



Review

The neural code of intelligence: From correlation to causation

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Abstract

Research into the neural underpinning of intelligence has mainly adopted a *construct perspective*: trying to find structural and functional brain characteristics that would accommodate the psychological concept of *g*. Few attempts have been made to explain intelligence exclusively based on brain characteristics – the *brain perspective*. From a methodological viewpoint the brain intelligence relation has been studied by means of correlational and interventional studies. The later providing a causal elucidation of the brain – intelligence relation.

The best neuro-anatomical predictor of intelligence is brain volume showing a modest positive correlation with *g*, explaining between 9 to 16% of variance. The most likely explanation was that larger brains, containing more neurons, have a greater computational power and in that way allow more complex cognitive processing. Correlations with brain surface, thickness, convolution and callosal shape showed less consistent patterns. The development of diffusion tensor imaging has allowed researchers to look also into the microstructure of brain tissue. Consistently observed was a positively correlation between white matter integrity and intelligence, supporting the idea that efficient information transfer between hemispheres and brain areas is crucial for higher intellectual competence. Based on functional studies of the brain intelligence relationship three theories have been put forward: the neural efficiency, the P-FIT and the multi demand (MD) system theory. On the other hand, The Network Neuroscience Theory of *g*, based on methods from mathematics, physics, and computer science, is an example for the brain perspective on neurobiological underpinning of intelligence. In this framework network flexibility and dynamics provide the foundation for general intelligence.

With respect to intervention studies the most promising results have been achieved with noninvasive brain stimulation and behavioral training providing tentative support for findings put forward by the correlational approach. To date the best consensus based on the diversity of results reported would be that *g* is predominantly determined by lateral prefrontal attentional control of structured sensory episodes in posterior brain areas. The capacity of flexible transitions between these network states represents the essence of intelligence – *g*.

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1. Introduction

The only numerical measures of intelligence are test scores. They are theoretically based on psychometric *g*, which is an empirical outcome of factor analysis that accounts for a large proportion of variance in individuals' mental tests

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[1]. In other words, individuals who perform well on one mental task tend to perform well on most others. The higher the g -loading of a test is, the more it is considered to include the essence of intelligence. Although this is one of the most often replicated findings in psychology, it cannot conceal that intelligence is what the test is testing [2]. Therefore IQ scores are heavily criticized and demonized, especially when researchers try to answer questions which oppose the current Zeitgeist, such as, are there differences in cognitive abilities between ethnic groups or between genders? Sometimes the answers may even lead to violence, as was the case for Jensen's [3] statement that compensatory education in the US failed to produce lasting beneficial effects on children's IQ. One has to admit that based on IQ test scores, these two questions have no answer that would withstand scientific rigor. It is therefore not surprising that intelligence research has tried to find an IQ biomarker. This attempt makes sense because from a brain perspective, intelligence is just a specific sequence of action potentials.

Historically, the first general theory to present the idea that different parts of the brain relate to intelligence was developed by German anatomist Franz Josef Gall (1758–1828). His ideas began with an observation made in his youth. Reportedly, he was annoyed by students with good memories who achieved excellent marks but did not have an equivalent ability for original thinking. According to his recollection, the students with the best memories had large, protruding eyes. Using this crude observation, Gall developed a general theory of how the brain might produce differences in individual abilities into a theory called localization of function. For example, Gall proposed that a well-developed memory area of the cortex located behind the eyes would cause the eyes to protrude. Aliens featured in Hollywood science fiction movies are often portrayed as having bulging foreheads, reminiscent of Gall's idea that the frontal lobes are the seat of intelligence [4]. It is worth mentioning that the most influential contemporary theories of the brain intelligence relationship, the neural efficiency [5], the parieto-frontal integration theory (P-FIT) [6], and the Multiple-Demand (MD) System [7], have also positioned intelligence in frontal brain areas.

Our developing understanding of the brain IQ relation is a result of improved capabilities in brain imaging and the availability of new tools and methods for representing and analyzing this relation [8]. Some promising candidates in the past were string length and individual alpha frequency (IAF), which were later replaced by more sophisticated measures derived from mathematics – chaos and graph theories [9]. The disappointing part is that they on average still do not explain much more than about 25% of IQ test score variance [10].

This review will try to explain the brain intelligence relation from the viewpoint of correlational and interventional studies. The later providing a causal perspective on the link between a psychological construct and a physiological organ. Additionally some contemporary trends in the further development of the brain intelligence research will be highlighted.

2. The intelligence construct

The theoretical frame for psychometric intelligence was provided by Spearman's [1] g -factor, an empirical outcome of factor analysis derived from the first unrotated principal component that accounts for a large proportion of variance in individuals' mental test scores. Correlations obtained between mental test scores tend to be positive and are often moderately large – the positive manifold. The higher the g -loading of a test is, the more it is considered to include the essence of intelligence.

In models that have emerged during the past decades, such as the Cattell–Horn Gf–Gc and the Carroll Three-Stratum model, human intelligence forms a multilevel hierarchy, with a general factor at the pinnacle (third stratum), many very specific abilities at the bottom (first stratum), and separable but correlated group factors of ability in between (second stratum) [11]. For example, the most prominent second stratum factors include fluid and crystallized intelligence and short term memory, with specific first stratum factors such as inductive, deductive and quantitative reasoning, as well as speed of reasoning general information, foreign language proficiency and aptitude. Despite the exact numerical relations between factors the enigmatic characteristic of g lies in the fact that it is just an empirical result that cannot be explained by examining the tests from which it was derived. Test performance is only a vehicle for the measurement of g . Thus, giving this result a neural marker is one way to understand its nature and origin [12].

Research into the neural basis of intelligence has mainly adopted a *construct perspective*: trying to find structural and functional brain characteristics that would accommodate the psychological construct of intelligence [9,13]. Most often additional constructs such as working memory (WM), processing speed and attention have been introduced on an interim level of reductionism between g and biological intelligence [14]. The problem with such an approach is

that these constructs have considerable conceptual overlap and they are not readily localized into one or a few brain centers, what makes them at times vague and not entirely distinct [13].

For example, Colom et al. [15] used hierarchical factor analysis of the Wechsler Adult Intelligence Scale (WAIS) showing that among the eight WAIS subtests, block design and vocabulary had the highest g -loadings. In a second step, they correlated the test scores with voxel-based morphometry data obtained from 48 subjects. Based on the results they concluded (p. 1359): “[...] it is shown that two prototypical measures of verbal and nonverbal g (i.e., vocabulary and block design) correlate with the amount of regional gray matter across frontal, parietal, temporal, and occipital lobes, suggesting that the general factor of intelligence relates to areas distributed across the brain as opposed to the view that g derives exclusively from the frontal lobes.”

The opposing viewpoint that Colom and coworkers alluded to was put forward by Duncan [16]. In this study positron emission tomography (PET) was used while respondents solved high/low- g tasks with verbal and spatial content. Regions of significantly greater blood flow in high- g tasks compared to low- g tasks were observed for the spatial tasks bilaterally in the lateral prefrontal cortex, and in a discrete region of the medial frontal gyrus. For the verbal tasks, the only significant difference was visible in the lateral frontal cortex of the left hemisphere, corresponding to the activation observed for the spatial tasks. The conclusion put forward was (16, p. 458): “Such results argue strongly against the possibility that high- g tasks are associated with diffuse neural recruitment, as predicted by broad sampling of the brain’s major cognitive functions.”

Even though the conclusions in the two exemplary studies differ, the approach they used was the same, namely trying to find evidence in brain structure or function that corresponds to the construct of intelligence. Recently research has adopted an opposite perspective: explaining the construct of intelligence based on what is known about information processing in the central nervous system — the *brain perspective*. Given that the brain is conceived as a dynamic network of interconnected elements [12], and cognition is seen as the consequence of dynamic interactions among distributed brain areas operating in large-scale networks [17,18], network neuroscience [19,20] seems to be a promising candidate for explaining individual differences in intelligence and their relation to brain structure and function [12,13].

3. The biological background of intelligence

From a methodological viewpoint the brain intelligence relation has been studied by means of correlational and interventional studies. Correlational studies have adopted two approaches: (1) individuals are examined at rest, and correlation analyses are used to examine associations between different measures of brain structure (obtained with Magnetic Resonance Imaging – MRI, PET, Diffusion Tensor Imaging – DTI) and IQ test measures. In the case of neuroelectric procedures, such as the electroencephalogram (EEG), or magnetoencephalogram (MEG) the measures obtained indicate characteristics of the resting brain, mainly patterns of power and frequency while the participants’ eyes are closed or open. (2) In the second functional approach, brains of individuals who are under cognitive load are scanned, and the observed differences between rest and activity are examined in relation to IQ scores.

On the other hand, the experimental approach tries to influence intelligence and by that establish a potential causal relation between intelligence and brain activity. At present, behavioral training, and noninvasive brain stimulation (NIBS), such as transcranial electric (TES), or magnetic (TMS) stimulation seem to be the most promising methods for influencing cognitive processes linked to brain activity.

3.1. Correlational studies

3.1.1. Brain structure

Most studies that correlated intelligence with brain structure have done this on a macroscopic level. The development of brain mapping methods, such as DTI, caused a shift in research interest toward the microscopic level: analyzing the density and integrity of fibers, and the degree of myelination.

3.1.1.1. Brain volume. The best neuroanatomical predictor of intelligence is total brain volume. A positive correlation between different IQ tests and brain volume has been reported in several studies and metaanalyses [21–25]. The work of Darwin [26] propelled the idea that human intelligence is related to a correspondingly large brain. Modern brain imaging techniques, have allowed for in vivo noninvasive measurements of brain volume replacing crude

markers like head circumference. For example, Ritchie et al. [22] conducted a large-scale study ($N = 672$) in which structural modeling was used on six different brain variables among which were brain volume, cortical thickness, and different measures of white matter structure. In relation to g and fluid intelligence, brain volume accounted for the largest portion of variance (12%), followed by cortical thickness (5%). Similar findings were also reported in a recent study [25] utilizing MRI and cognitive tests data from the Human Connectome project ($N = 900$). In general the correlations between brain volume and intelligence show a robust positive association, explaining between 9% to 16% of variance. The positive correlation between brain volume and intelligence has been explained by a positive association between brain volume and overall number of neurons. It is reasonable to assume that larger brains contain more neurons, have greater computational power, and in that way allow more complex cognitive processing [25]. Additionally it was revealed that the relation between brain volume and intelligence is more complex than previously assumed [27]. During the lifespan, the brain undergoes several changes: an increase in brain volume between 9 and 13 years of age, followed by a gradual decrease starting at age 13, followed by another growth between 18 and 35 years of age, thereafter a steady annual volume loss occurred [28]. The interesting finding in relation to intelligence was that more intelligent individuals showed more pronounced total brain volume increases and attenuated decreases [27].

3.1.1.2. Brain tissue and surface. Measures of cortical thickness are thought to represent the density and arrangement of neurons per column, as well as glial support and dendritic arborization. In contrast, cortical surface area is related to the number and spacing of minicolumnar units of cells [29]. All in all, the few studies that have been conducted show a modest positive correlation ($r = 0.24$) between cortical thickness and intelligence in adults. The topography of significant correlations was mainly observed in frontal and to a lesser extent in temporal brain areas [22,30–32]. Similar findings were also reported in a recent large scale study involving Chinese high school students. Higher academic performance was related to greater regional gray matter density of the left dorsolateral prefrontal cortex. The analysis further suggested that general intelligence partially mediated this relationship [33]. On the other hand, Karama et al. [34] found positive correlations between intelligence and cortical thickness in different locations of the brain scattered over the frontal, temporal, parietal, and occipital areas. The correlations were mostly symmetrical although slightly lateralized to the left hemisphere. Yet in another study [35], significant correlations between IQ and cortical thickness were reported for the right parahippocampal gyrus, right occipital, and left parietal lobe.

Even less numerous are studies correlating cortical surface area with IQ. Román et al. [35] reported a positive correlation between cortical surface area and the higher order factor of g bilaterally in the dorsolateral prefrontal cortex. In a second study [36], a similar relation was observed when full-scale IQ was correlated with cortical convolution. Specifically, intelligence scores were positively associated with the degree of gyrification only in the temporo-occipital lobe, particularly in the posterior cingulate gyrus.

A second characteristic of the correlations between cortical surface area and thickness with intelligence is that they are not stable, and show considerable developmental fluctuations [29,31,32]. They shift from negative in early childhood to positive in late childhood. It was further shown that the trajectories of cortical thickening differed in relation to the level of intelligence. Children of superior intelligence (IQ 121–141) displayed a marked increase in cortical thickening peaking at around 11 years of age, even though they started from a relatively thinner cortex. On the other hand, the average intelligent (IQ 83–108) group tended to show a steady decline in cortical thickness. Changes in cortical thickness in high intelligent (109–120) children followed an intermediate pattern, approximating the average intelligence group. A second characteristic of the latter two groups was also a much shorter period of cortex thickening that peaked at 7–8 years of age [32].

3.1.1.3. Corpus callosum and subcortical structures. The corpus callosum (CC) is the largest bundle of fibers in our brain that connects homologous areas of the two hemispheres, therefore it may be involved in any aspect of cognitive functioning, especially in those that require complex problem solving [4]. However, empirical evidence for the relationship is rather inconclusive. Just one study reported a positive relation between callosal thickness and intelligence which was observed in the posterior parts of the CC [37]. In contrast, when the CC of younger individuals was analyzed the correlations with intelligence were mostly negative — especially for children, and the relation also showed complex sex specific patterns [38–41]. The problem is that some of the trends observed differ substantially and even point in opposite directions. Similarly inconclusive was also a study which instead of analyzing CC thickness focused on the shape of CC and its relation to specific cognitive variables. The only significant correlation observed was for

attentional control that was positively associated with a thinner and more curved CC shape [42]. In a recent study the association between corpus callosum characteristics and intelligence measures was reexamined [43]. Analyzing mid-sagittal measures of regional callosal thickness, a positive association in the splenium of the CC was found for full scale IQ. This association became insignificant when the participants' age was considered in the analysis, suggesting that the positive relation could be explained by a temporal co-occurrence of overall trends in intellectual development and structural callosal increase.

Correlational research on the brain structure–IQ relation has also addressed subcortical areas, such as basal ganglia, the thalamus and cerebellum. Few studies have examined this topic which does not allow for a generalization. In one study, mainly positive correlations were reported between basal ganglia (caudate nucleus and pallidum) volumes and figural and numerical components of intelligence, the former also being sex-specific [44]. In a second study, the volume of the caudate nucleus, but not the volumes of other subcortical structures, showed a significant positive association with IQ [45]. A third study found positive correlations between the shape of right striatal structures and thalamus with spatial and fluid intelligence but not with crystallized intelligence [46]. In yet another study it was revealed that both male and female networks in the cerebellum have small-world properties with differences in females (especially in higher IQ females) indicative of higher neural efficiency [47]. The positive correlations were observed in samples consisting of young adults of about 20–25 years of age. On the other hand, reverse patterns have been observed for children. In 6–10 year old, increased gray matter volume of the putamen was associated with poor performance on IQ tests and tests of working memory and response speed [48]. These results to some extent resemble those reported for cortical thickness and volume, as well as those reported for corpus callosum thickness in children and young adolescents.

3.1.1.4. Microstructure of white matter. DTI, an MRI-based imaging technique, measures the random motion (diffusion) of water molecules that have the tendency to move in the direction of the lowest resistance presented by obstacles, primarily in the direction of main fiber orientation [49]. The shape of diffusion can be round, that is, nondirectional (isotropic) or elongated, that is, directional (anisotropic). This anisotropy, called fractional anisotropy (FA) is used as a measure of axonal organization, a marker of the structural integrity of white matter [50]. FA is higher in heavily myelinated fiber tracts, and points potentially to more efficient transfer of information [51,52]. In addition to FA, the average magnitude of water diffusion, mean diffusivity (MD), as well as axial diffusivity (AD; parallel with the main direction of diffusivity, assumed as an indicator of axonal integrity) and radial diffusivity (RD; orthogonal to the main direction of diffusivity; an indirect measure of myelination), was measured [50,53,54].

To my knowledge 11 studies examined the IQ–white matter microstructure relationship including 3150 healthy individuals aged between 8 and 80 years [50–60]. In all studies, white matter integrity was indexed with fractional anisotropy (FA); some studies also used MD, AD and RD measures to indicate specific relations between myelination and the number of axons [53,56,60]. A finding consistently observed in all of the studies is a positive correlation between FA magnitude and intelligence. Given the considerable sample size, the correlation is as robust as the one reported for brain volume. To some extent this might be explained by the fact that white matter volume is strongly associated with whole brain volume [50]. It has been suggested that the positive correlation between FA and IQ supports the idea that efficient information transfer between hemispheres and brain areas is crucial for higher intellectual capabilities — a finding that is in line with recent trends in cognitive neuroscience describing brain structure and function as a dense connectome allowing for virtually unconstrained interactions among any pair of neurons in the brain, either through direct connections or via a few brain hubs [12,17–20]. In addition, this finding lends support to the P-FIT theory [6] that proposes that intelligent behavior is related to the fidelity of underlying white matter structures necessary to facilitate rapid and error-free transmission between brain areas.

Some studies also reported specific interactions related to measures of different components of intelligence, such as processing speed, working memory and executive control. It was reported that tests measuring the cognitive trait of processing speed had the strongest correlation with white matter FA and showed the most pronounced decline with age. Interestingly, individuals with higher baseline white matter integrity displayed a more attenuated age-related decline in processing speed [51]. This finding is similar to the one observed for age-related decreases in brain volume [27] and lends further support to the brain reserve hypothesis [61], suggesting that individuals with higher brain white matter integrity are able to maintain their processing speed more efficiently over time. It was further revealed that FA positively correlated with processing speed and reasoning components, but not with episodic memory [56]. A similar

distinction between information representation, which relied on the accumulation of tissue in gray matter regions, and executive control, which depends on long-range white matter pathways for efficient communication across distributed cortical networks was reported in a recent study [59].

3.1.2. Neuroelectric measures of the brain at rest

The alpha rhythm dominates the EEG power spectrum recorded from the scalp during relaxed wakefulness and may tap into general central nervous system functioning, as well as the status of mental health and cognitive performance. It has been suggested that alpha-band oscillations have two roles: inhibition and timing of cortical processing, both of which are related to two fundamental functions of attention (suppression and selection) that enable controlled knowledge access and semantic orientation [62,63]. Scalp alpha rhythms result from sequences of inhibitory and excitatory postsynaptic potentials at the dendrites of cortical pyramidal neurons. These potentials depend mainly on the influence of near and distant cortical modules, and on the interactions of excitatory cortico-thalamo-cortical relay fibers and inhibitory thalamic reticular fibers [64,65]. Alpha power is thought to reflect the number of neurons that discharge synchronously in these integrated systems. On the other hand, peak alpha frequency, or individual alpha frequency (IAF) is assumed to reflect a delay in the intracortical circuit at alpha baseline [66].

Given that IAF is thought to be related to white matter integrity and as discussed in the previous section, different characteristics of white matter structure were found to be positively related to intelligence, a similar relation would be also expected for individual alpha frequency (IAF). However, empirical research has mostly failed to find such a relation. Some early research conducted before 1960 reported positive correlations [67]. More recent studies provided mixed findings [68–72], some showing positive relations [68,69], while others found no relation [71,72]. A recent large-scale study ($N = 417$) further elucidate the IQ-IAF relationship suggesting that the inconsistency in results obtained might be due to test selection (more or less saturated with memory factors) and sex [70].

Research on the relationship between intelligence and different power measures has provided even less consistent results. Using a nonlinear dynamical analysis of multichannel EEG, it was shown that during resting conditions subjects with high IQs demonstrated higher dimensional complexity in the EEG pattern than subjects with low IQ's [73]. However, in a replication study this finding was not confirmed [74]. In a series of studies conducted in our lab, mixed findings were reported. High IQ individuals compared to low IQ ones showed lower alpha power [75], higher alpha power [76], or no differences were observed [77,78].

Recently, research has focused on functional brain network characteristics, the so-called small-world network attributes (high clustering and short path length) and their relation to psychometric intelligence [79]. The study showed that higher psychometric intelligence was associated with increased small-world organization of the upper alpha band in the right parietal cortex, whereas negative correlations were observed in the frontal cortex [79]. On the other hand, in a MEG resting-state connectivity analysis, an inverse relationship between functional connectivity across right anterior and left lateral/posterior MEG sensors in the low alpha band and verbal working memory capacity was reported [80]. At first glance the studies reported opposite findings, however, they can be viewed as complementary. Activity in the upper alpha band is related to abstract thinking and reasoning, whereas the lower alpha bands are related to attentional demands — active inhibition of task-unrelated areas [63]. These findings correspond to the Network Neuroscience Theory of Intelligence [12] suggesting complementary processes of efficiency in strongly connected hubs in easy-to-reach states (crystallized intelligence), opposed to weak connections that enable the system to function within many difficult-to-reach states (fluid intelligence). In this theory the capacity of flexible transitions between network states represents the essence of intelligence – g (see section 3.1.3.4). A similar conception of g based on the j -function [81], and operational architectonics that considers the brain as a metastable system [82], has been recently proposed [83]. The analogy of a searchlight spotting bits of information, where the frequency of brain oscillations determines the timing at which the focus of attention is shifted was suggested. High-frequency components increase the number of bits of information processed, which may explain the relationship between g and speed of information processing, as well as the scope of attention relation (working memory capacity). From a neural perspective the lateral prefrontal cortex is important for attentional control: it represents top-down influence on posterior sensory regions reactivating cortical memory traces — the memories themselves [9].

3.1.3. Neurobiological theories of intelligence: a functional perspective

Functional studies examine brain activation patterns during performance on cognitive tasks, ranging from simple to complex. Activity in brain areas and their interconnections can be visualized with two types of techniques: electrophysiological on the one hand and hemodynamic on the other. The three most influential neurobiological theories of intelligence: the neural efficiency [5], the P-FIT [6], and the multiple-demand theory [7], were proposed based on data obtained from hemodynamic techniques like PET and fMRI. The contribution of studies based on the electrophysiological approach has been substantial for the neural efficiency theory and to some extent for the P-FIT, but was less often used to support the MD theory.

3.1.3.1. The neural efficiency hypothesis. The gist of the theory summarized by Haier et al. [5, p. 415] is: “Intelligence is not a function of how hard the brain works but rather how efficiently it works. This efficiency may derive from the disuse of many brain areas irrelevant for good task performance as well as the more focused use of specific task relevant areas.”

Based on a review of research pertinent to the relationship between psychometrically determined intelligence and functional characteristics of brain activation observed during cognitive task performance, it can be concluded that most of the reviewed studies have demonstrated a negative correlation between brain activity under cognitive load and intelligence [84]. Some studies have shown a specific topographic pattern of differences related to the level of intelligence. High-ability subjects made relatively greater use of parietal regions, whereas low-ability subjects relied more exclusively on frontal regions [85,86]. The same activation pattern — more able individuals displayed less prefrontal but more parietal cortical activation — was also reported by two fMRI studies [87,88]. It was further reported that highly intelligent subjects displayed more brain activity in the early stages of task performance, while individuals of average intelligence showed a reverse pattern [86].

Moreover, neural efficiency seems to be corroborated mainly when participants work on tasks of low-to-medium difficulty or complexity, and is particularly prominent in frontal brain regions [89,90]. Another possible moderating variable influencing the neural efficiency hypothesis is task content, differentiating between tasks requiring the involvement of long-term memory and tasks with less memory involvement. The former showing brain activation patterns opposite to the neural efficiency hypothesis [84].

The central question that remains: What actually is neural efficiency?

In a review of literature explaining the theory, Haier [91] proposed that a failure of neural pruning may lead to an overabundance of synaptic connections or redundant brain circuitry that could result in more brain activity displayed in less intelligent individuals. A variant of Haier’s explanation was the neural plasticity model [92]. The argumentation was that a better environmentally adapted brain with stronger and more appropriate network connections would on the one hand perform faster, and on the other more efficiently. In that way, two characteristics of more intelligent individuals could be explained: First, faster and less variable reaction times when solving simple tasks, and second better performance on more complex tasks requiring less brain activity. Miller [93] put forward the brain myelination hypothesis, suggesting that better myelinated axons would allow for faster communication between brain areas and for less cross-talk between neurons. This would explain faster processing of intelligent individuals, as well as less brain activity in comparison with low intelligent individuals during problem solving. The explanation is tempting because it gains support by recent DTI research indicating a rather robust relation between intelligence and axonal organization. Specifically, greater white matter structural integrity has been observed in more intelligent individuals (see section 3.1.1.4).

3.1.3.2. The P-FIT theory. The landmark Parietofrontal Integration Theory (P-FIT) suggested that variations in a distributed network, mainly involving frontal and parietal brain areas, are responsible for individual differences in intelligence [6]. The P-FIT, as well as the MD theory that will be discussed in the next section, both address the question: where in the brain is intelligence? Two steps are usually involved in an attempt to answer this question. In the first step, a minimal number of converging brain areas involved in intelligent thinking is determined with neuroimaging techniques like PET, or fMRI. In the second step, knowledge about the function of identified areas derived from different domains (e.g., lesion studies, cognitive theory, and research) is used to provide the explanatory content of the theory.

The P-FIT describes rather large parts of the association cortices in the brain as relevant for individual differences in intelligence. To some extent it resembles Luria’s hierarchical structure model of the brain that involves

three cortical zones and the concept that human behaviors arise from the input of all parts and levels of the brain [94]. Hence, a critical comment about P-FIT was that these areas are probably activated for any kind of higher cognitive demand — even for tasks that have marginal loadings on g [95]. It is therefore surprising that attempts to validate the P-FIT failed. Two studies that applied similar methodology, although employing different test batteries to derive g , did not correspond very well with respect to brain areas related to g . The main problem was that a very small number of discrete brain areas approached 50% of convergence across both studies [96,97]. The only agreement was that the areas related to intelligence are distributed throughout the brain and not localized only in the frontal lobes. Likewise, in a meta-analysis of studies relating neuroimaging and intelligence it was reported that functional and structural results did not show any overlap, which is at odds with the principal assumption of the P-FIT [95].

A recent meta-analysis (involving 47 fMRI and PET studies) applying brain connectivity analysis of resting-state networks showed a much more narrow involvement of brain areas related to fluid intelligence than suggested by the P-FIT [98]. It was revealed that nodes of the dorsal attention network (intraparietal sulcus and the frontal eye fields of each hemisphere) displayed the most consistent correlate of intelligence, with additional contributions by regions of the anterior salience and left frontoparietal control network. This led the authors to conclude that individual differences in intelligence are more related to the ability to focus on the task at hand while suppressing distractors and by that maximizing cognitive capacity over relevant information [98]. A similar top-down guided voluntary allocation of attention was also proposed by the Multiple-Demand Theory of intelligence [7]. Furthermore, this finding sheds also light on the relationship between WM processes and intelligence, which is still to some extent mysterious. Different WM features were suggested as being central for intelligent reasoning: scope of attention [99], short-term storage [100], and relational integration [101]. In contrast, Engle [102,103] proposed that executive functioning, especially the control of attention over interference and conflict is the central process contributing to the shared variance with intelligence. This explanation of the WM-IQ relationship is rather close to the top-down guided attentional processes revealed as crucial for the brain intelligence relation [98].

3.1.3.3. The multiple-demand theory. John Duncan's idea of a multiple-demand system that can explain intelligence is based on functional neuroimaging data showing that many different tasks activate the same brain regions in the frontal cortex [7,16]. Even though the theory has lately expanded to include parietal areas (e.g., intraparietal sulcus), the focus and level of precision in explanation is mainly on the prefrontal cortex. This is consistent with the main assumption of the theory, namely that this network underlies attentional control mechanisms for goal-directed problem-solving [104]. The frontal cortex achieves this generality in activation by what Duncan dubbed adaptive coding. According to this principle, neurons of the prefrontal cortex have no specific function and, therefore, can respond to multiple demands by emphasizing relevant information and producing a representation of the outer world — a structured series of attentional episodes — allowing the organism to break complex problems into manageable subgoals [7]. Variability in the efficiency to build such models could explain individual differences in intelligence. Another aspect of this process, besides dividing the task into subgoals, is maintaining the plan via a sequence of attentional episodes. One has to keep the model and its parts in mind to understand the whole. According to Duncan, goal neglect — a mismatch between what should be done and what is actually done (occasionally reported in frontal lobe patients), can under specific circumstances be observed in normal individuals. Indeed, people with below average IQ (-1 SD) tend to neglect certain instructions as complexity increases: they do not perform the actions requested, even though they are able to accurately repeat what they were told to do. This suggests that in low intelligent individuals, an increase in the number of elements (complexity) gives rise to competition in task mode, which in turn leads to a loss of some elements [105].

3.1.3.4. The network neuroscience theory of g . The theory provides a brain perspective on the g enigma [12]. It is based on methods from mathematics, physics, and computer science enabling measurement and modeling of the interactions among network elements [19,20]. Fig. 1 shows a schematic diagram of the major building blocks of brain networks.

Brain efficiency is to minimize the cost of information processing while maximizing the output – performance. To achieve minimal costs the cortex is divided into anatomically localized modules, composed of densely interconnected regions or nodes which reduces the average length of axonal projections and by that increase signal transmission speed. On the other hand this local efficiency must be complemented by global efficiency, which enables the system

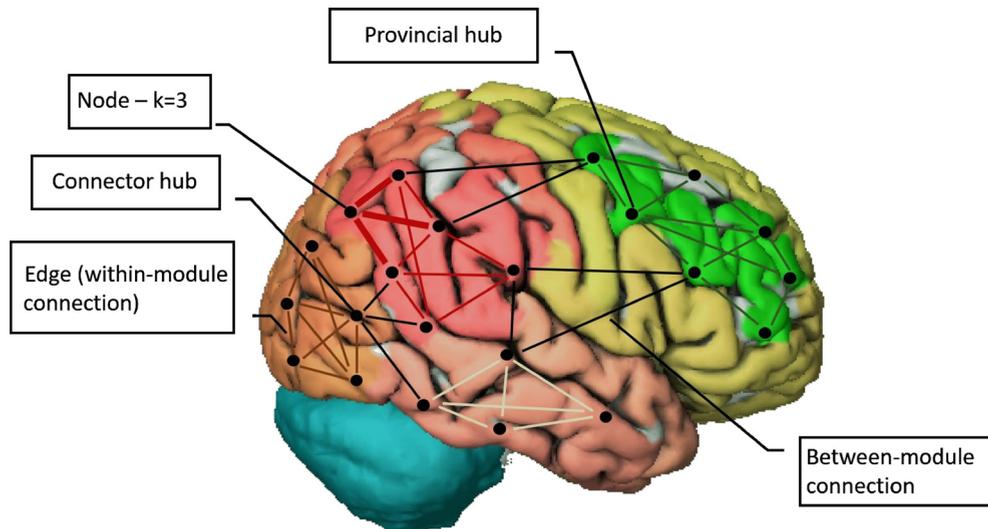


Fig. 1. Schematic diagram of a brain network introducing basic terminology. Networks consist of nodes and edges. The node degree corresponds to the number of edges that are attached to each node (e.g., $k = 3$). Highly connected nodes are hubs. Networks consist of modules which connect within or between them. When hubs connect with other nodes in the same module they are named provincial hubs, in contrast, connector hubs connect with nodes that belong to different modules. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

for global information processing. The human brain balances these competing constraints by creating a small-world topology [12,19,20]. In such a network strongly connected hubs enable a network to function within many easy-to-reach states which is the hallmark of crystallized intelligence being based on acquired knowledge and experiences. In contrast, fluid intelligence requires global information processing which depends on the formation of weak ties, which involve nodes with a small number of connections and by that enable the system to function within many difficult-to-reach states [106]. On the behavioral level this enables the organism to adapt to novel situations and problems which is central for fluid intelligence. In this framework “network flexibility and dynamics provide the foundation for general intelligence – enabling rapid information exchange across networks and capturing individual differences in information processing at a global level.” [12, p. 9].

Network flexibility relates to the ability of intrinsic connectivity networks for a rapid transition between easy-to-reach and difficult-to-reach network states providing the base for individual differences in g . This explanation is close to Jensen’s definition of intelligence being “. . . the periodicity of neural oscillation in the action potentials of the brain and central nervous system” [107, p. 173]. According to Jensen, oscillation rates determine the reaction times of individuals. Those with higher oscillation rates can react faster to stimuli with increasing response uncertainty (Hick’s law) in comparison to those with average or low oscillation rates. In that way, reaction time is a pure measure of oscillation rates, and therefore also of g . Jensen makes the analogy with a movie where motion is provided by the specific rate of projecting static pictures. The same is true for our perception of the outer world that is composed of a series of stimuli entering the focus of attention in working memory. Furthermore, Duncan’s structured series of attentional episodes – describing individual differences in intelligence with goal neglect: increased complexity of instruction makes less intelligent individuals perform a task by abandoning parts of the instruction – represents yet another facet of the same conception of information processing speed [105,108].

Support for the Network Neuroscience Theory comes also from empirical evidence showing positive correlations between levels of intelligence and nodal efficiency [109], increased age related genetic correlation between intelligence and global and local efficiency of brain networks [110], positive associations between intelligence and node-specific measures of within- and between-module connectivity, particularly in frontal and parietal brain regions [111–113]. A similar finding suggesting that higher intelligence is related to increased efficiency of local information processing and reduction of long distance connections that supports a small-world model of intelligence has been also established based on EEG data [114]. In yet another study a more complex connectivity pattern was revealed. Identified were 36 edges connecting regions distributed across the entire brain. These edges were related to high-order cognitive processes such as fluid and crystallized intelligence, learning, language, and visuospatial processing, suggest-

ing that one widespread, but limited number, of regions in the brain relates to individual differences in intelligence [115].

The few research findings analyzing network differences related to intelligence do not allow for a generalization, although most research seems to support a specialization model of intelligence with emphasis on the frontal-parietal lobes and global efficient allocation of resources in a small-world model of the brain.

3.2. *Testing for causality: behavioral training and noninvasive brain stimulation*

Many different interventions have been designed to influence intelligence. Among the most popular are: behavioral training, neurofeedback, music, mindfulness and meditation, nutrition and drugs, physical activity, and noninvasive brain stimulation (NIBS). For the purpose of a better understanding of the brain-intelligence relation the most promising results have been achieved with NIBS and behavioral training [9].

3.2.1. *Behavioral training*

The first wave of research that attempted to train intelligence was triggered by the studies of Klingberg et al. [116] and Jaeggi et al. [117]. The training targeted working memory processes and was therefore classified as a core training. Since then several studies have been conducted which were summarized in 20 meta-analysis and review papers [9]. In general, interventions show a positive near transfer effect on trained tasks, and a positive effect on tasks that are similar to the trained task measuring the targeted ability. Far transfer effects on measures of fluid intelligence are small and observed typically after WM training. Several studies, additionally to analyzing training influences on IQ test performance, investigated possible training-induced changes in patterns of brain activity and structure.

An early review paper based on the analysis of 10 studies reported several changes in brain activation patterns (fMRI) related to working memory training. Differences were mainly observed in the prefrontal and parietal areas, with two studies reporting differences also in the basal ganglia in the caudate nucleus. These findings are in line with the assumed function of the multimodal frontoparietal network. Another characteristic of the analyzed scans was that they did not show the same patterns of activity. Shorter trainings (less than 3 h) resulted in decreased brain activity, whereas longer periods of training showed mixed patterns of increased and decreased brain activity. A possible explanation was that increases in WM capacity are positively related to activity in the frontoparietal network, yet this effect cooccurs with deactivations linked to learned strategy refinement, priming effects, and decreased time needed to perform the task [118].

In a second review paper 18 studies were analyzed [119]. The analysis suggested four possible scenarios of brain activation patterns that could be induced by training: (1) decreased activity after training, (2) increased activity after training, (3) a combination of the first two patterns, and (4) a change in activation patterns in different brain areas which would indicate a reorganization of brain networks related to the trained characteristic. As previously discussed, decreased brain activity is in line with the neural efficiency hypothesis [6]. Thus, it is not surprising that eight studies reported activation decreases after practicing on different visuospatial working memory tasks. On the other hand, there is much less evidence for activation increases after WM training which was only observed in three studies. Increases in brain activity are usually found after sensory or motor practice reflecting an increase in cortical recruitment due to an increase in the size of cortical representations [120]. A mix of increases and decreases in brain activation patterns related to training suggests that some processes become more automated causing less brain activation (neural efficiency) due to training, whereas in areas supporting task-specific functions, activation increases. One would expect that frontal brain areas related to attentional control would become less involved in task performance throughout the training process therefore a frontal decrease in activity would be observed. However, these activation patterns were confirmed only in a few studies. The fourth possibility suggesting a reorganization of brain networks after WM training was not observed in this review. Due to the few studies published on this topic and the different brain activation patterns observed after training, the authors concluded that it was not possible to identify a specific neural mechanism that would fit within one single framework [119].

In a recent review of 22 studies using different cardiovascular (fMRI, near-infrared spectroscopy – NIRS, arterial spin labeling – ASL) and neuroelectric (EEG) indicators of brain activity, as well as 12 studies showing training-related changes in brain structure, were analyzed [121]. The conclusion was that training can improve higher cognitive function, and that these improvements are reflected in different brain activation patterns, as well as changes in gray and white matter structure that can be captured by a variety of neuroimaging techniques. The authors further sug-

gested that the brain connectome approach would be a useful framework for analyzing different brain states related to training interventions and their influence on higher cognitive functions like working memory and intelligence [121]. Hence, several recent studies have tried to analyze training induced changes from a neural network perspective.

In a pre–posttest experimental design, high-density eyes-closed EEG segments were used for the analysis of neural correlates induced by the WM training [122]. Pre–posttraining differences were significant only in the theta frequency band, showing posttraining power increases in relation to memory performance. The graph-theoretical network analysis showed a positive correlation for the clustering coefficient and a negative relationship for the path length. Both parameters are indicators of small-world networks characterized by high clustering and short path length. The former is a marker of local connectedness, whereas the latter points to the efficiency of information transfer in a network. The nodes identified as responsible for the observed training effects corresponded mainly to the frontoparietal network, showing increased dissociation in frontal areas and more associations in parietal areas. This finding is in good agreement with the neural efficiency theory suggesting that fewer neural resources, primarily in frontal brain regions, are related to better task performance in more intelligent individuals [84].

Furthermore, a similar frontoparietal dissociation during rest in relation to WM training was also observed in an fMRI/relative cerebral blood flow (rCBF) study [123]. The obtained posttest pattern could be regarded as indicative for superior WM performance, because exactly opposite activation patterns have been observed in many pathological conditions that reduce WM performance [123]. Changes in the frontoparietal network related to cognitive training were also observed in DTI studies measuring white matter integrity. It was reported that trained individuals displayed decreased radial diffusivity in white matter connecting frontal cortical areas and decreased mean diffusivity in left frontal and right parietal areas [124]. In a second study, it was found that long-term transfer of logical reasoning training was associated with increased structural integrity in corpus and genu of the corpus callosum [125].

In a recent study training induced changes in brain activity were assessed in EEG dynamics by examining fast-changing, recurring, topographically-defined electric patterns termed “microstates”, which characterize the electrophysiological activity of distributed cortical networks [126]. A video-game training based on multiple executive function tasks addressing WM, response-inhibition and task-switching was used. Among trained subjects there was a significant posttest difference in microstate C, which is most closely associated with the salience network. This may reflect reduced inhibition of frontal control networks, or a reduced inhibition by frontal control networks on others, indicating neural efficiency.

In summary, cognitive training not only shows transfer effects on performance but also significantly changes brain structure and activity. These changes were mainly observed in the frontoparietal network, which corresponds to brain areas that are central in most neurobiological explanations of intelligence (e.g., P-FIT, MD system, Network Neuroscience Theory). Moreover, the reported training-related decreases in frontal brain activity accompanied by increased parietal activity correspond to the neural efficiency theory [84]. These findings are also in line with the dual-process theory [127], which assumes that training increases automated task performance reducing the need for attentional control related to frontal brain regions, but increases activity in task-specific areas (parietal cortex).

3.2.2. NIBS: from brain connectivity to brain perturbation

Noninvasive brain stimulation is yet another approach that could disclose a causal relationship between intelligence and brain activity, overcoming the limitations of correlational evidence [128]. For this purpose two techniques have been used TMS and TES. The latter is the superordinate concept for at least three noninvasive brain stimulation techniques: (1) direct current (DC), (2) alternating current (AC), and (3) random noise (RN). The applied currents can be constant over a time (tDCS), or they can alternate at a specific frequency (tACS) or in a random frequency window (tRNS) [129]. These methods share several common characteristics. They are neuromodulatory techniques that do not induce activity in resting neuronal networks, but influence or alternate spontaneous nerve activity. Hence, the amount and direction of effects depend on the previous physiological state of the stimulated neural structures. The stimulation intensities of TES are not high enough to trigger discharge in resting neurons or axons and do not cause discharge of action potentials as TMS does [129,130].

The ideal experimental scenario proposed for a NIBS study would include several steps such as the identification of nodes and connections essential for intelligent performance which would serve as targets for subsequent rTMS. The next steps would then involve fcMRI to assess possible changes in brain networks targeted during rTMS, and analysis of behavioral measures. However, such stimulation approaches, especially when used in conjunction with brain imaging, are expensive and time consuming [128]. To my knowledge no study analyzing TMS effects on the brain

intelligence relation has been conducted. To date, there are only few studies that tried to influence fluid intelligence by directly stimulating brain activity with TES.

The first published study that explicitly aimed at influencing fluid intelligence with TES was the one by Santarnecchi et al. [131]. In this study tACS was delivered to the left middle frontal gyrus in a sham and four verum conditions at theta, alpha, beta, and gamma frequencies, while participants solved an IQ test (Raven matrices – RAPM). The only significant difference between sham and verum tACS conditions was observed for gamma stimulation, resulting in significantly shorter latencies on the more difficult Raven tasks. The authors concluded that the interactional effect of tACS improvements during gamma band stimulation with task difficulty might suggest a causal involvement of gamma oscillatory activity in the neural processes of higher order cognition, and highlights the importance of the left prefrontal cortex for inferential processes based on conditional arguments. These findings were replicated in a recent study by the same authors [132].

The objective of the study conducted in our lab was to explore the influence of offline tACS on measures of fluid intelligence [133]. Theta tACS was delivered to the left parietal and frontal brain areas. Verum theta tACS improved performance on tests of fluid intelligence. This influence was more pronounced in participants who received stimulation to the left parietal area, which increased performance on the difficult test items as compared to left frontal area stimulation that increased performance only on the easy test items. The observed behavioral tACS influences were also accompanied by changes in neuroelectric activity. The behavioral and neuroelectric data tentatively support the P-FIT neurobiological model of intelligence. These findings were recently replicated in a fMRI study [134].

A common characteristic of the above reported studies was that TES had a beneficial effect on tasks that are highly saturated with g (e.g., RAPM), even though different stimulation protocols with respect to the brain areas stimulated, frequencies employed, and current intensities were used. Another characteristic worth mentioning is that the positive effects were most pronounced for difficult tasks and were less significant (or not significant) for the easy ones. It is puzzling that such a diversity of stimulation parameters resulted in rather similar behavioral effects. In my opinion the only plausible explanation lies in the common characteristic of all these problems. In order to solve a matrix-reasoning test like RAPM, one must switch between different deduced relations and correlates. The more complex the problem becomes, a greater number of alternatives must be maintained and processed in WM. Perhaps the positive effects of theta and gamma tACS on performance on difficult tasks can be best explained by increased WM capacity. The hypothesis is further supported by recent evidence that cross-frequency coupling between theta and gamma oscillations plays an important role in working memory processing [135] and also relates to intelligence, showing a negative correlation with IQ scores in bilateral fronto-parietal brain areas in EEG patterns of resting individuals [136]. A similar decoupling between brain areas in high intelligent individuals was also reported in an resting state fMRI study [137].

In yet another study from our lab tACS was used to further elucidate the mixed findings between IAF and intelligence reported in section 3.1.2 [70]. For that purpose we increased IAF of individuals with tACS in the IAF + 1 Hz frequency band. Positive effects on IQ test scores were only observed for females while for males negative effects after tACS were observed. The verum tACS-related disruptive effect on male RAPM performance was unexpected. However, in our opinion it can be explained as a summation of several small effects, such as test characteristics and format of presentation, the sex-specific relation of endophenotypic IAF with factors of fluid intelligence, and preferred solution strategies. RAPM is based on abstract figures and therefore requires visuo-spatial ability [138]. Endophenotypic posterior IAF is strongly related to performance on mental rotation and shape manipulation tasks (rotation factor) in males. In contrast, anterior IAF is in males related to orientations involving attentional focus on details one at a time [70]. In addition, the reported male advantage in mental rotation tests has been most often attributed to sex-specific differences in strategy use. It was hypothesized that women performed mental rotation tasks in an effortful, top-down way, whereas men used an automatic, bottom-up strategy [139]. Therefore it could be speculated that tACS delivered to the left and right dorsolateral prefrontal cortex enhanced ordered step-wise problem solving processes that correspond to female solution strategies and conflict with male problem solving strategies. Furthermore, neuroelectric patterns based on event-related coherence measures showed increased decoupling mainly over a hub located in the right temporo-parietal area. In the upper alpha band the decoupling was observed between midfrontal and right parietal areas, whereas in the theta band it was mainly between right temporal and central locations. These locations are close to the main hubs of the salience and central executive networks; which may suggest switching of activity from the default mode network to the central executive network. A finding that corresponds with neuroelectric changes in brain networks induced with behavioral training [122,123].

This overview of studies that have tried to influence fluid intelligence with TES has demonstrated the great variety of possibilities the technique provides, in particular with respect to protocol design — which represents the positive part. On the negative side, one could critically remark that the studies are fishing in troubled waters, with no clear theoretical concepts that would justify why specific protocols were employed. Given that only a few studies have been conducted, it is probably premature to make a final assessment on the usefulness of TES to study the brain-intelligence relation.

4. Perspectives for future research

Whenever writing about predictions in science, the first landing on the Moon pops into my mind. Why? Because it is a scholarly example of false predictions. In 1969 it was seriously estimated that by the end of the century we will face lunar colonies living in bases build on the Moon, and missions to orbit or even land on Mars. At that time one would be probably diagnosed insane if predicting that in 2018 a mission to Moon would be regarded a mission impossible, not to speak about Mars.

In my opinion the brain-intelligence enigma can only be unraveled by analyzing brain oscillations in the framework of a brain perspective such as the proposed Network Neuroscience Theory of g [12]. Action potentials are the building blocks of all our thoughts and consciousness and their spatio-temporal architecture represents the brain code [82]. It was recently demonstrated that brain oscillations measured with EEG encompass the real part of a modular function suggesting that the human brain displays a pattern resulting from elliptic, intertwined oscillations resembling the waves described by the j -function. Such oscillations endowed in the brain spikes result from the delicate interaction of the countless moving trajectories that are at the very heart of modular functions [81]. Because the movements of the j -function take place on the plane of complex numbers, therefore in brain electric activity there must be also an unexplored complex part – hidden or undetected with EEG. Thus, it could be hypothesized that the mathematical superimposition between modular functions and EEG spikes might be correlated with the presence of further brain dimensions as recently discussed [82]. The Authors described the occurrence of multi-dimensional toruses, where trajectories take place in guise of particles traveling on donut-like manifolds. Suggesting that neural networks are limited by the dynamics of short-term local and global metastable brain states. A similar conception was suggested by Jerison [140], who viewed the brain as a “mapping machine”, in which maps are different representations of the external world. The number of these maps is related to the complexity of viewing and representing the external world. Therefore, the enlargement of the human brain during evolution could be explained as a need for improving ways of knowing reality. For example, the squirrel has three visual areas, the owl monkey has 14 representations of the visual world, and for humans it is estimated that there are 30 visual areas, therefore we can “see” 27 kinds of things which the squirrel cannot [141].

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