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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

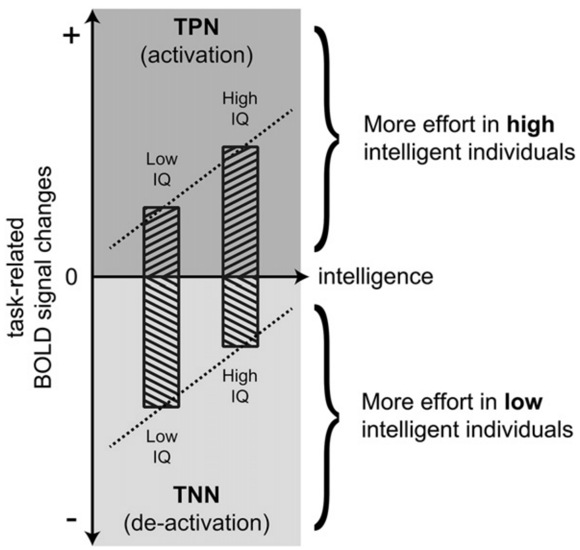

Fig. 1. Schematic illustration of possible associations between BOLD signal changes and intelligence. Positive correlations (dotted lines) may either result from higher intelligent individuals displaying larger BOLD signal increases (more activation) in the task-positive network (TPN; upper part of figure)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