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# Where smart brains are different: A quantitative meta-analysis of functional and structural brain imaging studies on intelligence

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ABSTRACT

Individual differences in general intelligence have been associated with differences in brain structure and function. The currently most popular theory of the neural bases of intelligence – the Parieto-Frontal Integration Theory of Intelligence (P-FIT) – describes a network of frontal and parietal brain regions as the main neural basis of intelligence. Here, we put the theory to an empirical test by conducting voxel-based quantitative meta-analyses of 12 structural and 16 functional human brain imaging studies, testing for statistically significant spatial convergence across studies. We focused our analyses on studies reporting associations between individual differences in intelligence (as assessed by established tests of psychometric intelligence) and either (a) brain activation during a cognitive task (functional meta-analysis) or (b) amount of grey matter as assessed by voxel-based morphometry (structural meta-analysis). The functional meta-analysis resulted in eight clusters distributed across both hemispheres, located in lateral frontal, medial frontal, parietal, and temporal cortices. The structural meta-analysis of VBM studies resulted in 12 clusters distributed in lateral and medial frontal, temporal, and occipital cortices, as well as in subcortical structures. Results of the functional and structural meta-analyses did not show any overlap — although both independently showed good match with the P-FIT. Based on the meta-analyses, we present an updated model for the brain bases of intelligence that extends previous models in also considering the posterior cingulate cortex and subcortical structures as relevant for intelligence, and in differentiating between positive and negative associations of intelligence and brain activation. From a critical review of original studies and methods, we derive important suggestions for future research on brain correlates of intelligence.



## 1. Introduction

Understanding the bases of individual differences in general cognitive ability constitutes an important topic in psychological research since more than a century (Spearman, 1904). Already in the early days of this research endeavour, scientists thought about human cognitive ability as being determined by biological factors, first and foremost by characteristics of the central nervous system (Galton, 1883). Today, the assumption that human intelligence has a biological basis in the structure and function of the brain, is commonly accepted (Deary, Penke, & Johnson, 2010; Duncan, 2010; Gray & Thompson, 2004; Jung & Haier, 2007). Based on neuropsychological studies evaluating deficits in cognitive functioning and intelligent behaviour following brain lesions, it first became apparent that human intelligence crucially relies on the proper functioning of the frontal lobes, especially the prefrontal cortex (Duncan, 1995; Duncan, 2005; Duncan, Burgess, & Emslie, 1995; Duncan, Emslie, Williams, Johnson, & Freer, 1996; Duncan et al., 2000).

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Later, brain imaging studies confirmed the involvement of the frontal cortex in intelligent behaviour, but extended this finding by suggesting a role also for regions in parietal and sensory cortices (Duncan, 2010; Jung & Haier, 2007). To date it is widely accepted that intelligence is a product of the human brain that arises from the interaction of a distributed set of brain regions, primarily comprising regions in frontal and parietal cortices.

Brain imaging research on the neural bases of intelligence has targeted functional as well as structural correlates of general cognitive ability. Functional correlates of intelligence have been studied using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), which provide a proxy for neural activity in the brain by assessing changes in metabolism and hemodynamics. Studies on the structural bases of intelligence considered properties of grey matter and white matter. Grey matter properties have been studied with different techniques for the analysis of data from high-resolution structural magnetic resonance imaging (sMRI), mainly including voxel-based and surface-based morphometry methods. Voxel-based morphometry (VBM; Ashburner & Friston, 2000; Mechelli, Price, Friston, & Ashburner, 2005) was predominantly used to examine the amount of grey matter in different parts of the brain, while surface-based methods focus on properties of the cortex, such as cortical thickness or surface area (e.g., Lyttelton, Boucher, Robbins, & Evans, 2007). Properties of white matter have been studied with VBM, diffusion tensor imaging (DTI), and magnetic resonance spectroscopy (MRS). Based on the finding that individual differences in these measures of brain function and structure are correlated with individual differences in psychometric intelligence (e.g., Gray, Chabris, & Braver, 2003; Haier, Jung, Yeo, Head, & Alkire, 2004), a broad consensus arose that intelligence is linked to characteristics of our neural system in a circumscribed set of brain regions, mainly located in frontal and parietal cortices (Deary et al., 2010; Duncan, 2010; Gray & Thompson, 2004; Jung & Haier, 2007).

In a seminal review by Jung and Haier (2007), 37 neuroimaging studies on intelligence were reviewed, and the reported effects of intelligence on brain structure and function were counted by Brodmann's areas. From summarising these data, the authors concluded that differences in intelligence are linked to structural and functional variations in the lateral prefrontal cortex (dorsolateral and ventrolateral prefrontal cortices, DLPFC and VLPFC), medial frontal cortex (anterior cingulate cortex, ACC, and pre-supplementary motor area, preSMA), parietal cortex (inferior and superior parietal lobule, intraparietal sulcus, IPS), and sensory areas in the temporal and occipital cortices. In addition, the review of Jung and Haier (2007) considers white matter tracts connecting these regions, in particular the arcuate fasciculus and the superior longitudinal fasciculus. The authors termed their model of the brain basis of intelligence the *Parieto-Frontal Integration Theory* of intelligence (P-FIT, Jung & Haier, 2007).

Other authors and reviews come to similar conclusions. For instance, Duncan (2010) discusses roughly the same regions, i.e., prefrontal and parietal cortices, as relevant for diverse cognitive demands and intelligent behaviour, respectively, and subsumes them under the term *multiple-demand system* (MD system, see also Duncan & Owen, 2000). Notably, the brain regions considered in the P-FIT model and in the MD system largely resemble what in other – i.e., not intelligence-related – contexts is referred to as (*attention and*) *working memory system* (Cabeza & Nyberg, 2000), *cognitive control network* (Cole & Schneider, 2007), or – most generally – the *task-positive network* (Fox et al., 2005). The frontal and parietal brain regions under discussion show increased activation for a wide variety of different cognitive tasks — including tasks that are commonly used in intelligence tests, e.g., matrix problem solving tasks (Duncan & Owen, 2000; Duncan et al., 2000; Goel & Dolan, 2001; Noveck, Goel, & Smith, 2004). Furthermore, several studies suggested that variation in structure and function of these regions across individuals (i.e., individual differences in tissue properties and neural activity during cognitive challenges) can explain individual differences in general cognitive ability, i.e., (fluid) intelligence (e.g., Gray et al., 2003; Haier et al., 2004). However, while the P-FIT's assumption that frontal and parietal cortices support intelligent performance is widely approved, the authors of the P-FIT themselves evaluated their analyses as providing "provisional empirical support" for a model that was "very much still a hypothesis" (Jung & Haier, 2007, p. 152). Moreover, it has been noted early on that the convergences between the studies constituting the basis of the P-FIT may be smaller than commonly believed — particularly with respect to the structural correlates of intelligence and the synopsis of functional and structural findings (Colom, 2007, 2014).

Eight years after the first description of the P-FIT model, there are now several more studies available on this topic, many of which show considerable methodological improvements compared to older studies. One essential improvement in the functional neuroimaging of intelligence consists in the stronger focus on individual differences in brain activation in more recent studies. Previous reviews (e.g., Jung & Haier, 2007) included two types of studies that we call the *task approach* and the *individual differences (ID) approach*. With the *task approach*, researchers study the neural correlates of processing a particular task. In research on the neural underpinnings of intelligence following this approach, the tasks performed during functional imaging are related to intelligence. Often researchers used tasks taken from established intelligence tests. Typically, these studies report the mean task-induced brain activation for a whole group of subjects — not taking into account differences in brain activation related to differences in the individuals' levels of intelligence.

In contrast, the *ID approach* considers individual differences in brain activation during cognitive challenges and tests whether these can predict individual differences in intelligence. As, by definition, the theoretical construct of intelligence serves the purpose of describing differences between people, we claim that it must be the primary aim of a neurocognitive approach to intelligence to explain such individual differences in general cognitive ability with individual differences at the neural level. Consequently, we judge the *ID approach* to be more valid for identifying neural underpinnings of human intelligence. Considering that the review of Jung and Haier (2007) included a substantial proportion of studies (i.e., 16 of 26 functional studies) employing the *task approach*, it may appear little surprising that their synopsis resulted in a set of brain regions that is typically activated for any kind of higher cognitive demand (see above, comparison of P-FIT regions and the cognitive control or task-positive network). Yet, the fact that a brain region is commonly activated during cognitive challenge does not yet imply that individual differences in this activation are linked to individual