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MORPHOLOGIE ET IMAGERIE DU SYSTEME NERVEUX CENTRAL

STRUCTURAL AND FUNCTIONAL NEUROMARKERS OF HIGH GENERAL COGNITIVE ABILITY (*G*)

PAR

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INTRODUCTION

In 1869, the English polymath Sir Francis Galton published *“Hereditary genius: An inquiry into its laws and consequences”* (1). His book was the first social scientific attempt to study giftedness and genius – human differences and inheritance – through statistical methods and large biographical data of eminent men. Founder of modern psychometrics and historiometry, cousin of Charles Darwin, he is also considered as a pioneer in the very controversial practice of eugenics, which is the study to analyze and improve the genetic quality of the human population making up the society.

Since then, scientific research has sought to understand, define and measure intelligence through various means and different disciplines, from medicine to sociology. Among the many questions surrounding the study of intelligence, one appears to be particularly topical and raises many challenges and ethical questions for the (near) future: what does a smart brain look like? And, behind this idea, can brain mechanisms be tweaked to enhance intelligence with brain training, neurochemistry or even genetic engineering?

The considerable improvements made in brain imaging open new and promising ways to study the structural and functional neuromarkers associated with high intelligence. Obtaining reliable information about how high performance brains are organized (structure) and how they work (function) might provide very useful knowledge for designing effective training programs tailored to less efficient (compromised) brains, whatever causes.

In the first section, I will define concepts strongly related to intelligence then, in a second part, I will review some of the most recent neuroimaging studies using functional and structural approaches to examine the brain bases of intelligence. Finally, I will introduce an updated model for neural correlates of intelligence, based on these findings in brain imaging.

1. Definitions

In order to answer our research question, three related and often conflated concepts need to be precisely defined: intelligence, *g*-factor and intelligence quotient – mostly known as IQ.

1.1 Intelligence

The term *intelligence* comes from the combination of the Latin prefix *inter-* ("between") and the verb *lĕgĕre* ("choose, read"). Thus, etymologically speaking, intelligence means "making a choice, a selection" (2). However, in order to conduct rigorous scientific research, the definition below is the common definition, largely adopted among researchers:

> Intelligence is a very general mental capacity that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly, and learn from experience. It is not merely book learning, a narrow academic skill, or test—taking smarts. Rather, it reflects a broader and deeper capability for comprehending our surroundings—' catching on,' 'making sense' of things, or 'figuring out' what to do'' (3).

Thus, among the scientific community, intelligence is widely accepted as a general mental ability, including specific abilities that can be grouped into five more specific factors: reasoning, memory, spatial ability, vocabulary and speed of information processing. The figure 1 below shows how all these factors are related from one to another by the *g*-factor.

1.2 The g-factor

Firstly described by the English psychologist Charles Spearman, the *g*-factor (also known as *general intelligence factor*) is the basis of most intelligence assessment used in research today (4,5). *g* is a variable characterizing the positive correlations between all the different tests in a mental abilities test battery – or *positive manifold*. The positive manifold constitutes one of the core findings in intelligence research: individuals who score high on one test tend to score high on the others (4). Thereby, the *g*-factor is a common source of individual differences in all cognitive ability tests (5–7).

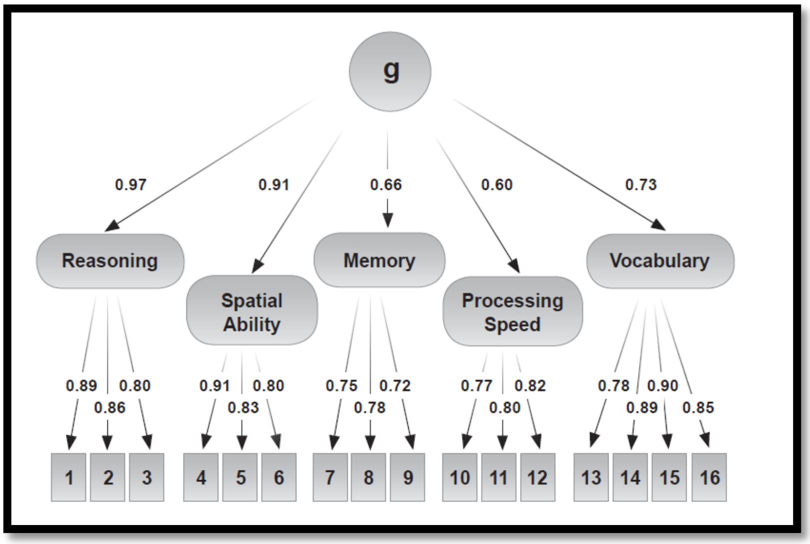

Figure 1. The structure of mental abilities. The g-factor is common to all mental tests. Number are the correlations that show the strength of relationship between tests, factors, and g. Note all correlations are positive. Source: Haier (2016, p. 6)

1.3 Intelligence quotient (IQ)

While the scientific construct of *g* relies on the correlations among test scores, IQ relies on the summation of standardized scores. It is based on a subset of the mental abilities that relate to everyday intelligence and is considered as a proper measure of intelligence (high *g*-loading[1]). It is worth mentioning that IQ is not an absolute measure (such as height or liquid) but an arbitrary variable – intelligence in general – that only has meaning relative to other people. However, despite various critics on its utility, IQ scores predict general learning ability and many real-world aspects in a person life (such as education level, health, etc.) (4).

In a normal distribution, about 68% of the population has an IQ comprised between 85 and 115 on the Weschler scale (see appendix 1). Research usually defines higher intelligence (or giftedness) when an individual scores over 130 (which is the top 2%) on the Weschler scale (for adults or children)[2].

2. Brain imaging reviews of (high) intelligence

2.1 The P-FIT model (2007): the first synthesis of 37 brain imaging studies of intelligence

[1] The *g*-loading is the amount of *g* represented in a test (Haier, 2013)

[2] There are three Weschler scales used to measure IQ, depending on the age of the individual: Wechsler Preschool and Primary Scale of Intelligence (WPPSI; 2 years and 6 months – 7 years and 7 months); Weschler Intelligence Scale for Children (WISC; 6 – 16 years old); Weschler Adult Intelligence scale.

In 2007, Jung and Haier (8) reviewed the 37 neuroimaging studies of intelligence published worldwide since the first PET study in 1988 (9). Despite using different intelligence tests and different imaging methods (PET, fMRI, structural MRI), consistent findings were found. Following a method used to review the emerging literature from cognitive neuroimaging studies (10), the authors showed that several brain areas were common in 50% or more of all the studies (4). The figure 2[3] presents the model of brain-intelligence relationships resulting from these findings and called the *parieto-frontal integration theory* (P-FIT) of intelligence. The 9 main identified salient brain areas are mostly located in the frontal and parietal lobes, in the left, right or both hemispheres. Most of them are related to fundamental cognitive processes, such as memory, language or attention.

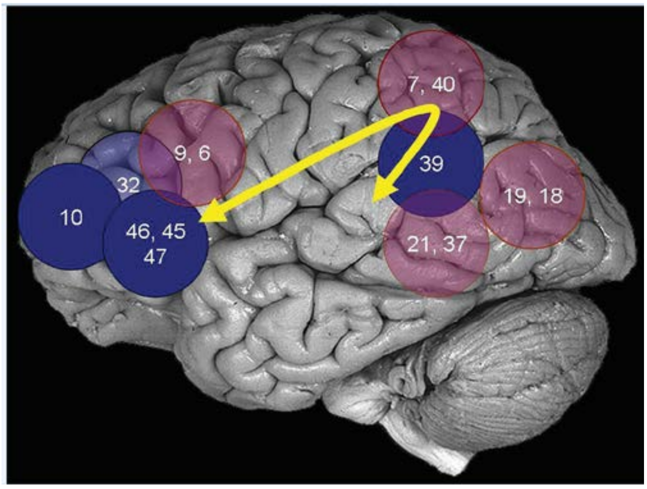

Figure 2. The Parieto-Frontal Integration Theory (P-FIT) showing brain areas associated with intelligence. Numbers = Brodmann areas; dark blue circles = predominant left hemisphere associations; red circles = predominant bilateral associations; yellow arrow = arcuate fasciculus. Source: Haier (2016)

Because it integrates information flow between parietal and frontal areas, the arcuate fasciculus, a major white matter tract of fibers, appears to play a substantial role in intelligence. Importantly, the way information flows around these regions seems to be the basis for individual differences in intelligence and reasoning tasks: the more efficient information flow is associated with higher scores in intelligence tests (4).

The basic proposal of the P-FIT model is that efficient brains integrate sensory information in back brain areas and then the information is further integrated to higher-level processing as it flows to frontal areas (8).

[3] An animated version of the P-FIT model can be found on the website www.cambridge.org/us/academic/subjects/psychology/cognition/neuroscience-intelligence.

Since this review, over than 100 imaging studies of intelligence have been published all across the world. Overall, these recent findings support the basic P-FIT model as we will describe below.

2.2 Recent brain imaging reviews of literature

For the last decade, considerable improvements have been made in brain imaging techniques and methodology, allowing the researchers to explore the neural bases of intelligence with much more precision, in both spatial and temporal resolutions. As pointed by Basten, Hilger and Fiebach, "one essential improvement in the functional neuroimaging of intelligence consists in the stronger focus on individual differences in brain activation in more recent studies" (7). Since the review of Jung and Haier in 2007, most of the brain imaging studies have been using PET or MRI to assess brain activation during a cognitive task (functional study) or investigating properties of grey and white matters with different analyze techniques. These techniques usually include voxel-based morphometry (VBM) – to examine the amount of grey matter in different brain areas – and surface-based morphometry (SBM) – to analyze cortical thickness or surface area (7).

This section provides a synthesis of three recent reviews (including a meta-analysis) on both functional and structural neural correlates of intelligence and the possible overlaps between these networks (7,11,12).

2.2.1 Functional neuromarkers of intelligence

Aiming at testing the P-FIT model empirically, Basten et al. (7) realized voxed-based quantitative meta-analysis of 16 functional and 12 structural human neuroimaging studies. In the same vein as Colom and Thompson (11), they focused the analyses on research reporting associations between individual differences in intelligence (as assessed by psychometric tests) and the functional or structural correlates supporting this ability.

Regarding the functional networks, both teams found that intelligence was associated with the strength of brain activation in left and right lateral prefrontal cortex (8,12), in medical frontal cortex, in bilateral parietal cortex (13) and in right temporal cortex (7).

In frontal and parietal areas, Basten and al. (7) suggested overlap of findings bilaterally in the inferior frontal sulcus (IFS), in the inferior frontal gyrus (IFG) and the right middle frontal gyrus (MFG) (14) and in the posterior part of the right superior frontal sulcus (SFS). Most of the studies reviewed by Basten et al. (7) or Colom and Thompson (11) support the P-FIT model of intelligence (8). Regarding giftedness specifically, reviews highlight:

- An increased involvement of the bilateral frontoparietal network (esp. lateral prefrontal, anterior cingulate) through preferential activation of the posterior parietal regions (6,13);

- An enhanced interhemispheric connectivity (8);

- Increased activations in Brodmann areas 7 and 40 (superior and intraparietal cortices) (6,13);

- A greater integration in brain mechanisms (12,14,15).

Elsewhere in the brain, Basten and al. (7) also suggest overlap of findings bilaterally in the pre-supplementary motor area (preSMA), in the dorsal part of the anterior cingulate cortex (dACC), in the left superior parietal lobule (SPL), adjacent to the intraparietal sulcus (IPS), in the right precuneus, and in the posterior part of the right middle temporal gyrus (MTG).

2.2.2 Structural neuromarkers of intelligence

In the reviews presented hereinabove, the authors included both functional and structural studies aiming at understanding where in the brain is intelligence. Structural approaches mostly use three measures: the cortical gray matter volume (GMV), the cortical surface area (CSA) and the cortical thickness (CT) (14). Because of their sensitivity to different attributes of cortical anatomy, cortical measures can be useful for assessing individual differences in brain structure and function (11).

Grey matter. Across studies using structural approaches, intelligence was significantly related to the amount of grey matter in specific areas, mostly in frontal and parietal regions but also in more internal structures. Thus, an important overlap seems to exist in lateral prefrontal cortex, especially the left frontopolar cortex (BA 10) (11,14,16) and the right superior and inferior gyri (7). Aiming at examining the commonality of brain areas between different intelligence factors (fluid, crystallized and spatial intelligence) and cognitive functions (such as working memory, attention or language) using a structural approach, Colom et al. (14) highlight that the main overlapping clusters between GMV and CSA are observed in the middle frontal gyrus. They strongly involve fluid intelligence and working memory.

In their meta-analyses, Basten, Hilger and Fiebach (7) relate the important association of frontal areas and more particularly the frontopolar cortex (FPC), with intelligence. In fact, the FPC appears to support more higher-order processes, which are critical for high performance scores in intelligence tests.

The amount of grey matter in the supplementary motor area, the dorsal part of the posterior cingulate cortex, the temporal and bilateral occipital cortices (BA 18, 19, 37) is also correlated with different measures of intelligence (7,11).

Finally, recent structural studies reviewed by Basten et al. (7) and Colom & Thompson (11) show the implication of specific subcortical areas, including the caudate nucleus. On account of its involvement in the striatal dopaminergic gating mechanism, the caudate controls dopamine concentration in prefrontal cortex and impacts on cognitive performance.

White matter. The integrity of white matter tracts can be assessed by fractional anisotropy (FA), which examines both myelination and axonal thickness. Yu and al. (17) studied correlations between the integrity of several tracts and intelligence scores in two groups: average and high intelligence adults. Using FA analyses, the authors showed that participants with higher intelligence displayed more white matter integrity than average IQ participants, but only in the right uncinate fasciculus, suggesting white matter might support the efficient flow of information in the brain (6).

In a recent study, Navas-Sánchez et al. (12) investigated the relationship between mathematical giftedness, IQ and the microstructure of white matter tracts in a sample of 36 adolescents divided in two groups: math-gifted subjects and age-matched controls. Confirming their hypothesis, results showed a positive correlation between IQ and FA, mainly in the corpus callosum. This result supports the idea that efficient information transfer between hemispheres is critical for higher intellectual capabilities. Moreover, the math-gifted participants had increased FA in white matter tracts linking frontal areas with basal ganglia and parietal regions.

These studies comfort the hypothesis that intelligence differences would be associated with the trajectory of cortical development in frontal brain regions and more plasticity in the developmental process of children with high IQ scores (11). Specifically, Shaw et al. (18) proposed that higher intelligent children are characterized by an accelerated and prolonged phase of increase in cortical thickness then a more vigorous thinning during early adolescence (7).

To conclude this section, the results presented above support the main ideas of the P-FIT model of intelligence proposed by Jung and Haier in 2007: frontal and parietal regions appear to be critical for high intelligence and the way information flows around these areas seems to be the basis for individual differences in intelligence.

2.2.3 From the P-FIT to an updated version for the brain bases of intelligence

Ten years after the P-FIT model of intelligence and based on the results of the meta-analyses they conducted, Basten et al. proposed an updated model for the brain bases of intelligence. The figure 3 summarizes the main areas involved in intelligence. As noted by the authors, it differs from the P-FIT model on three points:

1) It differentiates functional (brain activation) and structural (amount of grey matter) neuromarkers of intelligence;
2) It differentiates positive and negative associations of intelligence and brain activation;
3) It extends the set of brain regions considered relevant by including the insular cortex, the posterior cingulate cortex and subcortical structures (7).

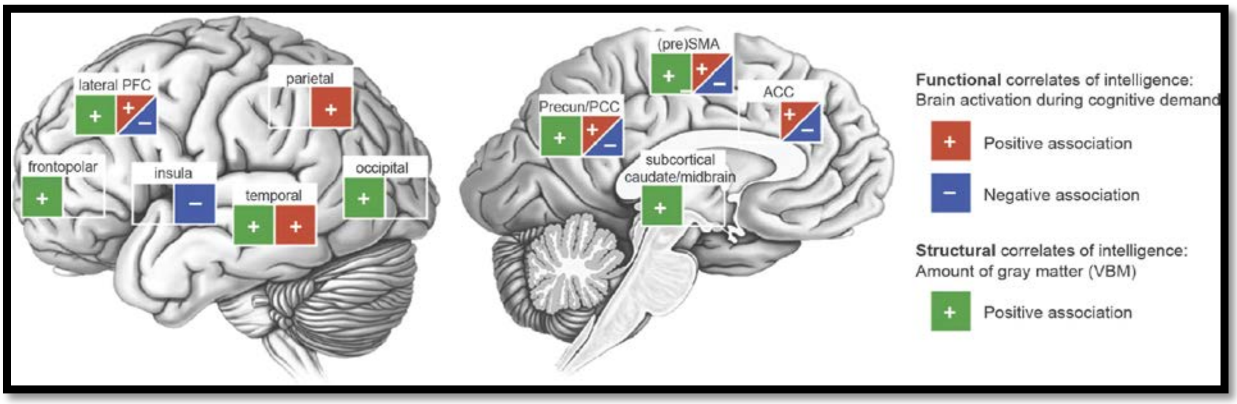

Figure 3. Updated model of the brain bases of intelligence. Abbreviations: ACC: anterior cingulate cortex; precun: precuneus; PCC: posterior cingulate cortex; PFC: prefrontal cortex; (pre)SMA: (pre-)supplementary motor area. Source: Basten et al. (2015)

FINAL REMARKS

This essay aimed at synthesizing recent brain imaging research regarding functional and structural neuromarkers of intelligence. The significant progress in the field of neuroimaging in the last decade helped shift intelligence research away from the controversies of predominately psychometric approaches to a more neuroscientific perspective (4).The recent techniques for seeing the brain (e.g. magnetoencephalography, diffusion tensor imaging) and analyzing data (e.g. fractional anisotropy, voxel-based morphometry), open promising ways to understand “how the brain generates the mind” (19) and works differently according to individuals.

However, some limits must be pointed and subjected to the reader’s consideration for deeper examination:

1- To date, intelligence can’t yet be measured as an absolute quantity (but measurements are still required to do scientific research in intelligence (4). Thus, the accumulation of research findings and the development of technological devices are necessary to increase our understanding of the field and elaborate proper measures and definition of intelligence.

2- In their meta-analyses, Basten et al. insist on the importance to extend research beyond the localization of single regions involved in intelligent performance and to “study connections and dynamic interactions within and between neural networks” (7). It is all the more essential that recent major advances in neuroimaging analysis, based on connectivity patterns among brain areas, have provided crucial clues for the identification of ‘brain fingerprints’ unique to individuals (20).

3- Until now, most studies in brain imaging have been principally focused on group analyses, neglecting the fact that every brain is unique and that individualized profiles act as an ‘identifying fingerprint’ (21). Connecting these two last limits, Finn & al. (20) showed that the obtained functional connectivity profiles predicted individual differences in fluid reasoning ability.

To summarize, one of the main take-home messages emerging from the studies herein below is the critical necessity to move from a group-based approach to an individual-based brain imaging research (4,7,11,20). Pursuing and favoring a “fully personalized investigation of brain function" (22) will allow designing interventions best fitted for each individual regarding their profile and the ability of interest to enhance, repair or improve (21).

In order to galvanize further reflections in the part of the reader, I would like to conclude this essay with this quote from P^{r} Haier in his online class *"The Intelligent Brain"* (2013, p. 2):

> One central issue is whether we have a moral obligation to increase intelligence if we could. Assuming that more intelligence is always better than less, would you take an IQ pill, or prevent your child from taking one? Research on intelligence is progressing so that such choices could be real in the not-so-distant future.

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APPENDIX

APPENDIX 1. THE NORMAL DISTRIBUTION OF IQ SCORES AND THE PERCEPT OF PEOPLE WITHIN EACH LEVEL (SOURCE: HAIER, 2016, P.14)