to intelligence. This is particularly so because previous investigations of intelligence-related differences in task-induced brain activation focused on activation changes in the TPN. Yet, there is a first hint from a recently published fMRI study that intelligence is indeed related to brain activation changes in the TNN during the processing of cognitive tasks: Lipp et al. (2012) report stronger deactivation for less intelligent subjects during the processing of a mental rotation task in one key region of the TNN, i.e., the posterior cingulate cortex. Here, we asked whether we can (a) replicate the negative association between intelligence and the amount of task-related deactivation in the posterior cingulate, (b) demonstrate the association not only for a single task-negative brain region, but for the TNN as a whole, and (c) dissociate intelligence effects in TPN and TNN.

Most previous studies relating intelligence test scores to measures of brain activation during the processing of cognitive tasks aimed at deriving conclusions about the efficiency of neural processing and whether it depends on intelligence (Haier et al., 1988; for a review, see Neubauer & Fink, 2009). Neural efficiency is commonly defined as task performance in relation to the neural effort expended on task processing, i.e., neural efficiency = performance/neural effort (e.g., Basten et al., 2011, 2012). The more neural effort is expended to reach a given level of behavioural performance, the less efficient the processing. To infer neural effort from BOLD signal changes in fMRI, one has to consider whether these signal changes were observed in regions of the task-positive network (TPN) – where the signal *increases* with effort expended on task-processing – or in regions of the task-negative network (TNN) – where the signal *decreases* with effort (Esposito et al., 2006; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003; Singh & Fawcett, 2008). The interpretation of a correlation between intelligence and changes in brain activation in terms of neural effort – and efficiency, respectively – thus critically depends on whether the correlation is observed in the TPN or the TNN (see Fig. 1). We argue that – given equal task performance – a positive correlation observed in regions of the TPN must be interpreted as higher intelligent individuals expending *more* neural effort, thus indicating reduced efficiency. In contrast, a positive correlation observed in regions of the TNN must be interpreted as higher intelligent individuals expending *less* neural effort, thus indicating increased efficiency of neural processing. The exact opposite is true for the interpretation of negative correlations between brain activation and intelligence. In either case, to derive a valid interpretation regarding intelligence-related inter-individual differences in neural efficiency, it is critical to take into account whether an effect was observed in the TPN or the TNN. Apart from the above-mentioned study by Lipp et al. (2012), this has not systematically been done in previous studies on the association of intelligence and fMRI BOLD signals.

To summarize, the current study aims at filling the gap between studies of task-induced brain activation that predominantly focussed on the TPN and studies of resting state functional connectivity that suggested a role for the TNN in intelligence. For that purpose, we investigated the relationship between individual differences in psychometric intelligence and the regulation of neural activity in both the TPN *and* the

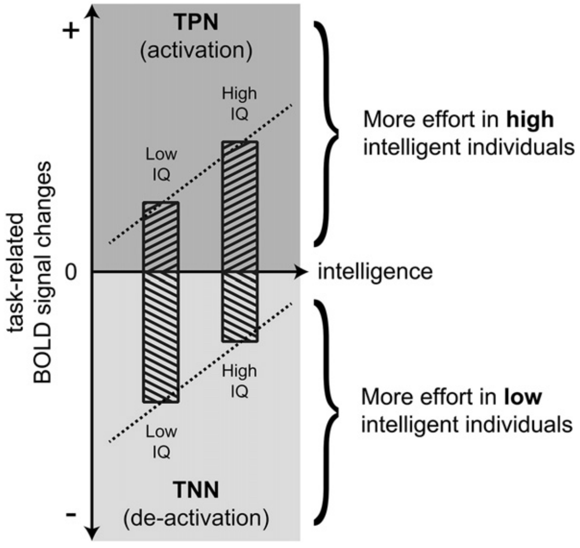

Fig. 1. Schematic illustration of possible associations between BOLD signal changes and intelligence. Positive correlations (dotted lines) may either result from higher intelligent individuals displaying larger BOLD signal increases (more activation) in the task-positive network (TPN; upper part of figure) or from higher intelligent individuals displaying smaller BOLD signal decreases (less deactivation) in the task-negative network (TNN; lower part of figure).

TNN during cognitive demand, considering average activation for the entire networks. In addition, we conducted a voxel-wise correlation analysis across the whole brain. This allowed us to resolve which specific regions within the two functional networks contributed to observed correlations between intelligence and task-induced BOLD signal changes.

Fluid intelligence was measured with Raven's Advanced Progressive Matrices (RAPM, Raven, Raven, & Court, 1998). As a measure of brain activation (in the TPN) and deactivation (in the TNN) under cognitive demand, we used fMRI BOLD signal changes during a working memory task. To test a potentially moderating effect of task difficulty on the intelligence–brain activation relationship, we chose a working memory task that comprised three conditions of increasing difficulty: the easiest condition merely required the *maintenance* of information (4 letters) in working memory, the medium difficult condition required the *manipulation*, and the most difficult condition required the *updating* of this information. This variation was included to take into account that task difficulty and associated aptitude-dependent differences in mental effort are assumed to moderate the relationship between psychometric intelligence and brain activation (Larson, Haier, Lacasse, & Hazen, 1995). Most specifically, higher neural efficiency (i.e., less neural effort) in more intelligent individuals is expected for easier tasks rather than for more difficult tasks, while in more difficult tasks, persons with higher intelligence are expected to invest more neural effort (for a review, see Neubauer & Fink, 2009). Furthermore, because previous studies found sex differences in the correlations between measures of intelligence and measures of brain structure (e.g., Haier, Jung, Yeo, Head, & Alkire, 2005; Narr et al., 2007) as well as function (e.g., Haier & Benbow, 1995; Neubauer & Fink, 2003), we also tested for an interaction of sex and RAPM scores on brain activation. Finally, to ensure that the observed associations between intelligence test scores and brain activation were unequivocally attributable to stable individual differences in general cognitive ability, we statistically controlled for variation in performance on the working memory task.

2. Material and methods

2.1. Participants

52 healthy volunteers participated in the study after giving informed consent according to a protocol approved by the local ethics committee. All were students of the University of Heidelberg, all were right-handed, had normal or corrected-to-normal vision, no structural brain abnormalities and no history of neurological or psychiatric diseases. The persons were paid for participation in the study. Of all 52 participants, 25 were male, 27 female. Age ranged from 19 to 27 years ($M = 22.23$, $SD = 1.92$). Fluid intelligence was assessed with the Raven's Advanced Progressive Matrices (RAPM; Raven et al., 1998). RAPM intelligence quotient (IQ) scores ranged from 77 to 139 ($M = 107.71$, $SD = 14.37$). For ANOVAs and the illustration of IQ effects, the sample was split into a low-IQ (IQ < 100; $n = 16$) and a high-IQ (IQ > 100; $n = 36$) group, differing significantly in RAPM IQ scores (low-IQ $M = 91.94$, $SD = 8.26$; high-IQ $M = 114.72$, $SD = 10.35$; $t(50) = 7.76$, $p < .001$). In the current sample, RAPM IQ scores did not significantly differ between men ($M = 107.68$, $SD = 16.13$) and women ($M = 107.74$, $SD = 12.83$; $t(50) = 0.02$, $p = .99$). Accordingly, there was no significant difference in the frequency of males/females in the groups of high-IQ (16/20) and low-IQ (9/7) individuals ($\chi^2(1) = 0.62$, $p = .43$).

2.2. Experimental procedure

Participants performed a modified delayed response task (Fig. 2; D'Esposito, Postle, Ballard, & Lease, 1999; Postle, Berger, & D'Esposito, 1999) including a maintenance, a manipulation, and an updating condition. The task consisted of three phases:

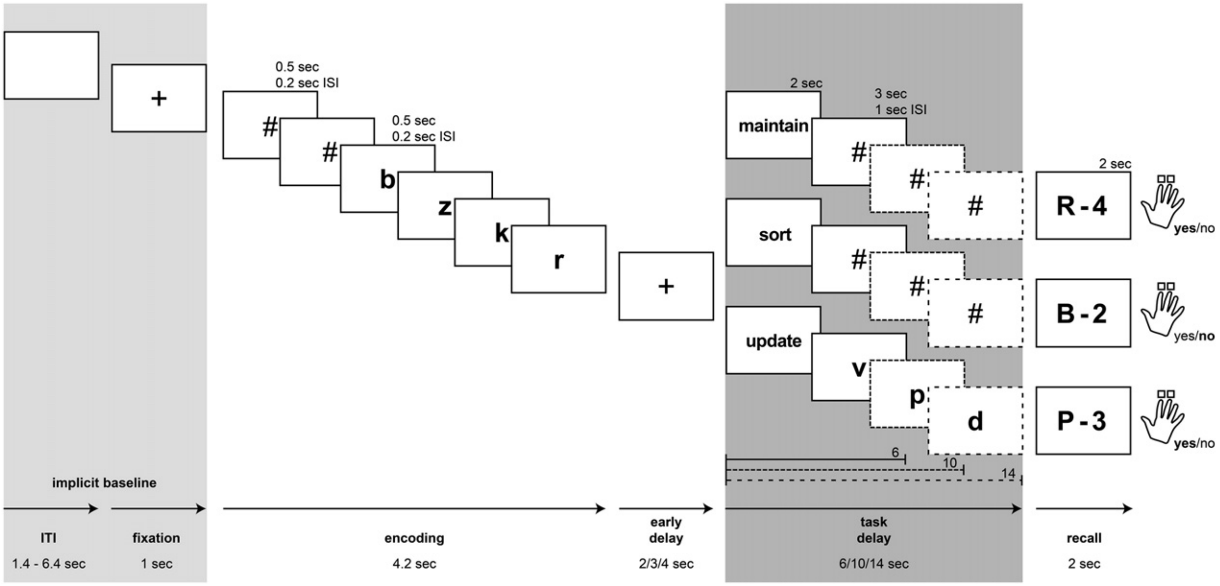

Fig. 2. Delayed response working memory task. Shaded areas mark the periods of the task contrasted in the fMRI analyses: light gray = implicit baseline, dark gray = task processing phase representing maintenance, manipulation (i.e., alphabetic sorting of memoranda), and updating of working memory contents.

encoding, delay (early delay and task delay), and recall. In the encoding phase, four sequentially presented letters had to be encoded into working memory. In the early delay phase, participants maintained the encoded set of letters in memory. In the task delay phase, a written cue indicated which task to perform on the four letters. In the maintenance condition (cued by the word 'maintain', in German: 'merke'), participants continued to maintain the letters in the order of presentation (top stream in Fig. 2). In the manipulation condition (cued by the word 'sort', in German: 'sortiere'), participants mentally rearranged the letters to alphabetical order (middle stream in Fig. 2). In the updating condition (cued by the word 'update', in German: 'aktualisiere'), new letters were presented in the task phase. For each new letter that was presented, participants had to cancel the first letter and attach the new letter to the end of their four-letter memory set (bottom stream in Fig. 2). In the maintenance and the manipulation condition, no new letters were presented in the task delay phase. Instead, participants saw hash keys (#) that served as placeholders to ensure perceptual equivalence with the updating condition. In the recall phase, a probe stimulus, consisting of a letter and a number (the latter indicating the position of the letter in the memory set) required retrieval of information from working memory. By pressing a button with the index or middle finger of their right hands, participants indicated whether or not the respective letter took the indicated position in the 4-letter memory set (response options: yes, no). The probe 'P-3', for instance, asked participants to decide whether or not the letter 'P' took the third position in the original (maintenance condition) or alphabetized (manipulation condition) or partly new (updating condition) memory set. Timing information is included in the schematic of the task procedure in Fig. 2. Participants were trained on the task prior to the fMRI session, and during training received feedback whenever a response was incorrect or too slow. Participants were instructed to respond fast and accurately. During image acquisition in the scanner they received no feedback on performance. The presentation of the task in the scanner was split into 4 blocks. Across all blocks, participants completed 24 trials of each condition.

2.3. Behavioural data analyses

To test whether behavioural performance on the working memory task was affected by task condition and intelligence level, we conducted separate 2-way repeated measures ANOVAs for error rates and response times as dependent variables, including *task condition* as a within-subjects factor (3 levels: maintenance, manipulation, updating) and *intelligence group* as a between-subjects factor (2 levels: high, low). For the three levels of the *task condition* factor, we conducted pair-wise post hoc comparisons of the three conditions, applying Bonferroni correction for multiple comparisons.

2.4. FMRI acquisition procedures

MRI data were acquired on a Siemens Trio 3 T MRI scanner equipped with a fast gradient system for echo-planar imaging (EPI) and a birdcage head coil. Participants were stabilized with cushions to restrict head motion. A screen, attached to the end of the bore, was visible for participants through a mirror in the head coil. Visual stimuli were presented on a dark background in the centre of the screen, using the software Presentation (Neurobehavioural Systems, http://nbs.neuro-bs.com). Functional data were acquired using a T2*-weighted BOLD-sensitive gradient-echo EPI sequence with 32 oblique axial slices of 3 mm thickness, 1 mm inter-slice gap, field of view (FOV) 192 mm, matrix size 64 × 64, in-plane resolution 3 × 3 mm, repetition time (TR) 2000 ms, echo time (TE) 30 ms, and flip angle 80°. Four runs of 440 volumes were acquired. The experiment was set up in an event-related design, jittered to improve BOLD signal estimation (Dale, 1999). The first six volumes of all four runs were discarded to allow for stable magnetization. For coregistration, a T1-weighed anatomical scan with the identical slice prescription as the functional scans was acquired. Three-dimensional high-resolution structural data were obtained via a sagittal T1-weighted, Magnetization Prepared-RApid Gradient Echo (MP-RAGE) scan with 192 slices of 1 mm thickness, FOV 256 mm, matrix size 256 × 256, in-plane resolution 1 × 1 mm, TR 1570 ms, TE 2.63 ms, and flip angle 30°.

2.5. FMRI data analyses

All MRI data analyses were carried out using the Statistical Parametric Mapping software package (SPM5, Wellcome Trust Centre for Neuroimaging, London, UK, http://www.fil.ion.ucl.ac.uk/spm/spm5.html).

2.5.1. Preprocessing

The acquired EPI time series were first slice-time and then motion corrected. All functional volumes were spatially normalized into standard (MNI 152) space according to the normalization parameters resulting from the segmentation of the high-resolution anatomies (voxels resampled to 2 × 2 × 2 mm). Finally, spatial smoothing was applied (8 mm FWHM Gaussian kernel).

2.5.2. Task-related brain activation

To identify regions showing task-related changes in the measured BOLD signal, a general linear model (GLM) accounting for serially auto-correlated data (Friston et al., 1995) was set up for each participant, applying a canonical hemodynamic response function and a temporal highpass filter (cut-off 128 s). Functional runs were modelled as separate sessions. The GLMs included separate regressors for all experimental conditions (i.e., maintenance, manipulation, updating, and three other conditions not evaluated for the current research question) and task periods (i.e., encoding, early delay, task delay, and recall; see Fig. 2). In addition, the model included covariates of no interest for incorrectly answered trials and the realignment parameters derived from the motion correction in data preprocessing. Subsequently reported results focus on the task delay period regressors.

2.5.3. Identification of the task-positive and task-negative network

To identify regions of the task-positive network (TPN), for each subject, we contrasted activation for all experimental conditions during the task phase with the implicit baseline of our model (i.e., [maintenance & manipulation & updating] > baseline), by linear combination of beta weights obtained from the estimation of the GLM. The task-negative network (TNN) was identified using the reverse contrast (i.e. baseline > [maintenance & manipulation & updating]). Individual maps of contrast values were integrated at the group level in a model treating participants as random effects (Holmes & Friston, 1998). Analyses of task-related increases and decreases in BOLD signal included all voxels in the brain. We report results for an overall threshold of $p < .05$ (FWE-corrected for multiple comparisons), constituted by an individual-voxel-probability threshold of $p < .001$ (uncorrected, $t(51) > 3.26$) in combination with a minimum-cluster-size threshold of $k > 64$ voxels as determined via Monte Carlo Simulation using the AFNI routine AlphaSim (Ward, 2000; cf. Forman et al., 1995).

2.5.4. Effects of task condition and intelligence on brain activation

To investigate effects of task condition and intelligence on brain activation, in our main analysis, we averaged individual contrast values (maintenance > baseline, manipulation > baseline, updating > baseline) across all voxels of the respective functional networks, i.e., TPN vs. TNN, as defined by the current task at a threshold of $p < .001$ and $k > 64$ (see above). The resulting mean contrast values were subjected to off-line statistical analyses. We conducted separate 2-way repeated measures ANOVAs for the TPN and the TNN, respectively, that were analogous to those conducted for the behavioural data. In addition, we conducted a joined 3-way ANOVA for TPN and TNN using as dependent variable the neural effort – as indicated by TPN activation increases and TNN activation decreases, respectively – and including the three factors *network* (2 levels: TPN, TNN), *task condition* (3 levels: maintenance, manipulation, updating), and *intelligence group* (2 levels: high, low). To control for subtle performance differences between the high- and low-intelligence groups in our analyses, we included task performance measures (mean errors and response times across the three conditions) as covariates into the ANOVAs testing for effects of intelligence on brain activation. For all AN(C)OVAs conducted, Greenhouse–Geisser correction (GGC) was applied to *p*-values and degrees of freedom whenever Mauchly's test indicated that the assumption of sphericity had been violated.

Finally, to investigate the effects of intelligence on brain activation not only for the average levels of activation within the two functional networks of interest (TPN and TNN) but also across the whole brain, in a secondary analysis, we included individual RAPM IQ scores as a predictor in the group analysis of task activation that contrasted all task conditions against the implicit baseline (i.e., [maintenance & manipulation & updating] > baseline) and tested for its effects in every single voxel of the whole brain volume. This also allowed us to resolve which specific regions within the two functional networks contributed to observed correlations between intelligence and task-induced BOLD signal changes.

2.5.5. Effects of sex on the association between intelligence and brain activation

To test whether sex had an influence on the relation between intelligence test scores and brain activation, we tested for an interaction of sex and intelligence on brain activation in two separate 3-way ANOVAs for the TPN and TNN, respectively, including the three factors *task condition* (3 levels: maintenance, manipulation, updating), *intelligence group* (2 levels: high, low), and *sex* (2 levels: males, females).

3. Results

3.1. Behavioural performance

Behavioural performance on the working memory task varied with task condition, but was not significantly influenced by intelligence (see Fig. 3). Repeated measures ANOVAs revealed a significant effect for the within-subjects factor *task condition* (3 levels: maintenance, manipulation, updating) for both error rates and response times; error rates: $F(2, 100) = 23.02$; $p < .001$; response times: $F(2, 100) = 73.79$; $p < .001$. The between-subjects factor *intelligence group* (2 levels: high, low) did not significantly influence performance, though there was a tendency for the group of high-intelligent subjects to respond faster; $F(1, 50) = 2.73$; $p = .11$. The increase in error rates and response times observed across the three conditions confirmed an increase in task difficulty as intended, with the simple maintenance condition showing the lowest, the manipulation condition a medium, and the updating condition the highest level of difficulty realised in the current paradigm. Pair-wise post hoc comparisons of the three conditions (with Bonferroni correction for multiple comparisons) revealed that manipulation as contrasted to simple maintenance was associated with significantly more errors ($p < .001$) along with a nominal though statistically not significant increase in response times ($p = .05$). Updating as contrasted to manipulation was associated with significantly longer response times ($p < .001$), whereas the two conditions did not differ with respect to error rates ($p = .10$). We conclude that in sum, the three experimental conditions were characterized by increasing levels of difficulty.

3.2. Task-positive and task-negative brain networks

In the present study, the TPN, characterized by *increases* in BOLD signal during task processing as compared to the implicit baseline, comprised lateral PFC, dorsal ACC, intraparietal sulcus, anterior insula, thalamus, visual cortex, and superior cerebellum — all bilaterally. The TNN, characterized by task-related *decreases* in BOLD signal, comprised ventromedial PFC, rostral ACC, superior frontal gyri, posterior cingulate cortex, medial temporal gyri, and the temporo-parietal junction area (TPJ) — also all bilaterally. Both TPN and TNN are illustrated in Fig. 4 A (see also Table 1), and both are consistent with previously published characterizations of TPN and TNN (e.g., Fox et al., 2005). Activation in the TPN as well as deactivation in the TNN increased with task difficulty. Both measures yielded lowest values for the easiest task condition (maintenance of working memory contents) and highest values for the most difficult task condition (updating of working memory contents), see Fig. 4 B; TPN main effect of condition: $F(1.78, 89.07) = 95.23$, $p < .001$ (GGC); TNN main effect of condition: $F(1.83, 91.38) = 42.09$, $p < .001$ (GGC). Pair-wise post hoc comparisons of the three conditions (with Bonferroni correction for multiple comparisons) revealed that manipulation as contrasted to simple maintenance was associated with significantly stronger activation in the TPN ($p < .001$) and stronger deactivation in the TNN ($p < .001$). Updating as contrasted to manipulation was

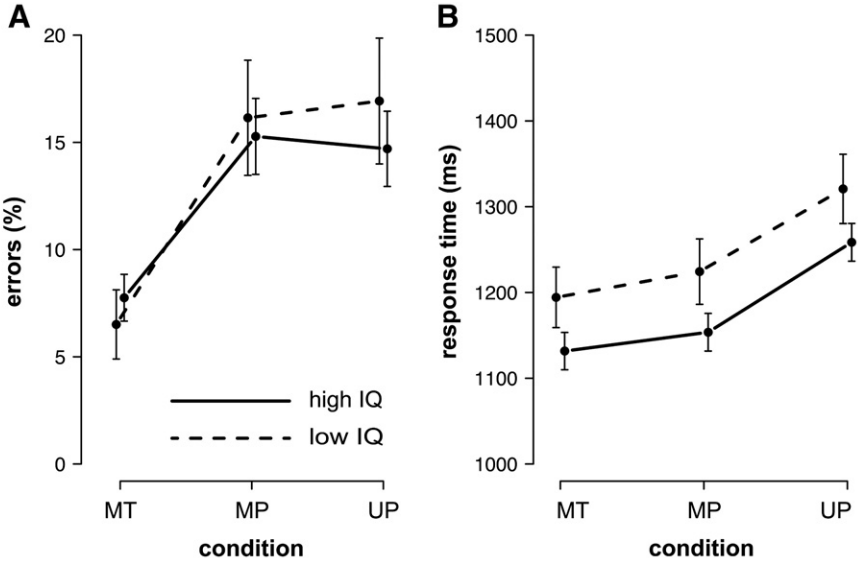

Fig. 3. Behavioural performance. (A) error rates and (B) response times by task condition (MT = maintenance, MP = manipulation, UP = updating) and intelligence group (continuous line = high-IQ group, dashed line = low-IQ group). Error bars show the standard errors of the means.

associated with significantly stronger activation in the TPN ($p = .002$) and numerically but not significantly stronger deactivation in the TNN ($p = .38$).

3.3. Intelligence and brain activation

RAPM IQ scores were significantly associated with both the strength of activation in the TPN and the strength of deactivation in the TNN (Fig. 4 B). Across conditions, the high-IQ group showed stronger activation increases in the TPN than the low-IQ group; TPN main effect of intelligence: $F(1, 50) = 4.29$; $p = .044$. In contrast, in the TNN, the high-IQ group showed weaker decreases in activation than the low-IQ group; TNN main effect of intelligence: $F(1, 50) = 8.87$, $p = .004$. The differential effect of intelligence on activation in the TPN and the TNN was confirmed in a joined ANOVA for both TPN and TNN where neural effort – as indicated by TPN activation increases and TNN activation decreases, respectively – was predicted by the three factors *network* (2 levels: TPN, TNN), *task condition* (3 levels: maintenance, manipulation, updating), and *intelligence group* (2 levels: high, low). The analysis revealed a significant interaction of network and intelligence on neural effort; $F(1, 50) = 7.84$, $p = .007$ (GGC). The association between intelligence and neural effort depended on the functional network. While in the TPN, higher intelligence was associated with greater neural effort, in the TNN, higher intelligence was associated with less neural effort. When assessed separately, none of the two networks showed an interaction of intelligence and task condition on brain activation; TPN interaction of intelligence and condition: $F(1.78, 89.07) = 0.49$, $p = .60$ (GGC); TNN interaction: $F(1.83, 91.38) = 1.68$, $p = .20$ (GGC).

Fig. 4 C shows the results of the voxel-wise whole brain correlation between RAPM IQ scores and task activation for all task conditions as contrasted to the implicit baseline (i.e., [maintenance & manipulation & updating] > baseline). IQ scores were positively correlated with the BOLD signal in an extensive cluster in the anterior medial cortex, furthermore, in the posterior cingulate cortex, as well as bilaterally in superior frontal and superior temporal cortex, posterior insula, hippocampus, and putamen. In the right hemisphere, additional effects were found in the dorsolateral prefrontal cortex and the inferior frontal junction area (Table 2). No significant negative correlations were observed. Overlaying the correlation map onto the maps of the task-positive and task-negative networks (as done in Fig. 4 C), revealed that the main portion of the regions showing a positive correlation between IQ scores and BOLD signal fell within the TNN. This result is consistent with the observation that in the above-reported analyses conducted separately for the TPN and the TNN, the effect of IQ scores on BOLD signal appeared more pronounced for the TNN than for the TPN.

Our analyses testing whether males and females differed in the relation between IQ scores and brain activity revealed a numerically stronger difference in TPN activation depending on intelligence for females than for males. However, there was no significant interaction of sex and intelligence group on BOLD signal changes in neither TPN, $F(1, 48) = 2.33$, $p = .134$, nor TNN, $F(1, 48) = 0.30$, $p = .586$.

3.4. Controlling for individual differences in task performance

Crucially, as intra-individual variation in the strength of deactivation in the TNN has been associated with trial-to-trial variation in working memory performance (Anticevic, Repovs, Shulman, & Barch, 2010; Eichele et al., 2008; Li, Yan, Bergquist, & Sinha, 2007; Weissman, Roberts, Visscher, & Woldorff, 2006), it is important to ensure that the reported effects of intelligence on brain activation were not simply mediated by inter-individual performance differences between high- and low-intelligent subjects. Importantly, for our sample, performance on the working memory task did not significantly differ

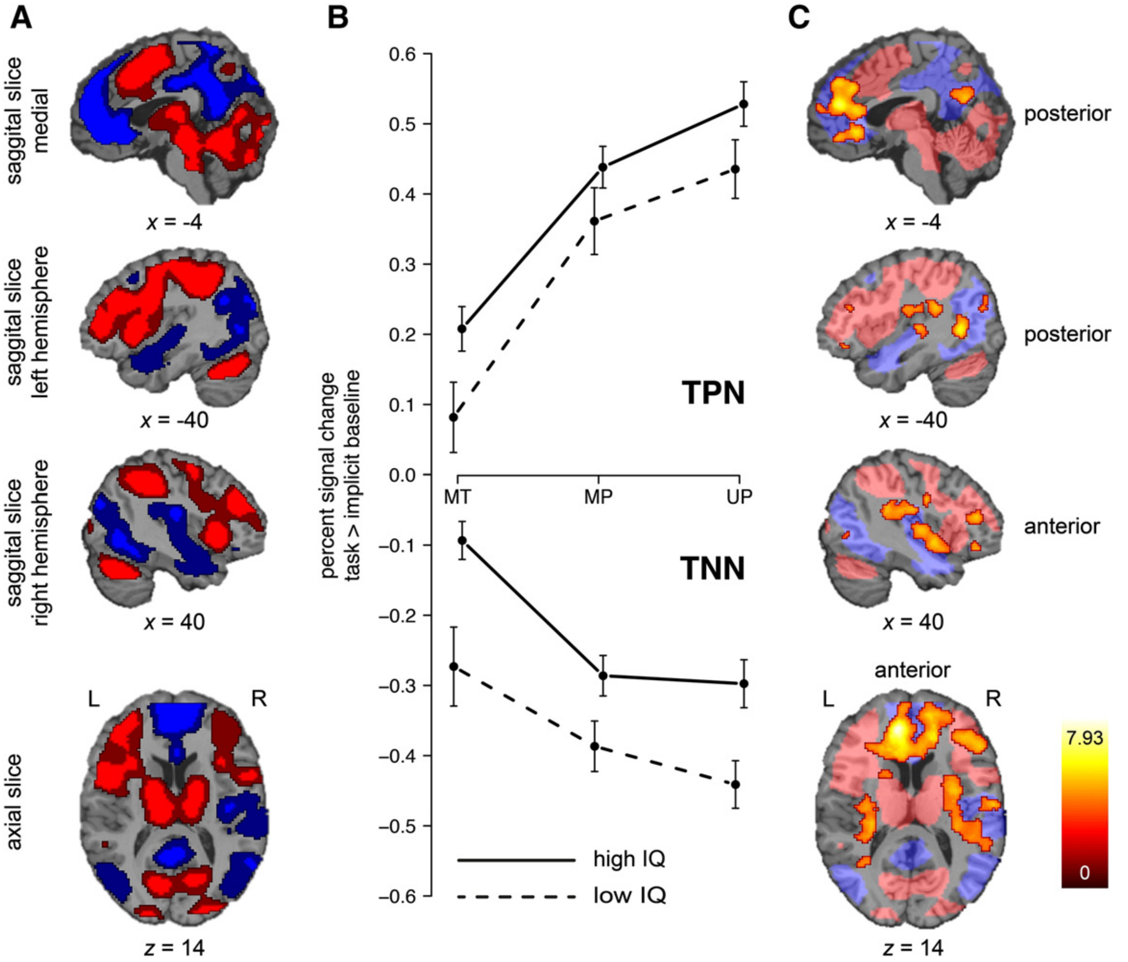

Fig. 4. Brain activation as measured by fMRI during the working memory task depends on intelligence. (A) Task-positive network (i.e., all 3 task conditions > implicit baseline; red) and task-negative network (i.e., all 3 task conditions < implicit baseline; blue) for the working memory task. Dark colours show clusters significant at voxel threshold $p < .001$ (uncorrected) and cluster threshold $k > 64$ voxels (AlphaSim .05, corrected); light colours show clusters significant at voxel threshold $p < .001$ (FWE corrected). (B) Task-related BOLD signal changes across the entire functional networks (TPN = task-positive network, TNN = task-negative network) by task condition (MT = maintenance, MP = manipulation, UP = updating) and intelligence group (dashed line = low intelligence group, continuous line = high intelligence group). Error bars show the standard errors of the means. (C) Red-to-yellow regions mark a positive voxel-wise whole brain correlation between intelligence (RAPM scores) and brain activation (i.e., all 3 task conditions > implicit baseline), $p < .001$, $k > 64$. Areas shaded in light blue and red mark the task-positive (transparent red) and task-negative (transparent blue) network ($p < .001$, $k > 64$, see panel A).

between the high- and the low-intelligent group (see above). As, nevertheless, there was a tendency for the high-intelligent group to respond quicker than the low-intelligent group, we statistically controlled for these subtle performance differences in our analyses. We included task performance measures (mean errors and response times across the three conditions) as covariates into the ANOVAs testing for effects of intelligence on brain activation. In a joined 3-way ANCOVA simultaneously considering TPN and TNN, the above-reported interaction effect of intelligence and network on neural effort remained significant when performance was controlled for; $F(1, 48) = 6.75$, $p = .01$ (GGC). Considering TPN and TNN separately in 2-way ANCOVAs controlling for performance, intelligence still had a significant effect on BOLD signal in the TNN; $F(1, 48) = 7.91$, $p = .007$. For the TPN, the effect just failed to reach significance; $F(1, 48) = 3.47$, $p = .07$. We conclude from these analyses that in the TNN, the effect of intelligence on task-related decreases in neural activity is robust against controlling for inter-individual differences in task performance.

4. Discussion

In the current study, we investigated how the relationship between brain activation and intelligence depends on the specific functional system under study. We found that the effects of fluid intelligence on the neural effort expended during performance of a working memory task strongly depended on the functional brain network that was being considered. Most specifically, we observed a *positive* association between intelligence and neural effort in the task-positive network (TPN), whereas we observed a *negative* association between intelligence and neural effort in the task-negative network (TNN). Our interpretation of the results in terms of neural efficiency

Table 1
Task-positive and task-negative networks: activation and deactivation for the working memory task ([maintenance & manipulation & updating] > baseline).

Brain region	BA	Hem	MNI			T_{max}	k
			x	y	z		
Task-positive network (activation: task > baseline)							
FWE-corrected with a combination of voxel strength ($p < .001$) and cluster extent ($k > 64$) threshold							
Extensive activation, see below for more differentiated characterisation of network.		L/R	4	12	48	20.92	57,715
FWE-corrected at the voxel level ($p < .001$) with Gaussian random field theory as implemented in SPM5							
DACC and SMA, left lateral PFC (inferior, middle, and superior frontal gyri, local peaks in DLPFC and IFJ), bilateral FEF, left anterior insula, left intraparietal sulcus	4, 6, 7, 8, 9, 10, 24, 32, 40, 44, 45, 46, 47	L/R	4	12	48	20.92	14,194
Thalamus, basal ganglia (caudate, putamen, pallidum), cuneus, occipital lobe (middle and superior gyri), lingual and fusiform gyri, cuneus, midbrain, cerebellum—all bilaterally	17, 18, 19, 23, 30, 31	L/R	30	−66	−30	16.43	11,608
DLPFC	9, 46	R	42	38	28	13.86	582
Inferior frontal junction	6, 8, 9, 44	R	56	12	32	9.40	462
Anterior insula		R	32	22	0	19.77	923
Intraparietal sulcus	7,40	R	36	−46	42	14.97	1,514
Precuneus	7	R	12	−64	52	9.51	65
Inferior temporal gyrus	37	L	−54	−52	−10	7.16	7
Task-negative network (de-activation: task < baseline)							
FWE-corrected with combination of voxel strength ($p < .001$) and cluster extent ($k > 64$) threshold							
Anterior medial frontal gyri (VMFPC, rostral ACC), superior frontal gyri, right inferior frontal gyrus	8, 9, 10, 11, 12, 24, 32, 45	L/R	2	56	4	15.01	8,656
Posterior cingulate cortex, precuneus, medial temporal lobes, parahippocampal gyri, middle and superior temporal gyri, inferior parietal lobes, temporo-parietal junction area (TPJ)	7, 8, 9, 10, 13, 19, 20, 21, 22, 23, 24, 28, 29, 30, 31, 34, 35, 36, 37, 38, 39, 40, 42	L/R	0	−18	38	12.34	26,180

Note. BA: approximate Brodmann's area; Hem: hemisphere, L: left, R: right; MNI: coordinates referring to the Montreal Neurological Institute template brain included in the SPM5 software package; T_{max}: maximum t-statistic in the cluster; k: cluster size in voxels.

suggests that while high-intelligent individuals are *more efficient* in deactivating the TNN during task processing, they put *more effort* into cognitive control-related activity in the TPN. In the following, we discuss the effects of intelligence on task-related changes in neural activation separately for the TNN and the TPN before integrating the results, relating our fMRI findings to those from previous EEG studies, and inferring implications for future studies.

4.1. Intelligence effects on task-negative activations

Brain activity in the TNN has been associated with so-called default mode processes: It is assumed that the brain has a default mode during which activity in regions of the TNN supports stimulus-independent, internally focused information processing – previously also summarized as "mind wandering" (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Mason et al., 2007; Raichle et al., 2001). During the processing of cognitive tasks, this default activity decreases (Raichle et al., 2001; Shulman et al., 1997), and this decrease in default activity seems to be crucial for successful performance on the tasks. The latter is suggested by studies that investigated within-subject variation in default activity and showed that across trials, greater TNN deactivation predicted better performance (Anticevic et al., 2010; Eichele et al., 2008; Li et al., 2007; Weissman et al., 2006). We interpret the negative correlation we observed between intelligence and the mean strength of task-related deactivation in the TNN as suggesting that higher-intelligent individuals get by with less deactivation in the TNN and thus less neural effort in the TNN. In terms of neural efficiency, we suggest that high-intelligent individuals are particularly efficient in reducing task-irrelevant and potentially disturbing default processes during task performance. They show weaker deactivation than less intelligent subjects. Still, the extent of deactivation is high enough to guarantee successful task performance. It is exactly the smaller extent of deactivation along with equal task performance that renders the high intelligent more efficient when compared to less intelligent.

Our present work was motivated by the fact that previous studies that used graph theoretical approaches to analyse functional connectivity within and between different regions of the brain during rest had suggested a role for the TNN in intelligence (Song et al., 2009; van den Heuvel et al., 2009). In these studies, higher intelligence was associated with higher global network communication efficiency — in particular between regions of the TNN. van den Heuvel et al. (2009) observed a negative association between intelligence (full-scale IQ from the Dutch version of Wechsler adult intelligence scale, WAIS) and characteristic path length that was most pronounced in core regions of the TNN, i.e., medial prefrontal cortex (BA 9/10), posterior cingulate cortex and precuneus (BA 7/31), and bilateral inferior parietal regions (BA 39/40). The characteristic path length is a graph theoretical measure of

Table 2
Brain regions where intelligence predicts strength of task-related BOLD signal changes ([maintenance & manipulation & updating] > baseline), analysed across the whole brain.

Brain region	BA	Hem	MNI			T_{max}	k
			x	y	z		
Positive correlation							
FWE-corrected with combination of voxel strength ($p < .001$) and cluster extent ($k > 64$) threshold							
Anterior medial frontal cortex (AMPFC), superior frontal gyrus (SFG), superior temporal gyrus (STG)	8, 9, 10, 11, 12, 13, 22, 24, 32, 41, 42, 43	L/R	−12	42	14	6.53	10,512
Posterior cingulate cortex, precuneus	23, 31	L/R	0	−62	22	4.88	322
Inferior frontal sulcus, middle and inferior frontal gyri	46	R	50	30	16	4.71	406
Inferior frontal junction area (IFJ)	6, 8, 44	R	46	−2	32	4.46	100
Superior temporal gyrus (STG)	13, 22, 41, 42	L	−32	−34	24	4.78	1,454
Middle temporal gyrus (MTG)	37	L	−42	−58	4	5.05	368
	21	L	−52	−20	−22	4.22	65
Posterior middle temporal gyrus	39	L	−26	−78	36	4.18	172
	37	R	48	−70	6	4.27	124
Hippocampus	27	L	−26	−32	−8	4.25	123
Cerebellum		R	16	−56	−30	4.04	75

Note. BA: approximate Brodmann's area; Hem: hemisphere, L: left, R: right; MNI: coordinates referring to the Montreal Neurological Institute template brain included in the SPM5 software package; T_{max}: maximum t-statistic in the cluster; k: cluster size in voxels.

global interconnectedness of a network. It is defined as the average number of connections on the shortest path from a given node to any other node in the network (Sporns, Chialvo, Kaiser, & Hilgetag, 2004; Watts & Strogatz, 1998). The shorter the characteristic path length, the less connections are necessary to travel from one point in the network to any other and the more efficient the global communication within the network. Song et al. (2009) also used graph theoretical procedures to analyse brain activity during a resting state. They restricted their analysis to the TNN and also found shorter path lengths and – accordingly – higher global network efficiency in subjects of superior as compared to average intelligence (full-scale IQ from the Chinese version of the WAIS). The findings of van den Heuvel et al. (2009) and Song et al. (2009) can be interpreted as high-intelligent people having more long distance connections between different regions of the brain that ensure integration of information. Consequently, global communication, especially between regions of the TNN, is more efficient in high-intelligent individuals.

While these graph-theoretical analyses of functional connectivity during resting states suggested a role for the TNN in intelligence, it was unclear whether intelligence also modulated task-induced BOLD signal changes during cognitive processing. First evidence for a link between intelligence and task-related brain activation changes in the TNN came from Lipp et al. (2012). These authors investigated the association of visuo-spatial intelligence (as measured with the German intelligence structure test I-S-T 2000-R; Amthauer, Brocke, Liepmann, & Beauducel, 2001) and task-related BOLD signal changes in fMRI during a mental rotation task. They report stronger deactivation for less intelligent subjects in one region of the TNN, i.e., the posterior cingulate cortex (PCC). With the current study, we confirm a role for the TNN in intelligence by showing that intelligence was related to the amount of deactivation observed in the TNN during a working memory task. Just like Lipp et al. (2012), we observed a negative association between intelligence and the extent of TNN deactivation. Importantly, unlike the earlier study, we demonstrate this relationship not only for the PCC, but across the entire TNN, which in addition to PCC comprised ventromedial PFC, rostral ACC, the superior frontal and medial temporal gyri, and the temporo-parietal junction area, all bilaterally. Moreover, we showed that – even when examining the brain activation-intelligence relationship voxel-wise across the whole brain – significant effects were observed in every single sub-region constituting the TNN (see Table 2). On the other hand, most of the brain regions where activation depended on intelligence were part of the TNN – and not TPN, respectively (see Fig. 4C). The fact that Lipp et al. (2012) used a mental rotation task in their investigation and we provide converging evidence for a working memory task furthermore points to TNN activity as a general phenomenon underlying individual differences in intelligence. The present study thus substantially extends the recently reported result by Lipp et al. (2012) and strongly indicates that – across different modalities – more intelligent persons reduce default mode activity more efficiently during the performance of cognitively challenging tasks.

In our view, there are two reasons why apart from the study of Lipp et al. (2012) effects of intelligence on TNN deactivation have not been reported previously. First, many studies have so far concentrated on brain activation in the TPN and explicitly excluded TNN regions from their analyses by testing for effects of intelligence/performance on brain activity only in regions of interest defined by activation during the cognitive task studied (e.g., Lee et al., 2006; Perfetti et al., 2009; Rypma et al., 2006; Tang et al., 2010). Second, where the whole brain was considered for the analysis, it was not differentiated between TPN and TNN regions (e.g., Gray et al., 2003; Preusse, van der Meer, Deshpande, Krueger, & Wartenburger, 2011). Positive correlations between intelligence and brain activation were simply interpreted as reflecting *stronger task-related activation increases* in higher intelligent individuals – no matter where in the brain they were observed. This interpretation ignores the possibility that a positive correlation may as well arise from *weaker task-related activation decreases* in the higher intelligent (see Fig. 1).

It will be an exciting challenge for future research to elucidate exactly how *efficiency of communication within the networks* as evaluated by graph analyses of resting state data (e.g., van den Heuvel et al., 2009) relates to *efficiency of activation in networks* during the processing of cognitive tasks (as assessed in the current study). We speculate that there may be a causal link, in the sense that higher efficiency of inter-areal neural communication within the TNN results in high-intelligent people having to invest less neural effort to reduce TNN default mode activity during cognitive demands.

4.2. Intelligence effects on task-positive activations

According to the neural efficiency hypothesis of intelligence (Haier et al., 1988; see also Neubauer & Fink, 2009), one would expect weaker task-related increases in brain activation in high- as compared to low-intelligent individuals. In this study, however, we observed the opposite, i.e., stronger task-related activation increases in the TPN for high- as compared to low-intelligent subjects. In fact, for studies using the method of fMRI, this appears to be a typical finding. Previous studies quite consistently reported a positive association between intelligence test scores and task-related BOLD signal changes in fMRI (e.g., Gray et al., 2003; Geake & Hansen, 2005; Lee et al., 2006; Rypma et al., 2006; Choi et al., 2008), while a negative association has rarely been reported for fMRI studies (e.g., Perfetti et al., 2009; Rypma et al., 2006; Tang et al., 2010). Stronger activation in regions of the TPN suggests that higher-intelligent people put more effort into task-specific – and presumably task-relevant – cognitive processes.

While the pattern of results from previous studies receives support from our findings, it is an open question how these results can be reconciled with the earlier findings from EEG studies that suggested higher neural efficiency in higher intelligent people (e.g., Neubauer, Grabner, Fink, & Neuper, 2005; Neubauer et al., 1995). In our view, there are two possible explanations. On the one hand, task difficulty has been suggested to moderate the relation between intelligence and brain activation such that only for easy tasks high-intelligent individuals are expected to be more efficient in neural processing. For difficult tasks, on the contrary, the high intelligent are expected to display stronger activation than the low intelligent (Neubauer & Fink, 2009). We cannot exclude that the limited number of fMRI studies available to date, including ours, used cognitive tasks that were at a level of difficulty where high-intelligent subjects put more effort into processing than low-intelligent ones. On the other hand, the ostensible conflict between findings from fMRI and EEG studies may be reconciled when taking into account the methodological issues discussed in the following paragraph.

4.3. Relating findings from EEG and fMRI studies

In EEG studies on IQ and brain activation (e.g., Neubauer et al., 1995, 2005), task-related increases in *brain activation* typically are inferred from event-related de-synchronisation of activity in the upper alpha band. FMRI studies, on the contrary, infer increases in brain activation from event-related increases in the BOLD signal. Today, it is not clear how exactly these two measures of brain activation acquired by two different methods, i.e., EEG and fMRI, relate to each other. Studies analysing data from simultaneous recordings of EEG and fMRI data came to the conclusion that there is an association between EEG alpha band power and fMRI BOLD signal fluctuations in the default mode network of the brain (roughly equivalent to the TNN) as well as in the dorsal attention network (roughly equivalent to the TPN; Mantini, Perrucci, Del Gratta, Romani, & Corbetta, 2007; Laufs et al., 2003; Laufs et al., 2003). Jann et al. (2009), differentiating between specific sub-bands of the EEG alpha frequency band, showed that global field synchronisation in the *upper* alpha frequency band was related to an increase in the fMRI BOLD signal in the default mode network whereas synchronisation in the *lower* alpha frequency band was related to an increase in BOLD signal in the dorsal attention network. These findings suggest that de-synchronisation of EEG activity in the upper alpha band is related to a decrease in default activity and thus to a decrease in TNN BOLD signal rather than to an increase TPN BOLD signal.

Based on these insights from simultaneous EEG-fMRI recordings, one would then expect that high-intelligent individuals (that show less de-synchronisation in the upper alpha band of the EEG) should also show less deactivation in the TNN during task processing. Indeed, this assumption is supported by our data, where a closer association was observed between intelligence and BOLD signal changes in the TNN than in the TPN. We consequently speculate that neural efficiency as measured with EEG in the studies cited above reflects the efficiency with which a person can deactivate the TNN as measured with fMRI. This interpretation would also imply the need to (at least partially) re-interpret findings from EEG studies: While de-synchronisation of EEG activity in the upper alpha band may still be taken as a measures of neural effort expended on cognitive processing, it has to be questioned whether it can be seen as a measure of "brain activation" in a strict sense. In our opinion, it has to be considered that it may be a measure of effort in terms of TNN deactivation – i.e., reduction of default mode activity – rather than TPN activation.

4.4. Task-difficulty effects on the intelligence-brain activation relationship

For the current study, we used a working memory task that comprised three conditions of increasing task difficulty, i.e., the maintenance, the manipulation, and the updating of working memory contents. It has been postulated that task difficulty moderates the relation between intelligence and brain activation during cognitive processing. Evidence supporting this hypothesis comes from EEG studies (e.g., Doppelmayr, Klimesch, Hodlmoser, Sauseng, & Gruber, 2005; for a review, see Neubauer & Fink, 2009). In our study, however, task difficulty did not affect the relation between intelligence and neural effort, neither in the TPN nor in the TNN, as effects of task difficulty and intelligence on brain activity were additive. Yet, we cannot exclude the possibility that all three task conditions realised in the current experiment were at levels of relatively high difficulty when compared to the above-mentioned EEG studies. In that case – at least for the TPN – high-intelligent subjects would be expected to show more neural effort than low-intelligent subjects in all conditions, as observed in the present study.

5. Conclusion and implications for future studies

We conclude that in our study individual differences in intelligence were associated with differences in the strength of brain activation during performance of a working memory task. Importantly, we showed that the relation between intelligence and neural effort inferred from fMRI BOLD signal changes differed between the functional brain networks under consideration: In the TPN, we found a *positive* association between intelligence and neural effort; in the TNN, we found a *negative* association. Future studies should routinely differentiate between the two functional networks, TPN and TNN, when investigating effects of intelligence on brain activation. In particular, when inferences are made about efficiency, it is crucial to take into account in which region of the brain an effect was observed, and if this region is typically activated or deactivated during cognitive demand. Like it was done for the current study, investigations on the association of intelligence and task-related changes in the fMRI BOLD signal should always identify the TPN and TNN for the task at hand before interpreting correlations between intelligence and BOLD signal strength. Furthermore, in addition to interpreting statistical correlation maps, it is desirable to visualize BOLD signal change profiles as a function of intelligence. Thereby, it can easily by clarified whether a given correlation results from stronger task-related activation increases or weaker decreases in high- as compared to low-IQ subjects – or vice versa.

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References

Amthauer, R., Brocke, B., Liepmann, D., & Beauducel, A. (2001). *Intelligenz-Struktur-test 2000 R.* Göttingen: Hogrefe.

Anticevic, A., Repovs, G., Shulman, G. L., & Barch, D. M. (2010). When less is more: TPJ and default network deactivation during encoding predicts working memory performance. *NeuroImage*, *49*, 2638–2648.

Basten, U., Stelzel, C., & Fiebach, C. J. (2011). Trait anxiety modulates the neural efficiency of inhibitory control. *Journal of Cognitive Neuroscience*, *23*, 3132–3145.

Basten, U., Stelzel, C., & Fiebach, C. J. (2012). Trait anxiety and the neural efficiency of manipulation in working memory. *Cognitive, Affective, & Behavioral Neuroscience*, *12*, 571–588.

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, *1124*, 1–38.

Choi, Y. Y., Shamosh, N. A., Cho, S. H., DeYoung, C. G., Lee, M. J., Lee, J. M., et al. (2008). Multiple bases of human intelligence revealed by cortical thickness and neural activation. *Journal of Neuroscience*, *28*, 10323–10329.

Christoff, K., Gordon, A. M., Smallwood, J., Smith, R., & Schooler, J. W. (2009). Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 8719–8724.

Cole, M. W., & Schneider, W. (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *NeuroImage*, *37*, 343–360.

D'Esposito, M., Postle, B. R., Ballard, D., & Lease, J. (1999). Maintenance versus manipulation of information held in working memory: An event-related fMRI study. *Brain and Cognition*, *41*, 66–86.

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping*, *8*, 109–114.

Doppelmayr, M., Klimesch, W., Hodlmoser, K., Sauseng, P., & Gruber, W. (2005). Intelligence related upper alpha desynchronization in a semantic memory task. *Brain Research Bulletin*, *66*, 171–177.

Eichele, T., Debener, S., Calhoun, V. D., Specht, K., Engel, A. K., Hugdahl, K., et al. (2008). Prediction of human errors by maladaptive changes in event-related brain networks. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6173–6178.

Esposito, F., Bertolino, A., Scarabino, T., Latorre, V., Blasi, G., Popolizio, T., et al. (2006). Independent component model of the default-mode brain function: Assessing the impact of active thinking. *Brain Research Bulletin*, *70*, 263–269.

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. *Magnetic Resonance in Medicine*, *33*, 636–647.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 9673–9678.

Friston, K., Holmes, A., Worsley, K., Poline, J., Frith, C., & Frackowiak, R. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.

Geake, J. G., & Hansen, P. C. (2005). Neural correlates of intelligence as revealed by fMRI of fluid analogies. *NeuroImage*, *26*, 555–564.

Gray, J. R., Chabris, C. F., & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience*, *6*, 316–322.

Haier, R. J., & Benbow, C. P. (1995). Sex differences and lateralization in temporal lobe glucose metabolism during mathematical reasoning. *Developmental Neuropsychology*, *11*, 405–414.

Haier, R. J., Jung, R. E., Yeo, R. A., Head, K., & Alkire, M. T. (2004). Structural brain variation and general intelligence. *NeuroImage*, *23*, 425–433.

Haier, R. J., Jung, R. E., Yeo, R. A., Head, K., & Alkire, M. T. (2005). The neuroanatomy of general intelligence: Sex matters. *NeuroImage*, *25*, 320–327.

Haier, R. J., Siegel, B. V., Nuechterlein, K. H., & Hazlett, E. (1988). Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence*, *12*, 199–217.

Holmes, A., & Friston, K. (1998). Generalisability, random effects & population inference. *NeuroImage*, *7*, 754.

Jann, K., Dierks, T., Boesch, C., Kottlow, M., Strik, W., & Koenig, T. (2009). BOLD correlates of EEG alpha phase-locking and the fMRI default mode network. *NeuroImage*, *45*, 903–916.

Jung, R. E., & Haier, R. J. (2007). The Parieto-Frontal Integration Theory (P-FIT) of intelligence: Converging neuroimaging evidence. *The Behavioral and Brain Sciences*, *30*, 135–154 (discussion 154–187).

Larson, G. E., Haier, R. J., Lacasse, L., & Hazen, K. (1995). Evaluation of a "Mental Effort" hypothesis for correlations between cortical metabolism and intelligence. *Intelligence*, *21*, 267–278.

Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., et al. (2003). EEG-correlated fMRI of human alpha activity. *NeuroImage*, *19*, 1463–1476.

Laufs, H., Krakow, K., Sterzer, P., Eger, E., Beyerle, A., Salek-Haddadi, A., et al. (2003). Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 11053–11058.

Lee, K. H., Choi, Y. Y., Gray, J. R., Cho, S. H., Chae, J. H., Lee, S., et al. (2006). Neural correlates of superior intelligence: Stronger recruitment of posterior parietal cortex. *NeuroImage*, *29*, 578–586.

Li, C. S., Yan, P., Bergquist, K. L., & Sinha, R. (2007). Greater activation of the "default" brain regions predicts stop signal errors. *NeuroImage*, *38*, 640–648.

Lin, P., Hasson, U., Jovicich, J., & Robinson, S. (2011). A neuronal basis for task-negative responses in the human brain. *Cerebral Cortex*, *21*, 821–830.

Lipp, I., Benedek, M., Fink, A., Koschutnig, K., Reishofer, G., Bergner, S., et al. (2012). Investigating neural efficiency in the visuo-spatial domain: An FMRI study. *PLoS One*, *7*, e51316.

Mantini, D., Perrucci, M. G., Del Gratta, C., Romani, G. L., & Corbetta, M. (2007). Electrophysiological signatures of resting state networks in the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13170–13175.

Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: The default network and stimulus-independent thought. *Science*, *315*, 393–395.

McDaniel, M. A. (2005). Big-brained people are smarter: A meta-analysis of the relationship between in vivo brain volume and intelligence. *Intelligence*, *33*, 337–346.

McKiernan, K. A., Kaufman, J. N., Kucera-Thompson, J., & Binder, J. R. (2003). A parametric manipulation of factors affecting task-induced deactivation in functional neuroimaging. *Journal of Cognitive Neuroscience*, *15*, 394–408.

Narr, K. L., Woods, R. P., Thompson, P. M., Szeszko, P., Robinson, D., Dimtcheva, T., et al. (2007). Relationships between IQ and regional cortical gray matter thickness in healthy adults. *Cerebral Cortex*, *17*, 2163–2171.

Neubauer, A., Freudenthaler, H. H., & Pfurtscheller, G. (1995). Intelligence and spatiotemporal patterns of event-related desynchronization (ERD). *Intelligence*, *20*, 249–266.

Neubauer, A. C., & Fink, A. (2003). Fluid intelligence and neural efficiency: Effects of task complexity and sex. *Personality and Individual Differences*, *35*, 811–827.

Neubauer, A. C., & Fink, A. (2009). Intelligence and neural efficiency. *Neuroscience and Biobehavioral Reviews*, *33*, 1004–1023.

Neubauer, A. C., Grabner, R. H., Fink, A., & Neuper, C. (2005). Intelligence and neural efficiency: Further evidence of the influence of task content and sex on the brain–IQ relationship. *Brain Research. Cognitive Brain Research*, *25*, 217–225.

Perfetti, B., Saggino, A., Ferretti, A., Caulo, M., Romani, G. L., & Onofrj, M. (2009). Differential patterns of cortical activation as a function of fluid reasoning complexity. *Human Brain Mapping*, *30*, 497–510.

Postle, B. R., Berger, J. S., & D'Esposito, M. (1999). Functional neuroanatomical double dissociation of mnemonic and executive control processes contributing to working memory performance. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 12959–12964.

Preusse, F., van der Meer, E., Deshpande, G., Krueger, F., & Wartenburger, I. (2011). Fluid intelligence allows flexible recruitment of the parieto-frontal network in analogical reasoning. *Frontiers in Human Neuroscience*, *5*, 22.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 676–682.

Raven, J., Raven, J. C., & Court, J. H. (1998). *Manual for Raven's progressive matrices and vocabulary scales*. Oxford: Oxford Psychologists Press.

Rypma, B., Berger, J. S., Prabhakaran, V., Bly, B. M., Kimberg, D. Y., Biswal, B. B., et al. (2006). Neural correlates of cognitive efficiency. *NeuroImage*, *33*, 969–979.

Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., et al. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, *9*, 648–663.

Singh, K. D., & Fawcett, I. P. (2008). Transient and linearly graded deactivation of the human default-mode network by a visual detection task. *NeuroImage*, *41*, 100–112.

Song, M., Liu, Y., Zhou, Y., Wang, K., Yu, C., & Jiang, T. (2009). Default network and intelligence difference. *Conference proceedings: Annual International Conference of the IEEE Engineering in Medicine and Biology Society. IEEE Engineering in Medicine and Biology Society. Conference*, *2009*, 2212–2215.

Sporns, O., Chialvo, D. R., Kaiser, M., & Hilgetag, C. C. (2004). Organization, development and function of complex brain networks. *Trends in Cognitive Sciences*, *8*, 418–425.

Tang, C. Y., Eaves, E. L., Ng, J. C., Carpenter, D. M., Mai, X., Schroeder, D. H., et al. (2010). Brain networks for working memory and factors of intelligence assessed in males and females with fMRI and DTI. *Intelligence*, *38*, 293–303.

van den Heuvel, M. P., Stam, C. J., Kahn, R. S., & Hulshoff Pol, H. E. (2009). Efficiency of functional brain networks and intellectual performance. *Journal of Neuroscience*, *29*, 7619–7624.

Ward, B. D. (2000). Simultaneous inference for FMRI data. (From) http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf

Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature*, *393*, 440–442.

Weissman, D. H., Roberts, K. C., Visscher, K. M., & Woldorff, M. G. (2006). The neural bases of momentary lapses in attention. *Nature Neuroscience*, *9*, 971–978.