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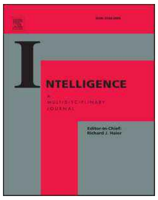

The biological basis of intelligence: Benchmark findings

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ABSTRACT

The scientific study of the biological basis of intelligence has been contributing to our understanding of individual differences in cognitive abilities for decades. In particular, the ongoing development of electrophysiological, neuroimaging, and genetic methods has created new opportunities to gain insights into pressing questions, allowing the field to come closer towards a comprehensive theory that explains how genotypes exert their influence on human intelligence through intermediate biological and cognitive endophenotypes. The aim of this article is to provide a focused overview of empirical benchmark findings on biological correlates of intelligence. Specifically, we summarize benchmark findings from electrophysiological, neuroimaging, and genetic research. Moreover, we discuss four open questions: (1) The robustness of research findings; (2) the relation between neural parameters and cognitive processes; (3) promising methodological developments; and (4) theory development. The aim of this paper is to assemble the most important and robust findings on the biological basis of intelligence to stimulate future research and to contribute to theory development.

1. Introduction

Intelligence is a psychological construct that refers to the ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, and to engage in various forms of reasoning (Neisser et al., 1996). Intelligence is an important predictor of educational and occupational success (Schmidt & Hunter, 2004) and relates closely to positive life outcomes such as health and longevity (Deary, Whiteman, Starr, Whalley, & Fox, 2004). Understanding the neurobiological basis of intelligence is therefore an important aim of ongoing research across multiple scientific disciplines. This article provides a focused overview of the current state of research. Specifically, we emphasize robust and well-established empirical benchmark findings from electrophysiological, neuroimaging, and genetic research on intelligence (see Fig. 1 for a summary of those benchmark findings). As a result, less well-established or relatively new findings are not included in this review unless considered groundbreaking. In those areas where systematic reviews of the literature were not yet available, we refrained from stating specific estimates or ranges of effect sizes but followed the recommendations by Funder and Ozer (2019) in labeling correlations as small, medium, large, or very large (for a very broad overview over typical effect sizes in intelligence research see Nuijten, Van Assen, Augusteijn, Crompvoets, & Wicherts, 2020). We discuss general topics concerning the robustness of research findings, highlight challenges in linking biological to cognitive processes parameters, and outline promising methodological developments that will contribute to our understanding about the biological underpinnings of intelligence. Finally, we discuss how theory development in intelligence research might benefit from accounting for those benchmark findings. A companion article by Frischkorn, Wilhelm, and Oberauer (submitted) provides a similar overview of research pertaining to cognitive processes.

2. Electrophysiology

A wide range of measures derived from the electroencephalogram (EEG) has been examined for a potential relationship with intelligence. For the sake of conciseness, we will summarize empirical results from the last thirty years that have been (conceptually) replicated at least a few times (for earlier studies and studies on the relation of intelligence to other EEG measures not discussed here see Deary and Caryl (1993) and Stelmack and Houlihan (1995)). Specifically, we will focus on a) two established components of the event-related potential (ERP), b)

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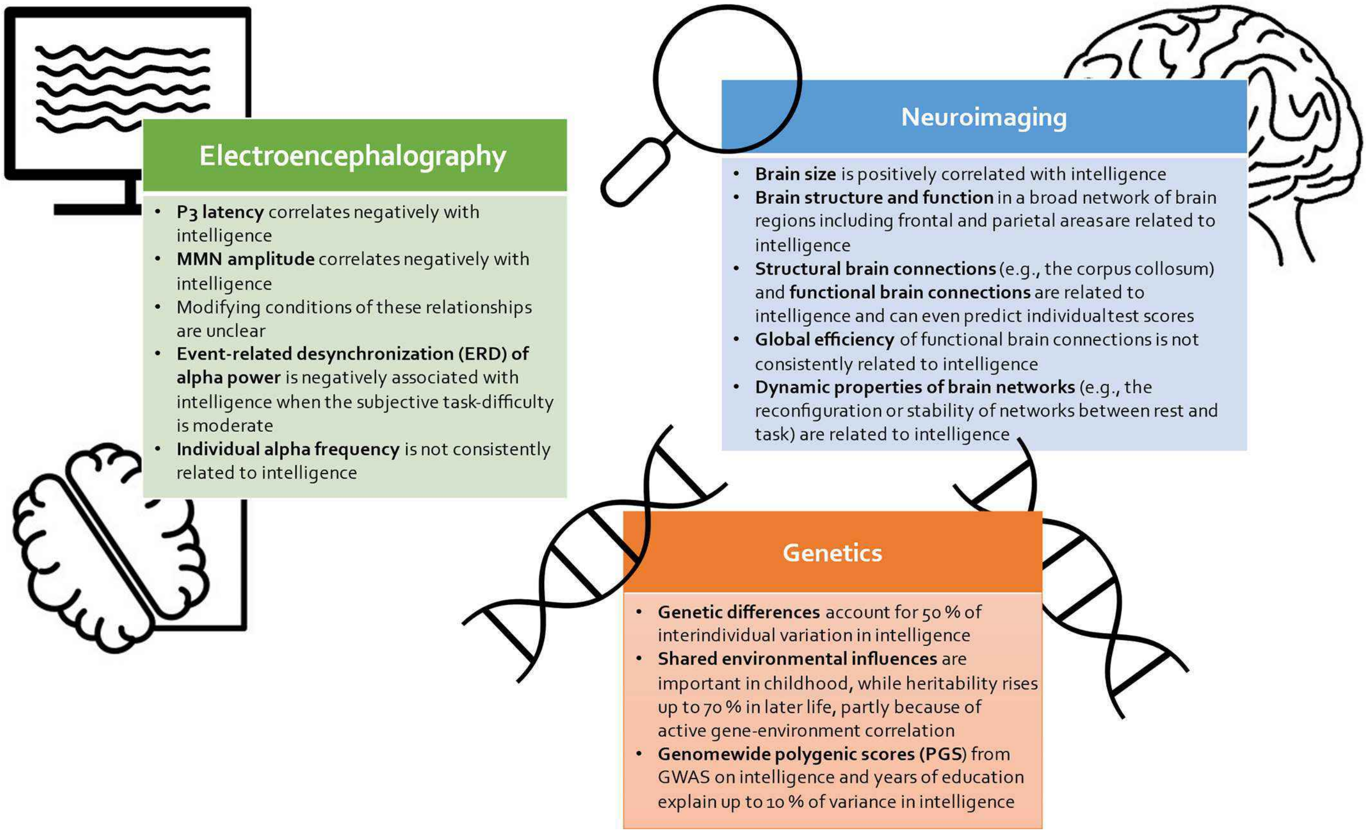
frequency band power, and c) individual alpha frequency (IAF).

2.1. The event-related potential

The ERP is the average electrophysiological response to a frequently presented stimulus. When the presented stimuli are attentively processed and a specified target stimulus is consciously detected, a pronounced P3 component emerges in the ERP as the third positive deflection (Luck, 2014). In the oddball task, for example, infrequent target stimuli are embedded in a series of standard stimuli. Here, the P3 component can be observed in the target-related but not (or strongly attenuated) in the standard-related ERP. A medium-to-large negative association (roughly in the range from $r = -.20$ to $-.40$) between intelligence and P3 latency has been reported consistently when oddball tasks were used (e.g., Bazana & Stelmack, 2002; De Pascalis, Varriale, & Matteoli, 2008; Saville et al., 2016; Stelmack & Houlihan, 1995; Troche, Houlihan, Stelmack, & Rammsayer, 2009; Walhovd et al., 2005), which can be interpreted as support for the mental speed approach of intelligence (Der & Deary, 2017). In contrast, the relation between intelligence and the P3 latency in other tasks is less consistent. For example, for the Hick task, the Sternberg Short-Term Memory Scanning task, and the N-back task some studies reported negative correlations (Jungeblut, Hagemann, Löffler, & Schubert, 2021; Saville et al., 2016; Schubert, Hagemann, & Frischkorn, 2017; Schubert, Löffler, Hagemann, & Sadus, 2022) whereas others did not (Euler, McKinney, Schryver, & Okabe, 2017; Houlihan, Stelmack, & Campbell, 1998; Schubert, Hagemann, Frischkorn, & Herpertz, 2018; Troche, Merks, Houlihan, & Rammsayer, 2017). This is in contrast to the very consistent relationship between intelligence and response time (RT) measures that has been observed across a wide variety of different tasks (Doebler & Scheffler, 2016; Schubert, 2019; Sheppard & Vernon, 2008), and cautions against a simple interpretation of the P3 latency as the non-motoric part of RT or stimulus-evaluation time (see Verleger, 2010). To date, neither the specific meaning of the P3 latency nor its relationship with intelligence are sufficiently understood. One step towards explaining the heterogeneity of findings might be to identify the specific conditions under which the P3 latency is related to intelligence and how this relationship changes under experimentally induced processing demands. For example, increasing the attentional demands in different conditions of a continuous performance task led to an increasing negative relationship between P3 latency and intelligence (Kapanci, Merks, Rammsayer, & Troche, 2019). More research tracking how the relationship between P3 latencies and intelligence changes as a function of experimental demands and subsequent systematic meta-analyses might be required to gain a more comprehensive understanding about the relation between P3 latencies and intelligence.

The auditory mismatch negativity (MMN) is a different ERP component for which relationships with intelligence have been reported in multiple electrophysiological studies. It is elicited when, within a series of frequent standard sounds or sound patterns, rare deviant sounds (e.g., of higher pitch, duration, or loudness) or deviant sound patterns are presented – even if participants are instructed to ignore those sounds. The MMN is considered an index of an automatic discrimination process (Näätänen, Paavilainen, Rinne, & Alho, 2007) and larger (i.e., more negative) MMN amplitudes have been observed in more intelligent individuals in several studies (De Pascalis & Varriale, 2012; De Pascalis, Varriale, Fulco, & Fracasso, 2014; Houlihan & Stelmack, 2012; Sculthorpe, Stelmack, & Campbell, 2009; Troche et al., 2009; Troche, Houlihan, Stelmack, & Rammsayer, 2010). However, the observed correlational associations were of rather moderate size (roughly between $r = -.15$ and $r = -.42$), and, most critically, also inconsistent. For example, Troche et al. (2010) observed a significant relationship when deviant sounds were of higher pitch than standard sounds, while no relation was found when deviant sounds were of longer duration than standard sounds. In the study by Houlihan and Stelmack (2012), an association between MMN amplitude and intelligence was



Electroencephalography

- **P3 latency** correlates negatively with intelligence
- **MMN amplitude** correlates negatively with intelligence
- Modifying conditions of these relationships are unclear
- **Event-related desynchronization (ERD) of alpha power** is negatively associated with intelligence when the subjective task-difficulty is moderate
- **Individual alpha frequency** is not consistently related to intelligence

Neuroimaging

- **Brain size** is positively correlated with intelligence
- **Brain structure and function** in a broad network of brain regions including frontal and parietal areas are related to intelligence
- **Structural brain connections** (e.g., the corpus collosum) and **functional brain connections** are related to intelligence and can even predict individual test scores
- **Global efficiency** of functional brain connections is not consistently related to intelligence
- **Dynamic properties of brain networks** (e.g., the reconfiguration or stability of networks between rest and task) are related to intelligence

Genetics

- **Genetic differences** account for 50 % of interindividual variation in intelligence
- **Shared environmental influences** are important in childhood, while heritability rises up to 70 % in later life, partly because of active gene-environment correlation
- **Genomewide polygenic scores (PGS)** from GWAS on intelligence and years of education explain up to 10 % of variance in intelligence

Fig. 1. Summary of benchmark findings in research on the biological basis of intelligence: Electrophysiological, neuroimaging, and genetic correlates of intelligence.

reported when simple, but not when more complex sound patterns were interspersed with deviant sound patterns. Furthermore, when backwardly masked stimuli were used (i.e., stimuli immediately followed by a masking stimulus), only the MMN latency, but not its amplitude, was negatively related to intelligence (Bazana & Stelmack, 2002; Beauchamp & Stelmack, 2006; but see De Pascalis & Varriale, 2012). A recent study analyzed the relationship between intelligence and MMN as marker of pre-attentive discrimination processes in the visual domain but found no significant relationship between the two (Hilger & Euler, 2022).

Overall, relations of amplitudes and latencies of ERP components with intelligence are very heterogeneous. One limitation of many studies is a mismatch between the hierarchical levels used to measure amplitudes and/or latencies of ERP components on the one hand and intelligence on the other hand: While specific ERP components were often recorded during specific tasks (e.g., the P3 component in the oddball task), intelligence was mostly operationalized as a rather broad construct (e.g., *g* at a higher hierarchical level). Measuring both constructs at a higher hierarchical level and estimating their associations by means of latent correlations may yield higher and possibly more consistent correlations between properties of ERP components and intelligence (up to $r = -.89$, see Schubert et al., 2017), in particular when noticeable parts of measurement error can be reduced at both sides (Schubert et al., 2017, 2022; Schubert & Frischkorn, 2020; Schubert, Hagemann, Voss, Schankin, & Bergmann, 2015).

2.2. Frequency band power

The EEG signal can be decomposed into multiple frequency bands (e.g., alpha, beta, gamma, delta) which allow for investigations of individual differences in neural oscillations, interregional synchronization, and cross-frequency coupling (Donoghue, Schaworonkow, & Voytek, 2021). Alpha activity reflects oscillatory dynamics in the frequency range from 8-12 Hz and is particularly dominant in a relaxed but awake state of rest (Klimesch, 2012). A functional positive relationship between the power of the alpha band during rest and intelligence could not be consistently established (see Jaušovec, 2019). More congruent results were obtained by investigating the decrease of alpha power from a state of cognitive rest to a state of cognitive activity. This decrease, referred to as event-related desynchronization (ERD; Pfurtscheller & Aranibar, 1977), is suggested to reflect increasing cortical activation (Neuper & Pfurtscheller, 2001) or the release from inhibition (Klimesch, 2012). In line with the neural efficiency hypothesis of intelligence (Neubauer & Fink, 2009), multiple studies observed a negative association between intelligence and ERD (see Neubauer & Fink, 2009, for an overview), and interpreted this as support for the assumption that more intelligent individuals show less task-evoked cortical activation than less intelligent ones when performing the same task with the same or even more success. In their overview, Neubauer and Fink (2009) identified a couple of moderating influences on this association (task demands, brain regions, sex, and learning effects). For example, the negative relationship between intelligence and ERD was primarily found for tasks with moderate task demands (see also Nussbaumer, Grabner, & Stern, 2015). However, a moderating effect of learning on the intelligence-ERD relationship could not be confirmed in a subsequent study by Nussbaumer et al. (2015). Subsequently, Dix, Wartenburger, and van der Meer (2016) proposed that the subdivision of the alpha band into lower and upper frequencies might also play a crucial role. Overall, only a very limited number of studies examined the proposed moderating factors systematically, which would be required to empirically establish the role of moderating factors in the intelligence-neural efficiency relationship.

Beyond alpha, the power of other frequency bands such as beta and theta has also been related to intelligence (e.g., Liu, Shi, Zhao, & Yang, 2008), albeit in fewer studies and with less promising results. Furthermore, the coherence (coupling, connectivity) between neural oscillations arising from different brain regions has been related to intelligence, both within the same frequency band as well as across different bands (e.g., theta-gamma cross-frequency coupling, Pahor & Jaušovec, 2014, 2017; delta-gamma cross-frequency coupling, Gągol et al., 2018; long-range theta connectivity, Schubert, Hagemann, Löffler, Rummel, & Arnau, 2021; for review see Chuderski, 2016). While negative associations between coherence and intelligence were observed in some studies (e.g., Cheung, Chan, Han, & Sze, 2014; Pahor & Jaušovec, 2014) and interpreted as indicating higher spatial differentiation potentially facilitating higher processing speed and neural efficiency (Thatcher, North, & Biver, 2005), positive relationships were reported in other investigations and understood as reflecting stronger and thus more effective inter-regional communication in more intelligent people (e.g., Anokhin, Lutzenberger, & Birbaumer, 1999; Lee, Wu, Yu, Wu, & Chen, 2012; Schubert et al., 2021). Other studies did not find any association between measures of oscillatory coherence and intelligence (e.g., Ujma et al., 2019). However, differences in the range of investigated frequency bands, in the type of coherence or connectivity measure, in the analyses space (source space vs. sensor space), and in the cognitive state during which EEG was acquired (task vs. resting-state vs. sleep, eyes open vs. eyes closed), make a comprehensive comparison of those findings difficult. Hence, we do not identify the relation between oscillatory synchrony and intelligence as a benchmark finding, but rather as a promising future line of research.

2.3. Individual alpha frequency

The frequency band within the spectral distribution of the alpha band (8-12 Hz) that depicts the highest overall power is referred to as the alpha peak and is typically located in the range of 10-11 Hz (Angelakis, Lubar, Stathopoulou, & Kounios, 2004). This peak exhibits large individual differences, high temporal stability, and was proposed to possess a trait-like character (Kondacs & Szabó, 1999). Depending on the method of quantification, this peak is called individual or peak alpha frequency (IAF/PAF; Klimesch, 1997) and has been considered a measure of the speed of information processing (Posthuma, Neale, Boomsma, & de Geus, 2001) or, more specifically, speed of memory retrieval (Klimesch, Schimke, Ladurner, & Pfurtscheller, 1990).

A positive relationship between IAF and intelligence was reported by Anokhin and Vogel (1996) as well as Grandy et al. (2013). In larger samples, however, Posthuma et al. (2001), Pahor and Jaušovec (2016) as well as Ociepka, Kałamała, and Chuderski (2022) failed to observe such a relation. Somewhat more consistent are empirical results on the association between IAF and performance on memory tests (Pahor & Jaušovec, 2016), potentially suggesting that IAF is linked to more specific abilities such as memory rather than to general cognitive ability, i.e., intelligence. Furthermore, it has been hypothesized that IAF reflects both a stable trait and a cognitive state, as it has been shown to be influenced by situational characteristics such as sensory input, mood, and attentional task demands (Mierau, Klimesch, & Lefebvre, 2017). Hence, momentary IAF is also interpreted as an indicator of cognitive preparedness (Angelakis et al., 2004). Whether trait aspects of IAF or task-related (state) changes in IAF are more consistently related to intelligence is still an open but interesting question (Grandy et al., 2013).

2.4. Open questions and future directions

Taken together, there seems to be no EEG measure which is unambiguously related to intelligence. Of note, this is not necessarily a symptom of the replication crisis in psychological science (Open Science Collaboration, 2015), but may rather be explained by moderators which should be studied with more complex experimental designs. Thus, systematic reviews and large-scale replication studies are needed to estimate the generalizability of EEG-intelligence relationships and to identify moderators of those associations. None of the above-mentioned EEG measures is a pure reflection of a single cognitive (let alone cortical) process. This impedes the interpretation of correlations between intelligence and single EEG measures and makes conclusions regarding potential intermediate phenotypes difficult. Less ambiguous interpretations might be obtained from experimental designs in which *changes* in EEG measures are induced by experimental manipulation and, thereby, directly related to the experimentally manipulated cognitive process (for some initial results see Euler, 2018; Jungeblut et al., 2021; Kapanci et al., 2019). However, this will inevitably introduce other problems due to the low reliabilities of individual differences in experimental effects (Hedge, Powell, & Sumner, 2018). Furthermore, research on the relation between EEG measures and intelligence should also speak to the cognitive processes associated with those EEG measures. Speed measures such as ERP latencies or IAF, for example, should be assessed together with behavioral speed measures such as reaction or inspection times or drift rates. Finally, a systematic decomposition of task/state-specific and domain-general (trait-related) portions of variance in EEG measures by factor-analytical approaches might be a promising avenue to less ambiguous estimates of the relation between individual differences in intelligence and EEG measures (Jungeblut et al., 2021; McGarry-Roberts, Stelmack, & Campbell, 1992; Schubert et al., 2017, 2022).

3. Neuroimaging

3.1. Structural imaging of intelligence

One of the best-established neural correlates of intelligence is total brain size, explaining up to 5% of the variation in intelligence test scores (e.g., Cox, Ritchie, Fawns-Ritchie, Tucker-Drob, & Deary, 2019; for meta-analyses see McDaniel, 2005; Nave, Jung, Karlsson Linnér, Kable, & Koellinger, 2019; Pietschnig, Penke, Wicherts, Zeiler, & Voracek, 2015; for sex differences see van der Linden, Dunkel, & Madison, 2017). Brain region-specific correlates of intelligence were identified in gray matter volume (e.g., Haier, Jung, Yeo, Head, & Alkire, 2004), cortical thickness (e.g., Román et al., 2014), and in additional region-specific morphometric characteristics (e.g., Basten, Hilger, & Fiebach, 2015; Colom et al., 2013) by studies using techniques like voxel-based morphometry (VPM; Ashburner & Friston, 2000). Intelligence-related variations in white matter have mostly been studied with diffusion tensor imaging (DTI) and have been reported at a whole-brain level (e.g., Chiang et al., 2009) as well as at the level of single tracts linking specific brain regions to each other (e.g., Kievit et al., 2016; for review see Genç & Fraenz, 2021). As white matter tracts can be understood as defining a structural brain network, those findings are discussed in detail in the section 'intelligence from a network neuroscience' perspective. Studies applying magnetic resonance spectroscopy (MRS) revealed insights into intelligence-associated biochemical properties of brain tissue and significant correlations were reported ranging from $r = -.35$ (Anderson et al., 1998) to $r = .91$ in specific subpopulations (here: only women, Jung et al., 2005). Although the general trend suggests a positive association between N-acetylaspartate (NAA) and intelligence as well as more pronounced associations in women than in men (e.g., Jung et al., 2005; Pfleiderer et al., 2004), conclusions that can be drawn from these investigations are limited due to the use of very small samples ($N \sim$ 10–60) that could lead to overestimated effect sizes (e.g., Anderson et al., 1998; Jung et al., 1999, 2005, 2009; Moss, Talagala, & Kirisci, 1997; Pfleiderer et al., 2004; Rae et al., 1996; for a more general review on MRS in cognitive research see Ross & Sachdev, 2004). Finally, most recent neuroanatomical investigations suggest that even individual intelligence test scores can be significantly predicted from variations in brain structure, albeit with a relatively large absolute error ($\sim$ 10 IQ points, i.e., $\sim$ 0.77 SD in e.g., Hilger et al., 2020a; Mihalik et al., 2019; Wang, Wee, Suk, Tang, & Shen, 2015; for a discussion on the differentiation between explanatory and cross-validated predictive analyses see Yarkoni & Westfall, 2017).

While the positive association between intelligence and brain size was mostly interpreted as indicating higher computational power due to larger neural capacities (Genç et al., 2018), brain region-specific associations, as summarized in the Parieto-Frontal Integration Theory (Jung & Haier, 2007), were set in relation to multiple information processing stages from perception to problem solving. Specifically, Haier (2017) proposed four processing stages as relevant for variations in intelligence, each associated with specific brain regions: Stage 1: Information enters the brain through perception channels. Stage 2: Information flows to association areas of the brain and relevant memories are integrated. Stage 3: Information continues forward and is integrated in the frontal lobes, options are weighted against each other, and actions are initiated. Stage 4: Motor or speech areas are innervated if required. However, more recent work broadened the initial parieto-frontal focus to a more wide-spread set of brain regions and suggested a more heterogeneous picture when structural studies on intelligence are compared meta-analytically (Basten et al., 2015; Santarnecchi et al., 2017a; for reviews see Colom, Karama, Jung, & Haier, 2010; Colom & Thompson, 2011; Deary, Cox, & Hill, 2021; Deary, Penke, & Johnson, 2010; Dizaji et al., 2021; Drakulich & Karama, 2021; Goriounova & Mansvelder, 2019; Gray & Thompson, 2004; Haier, 2017; Jaušovec, 2019; Luders, Narr, Thompson, & Toga, 2009; for a review about longitudinal changes in the relationship between brain structure and intelligence see Oschwald et al., 2020). This heterogeneity can partially be explained by different methodological choices (e.g., whether to control for brain size or not; Hilger, Winter, et al., 2020a) and makes it difficult to derive concrete conclusions about intelligence-relevant cognitive processes from studies of brain structure.

3.2. Functional imaging of intelligence

The neural efficiency hypothesis of intelligence proposes that more intelligent individuals require less effort to achieve a given performance level (Neubauer & Fink, 2009, see above). Early PET and EEG findings of globally less neural activation during task performance in more intelligent individuals' brains form the basis for this theory (Grabner, Fink, Stipacek, Neuper, & Neubauer, 2004; Haier et al., 1988; Jaušovec & Jaušovec, 2000). Subsequent fMRI studies, however, pointed in the opposite direction (i.e., more neural activation in more intelligent individuals), and contributed to the identification of multiple moderator variables (e.g., sex, task difficulty; Dunst, Benedek, Koschutnig, Jauk, & Neubauer, 2014; Neubauer & Fink, 2009, see above). Results from studies which focused on brain region-specific activation levels suggest the involvement of frontal and parietal brain regions (e.g., of the dorsolateral prefrontal cortex; Gray, Chabris, & Braver, 2003; for meta-analyses and reviews see Basten et al., 2015; Basten & Fiebach, 2021; Colom et al., 2010; Colom & Thompson, 2011; Deary et al., 2021; Deary et al., 2010; Dizaji et al., 2021; Goriounova & Mansvelder, 2019; Jaušovec, 2019; Jung & Haier, 2007; Haier, 2017; Santarneechi et al., 2017a,b). However, these investigations were often limited by a) a restricted focus of analyses to specific predefined regions of interest (ROI approach vs. whole brain approach) and b) by large variations in the tasks during which neural activation was assessed (from playing chess to passive viewing of video films, for an overview see Basten et al., 2015). While the former limitation prevents the identification of neural correlates in regions that were not hypothesized, the latter limitation hampers drawing more specific conclusions about the associated cognitive processes.

Recently, two pioneering studies (Sripada, Angstadt, Rutherford, Taxali, & Shedden, 2020; Wu, Li, & Jiang, 2020) applied machine learning-based predictive modelling (for reviews see Lemm, Blankertz, Dickhaus, & Müller, 2011; Poldrack, Huckins, & Varoquaux, 2020) to show that individual intelligence scores can be predicted from task-induced neural activation patterns (albeit with a rather large average error of ~10 IQ points, $\sim$ 0.67 SD; Sripada et al., 2020). Interestingly, and in accordance with previous reports (Basten, Stelzel, & Fiebach, 2013), the interplay between activation in fronto-parietal regions and deactivation in regions associated with the default mode of brain functioning contributed most to this prediction (Sripada et al., 2020) – an observation which can potentially be interpreted as support for the assumption that more intelligent individuals excel by keeping their cortical activation more focused, i.e., more effectively activating task-associated brain regions while also more effectively deactivating task-irrelevant regions.

In sum, functional neuroimaging research on intelligence was primarily focused on fMRI and identified positive as well as negative associations between intelligence and neural activation mostly in brain regions associated with functions of working memory, attentional control, and reasoning. Importantly, most inferences about potentially intelligence-relevant processes from this empirical background are indirect (reverse inference problem; Poldrack, 2008, 2011) and do thus require further investigation.

3.3. *Intelligence from a network neuroscience perspective*

The introduction of physical network theory to neuroimaging enabled the field to study the human brain as a complex network. Functionally specialized brain regions constitute network nodes that are interconnected via network edges (connections) and both together define a graph that can be investigated with specific graph-theoretical metrics (Bullmore & Sporns, 2009, 2012; Sporns, 2014). In structural networks, edges reflect anatomical brain connections that were mostly estimated from white-matter tracts based on diffusion-tensor imaging data (DTI). In contrast, functional networks are usually derived from time series of correlated neural activation and were mostly assessed during resting-state (intrinsic connectivity; Buckner, Krienen, & Yeo, 2013) or during ongoing cognitive demands (task-related connectivity; Cole, Bassett, Power, Braver, & Petersen, 2014). Over the last decade an increasing number of studies moved beyond the above outlined *localizationist* approach (aiming to localize intelligence in circumscribed brain regions) and highlighted the importance of structural and functional connections for understanding the brain bases of intelligence.

The majority of *structural connectivity* studies on intelligence reported a positive association between higher intelligence scores and higher levels of brain-wide white matter integrity (indexed by fractional anisotropy; e.g., Chiang et al., 2009; Navas-Sánchez et al., 2013; Penke et al., 2012). Respective associations lay typically in the range between $r = .30$ and .40 and became especially prominent in white matter tracts linking frontal to occipital brain regions (fronto-occipital fasciculus; Chiang et al., 2009; Kievit et al., 2012; Kievit et al., 2016; Malpas et al., 2016), frontal to parietal regions (arcuate fasciculus, longitudinal fasciculi; Malpas et al., 2016; Schmithorst, Wilke, Dardzinski, & Holland, 2005), different frontal regions to each other (uncinate fasciculus; Kievit et al., 2016; Malpas et al., 2016; Yu et al., 2008), and a large number of studies identified intelligence-related characteristics of white matter tracts connecting both hemispheres with each other with specific focus on the corpus callosum (e.g., Aydin, Uysal, Yakut, Emiroglu, & Yılmaz, 2012; Chiang et al., 2009; Damiani, Pereira, & Nascimento, 2017; Dunst et al., 2014; Ganjavi et al., 2011; Hutchinson et al., 2009; Kievit et al., 2012; Luders et al., 2007, 2011; Navas-Sánchez et al., 2013; Strauss, Wada, & Hunter, 1994; Tang et al., 2010; Westerhausen et al., 2018; Wolf et al., 2014; Yokota et al., 2022; Yu et al., 2008; for review see Colom et al., 2010; Deary et al., 2021; Dizaji et al., 2021; Genç & Fraenz, 2021; Hilger & Sporns, 2021). Interestingly, associations were proposed to be determined by common genetic factors (Chiang et al., 2009; Genç et al., 2022). Structural measures such as membrane density (Dunst et al., 2014) and myelination (Malpas et al., 2016) have also been linked to intelligence. Moreover, graph-theoretical investigations reported a globally more efficient (i.e., overall shorter path) structural network organization in more intelligent individuals (Koenis et al., 2015; Ma et al., 2017; Zalesky et al., 2011). Others, however, could not replicate this finding (Yeo et al., 2016). Recent studies applying machine learning-based algorithms including some form of cross validation showed that intelligence can also be predicted from structural connectivity (Lin, Baete, Wang, & Boada, 2020; Powell, Garcia, Yeh, Vettel, & Verstynen, 2018; Zhang, Allen, Zhu, & Dunson, 2019), and finally, longitudinal investigations suggested that white matter connectivity (computed from different indices of white matter integrity) could even predict individual intelligence scores not only at the same time (e.g., in childhood) but also in the future (e.g., in adulthood; Li et al., 2020; Ferrer et al., 2013; Wendelken et al., 2017).

Early studies addressing the relation between intelligence and *functional connectivity* used primarily seed-based approaches. These were mostly focused on fMRI data assessed during the (task-free) resting state in order to derive intrinsic connectivity characteristics. Intrinsic connectivity has been shown to be closely associated with the underlying anatomical connections (Greicius, Supekar, Menon, & Dougherty, 2009; Hagmann et al., 2008; Honey, Kötter, Breakspear, & Sporns, 2007) and to predict brain activity during cognitive tasks (Cole et al., 2014; Tavor et al., 2016). It is therefore suggested to reflect fundamental organizational principles of the brain. The emerging picture of seed-based studies on intelligence suggested that higher connectivity between regions of the fronto-parietal network (Dosenbach et al., 2007) together with lower connectivity between fronto-parietal regions and the default mode network (Greicius, Krasnow, Reiss, & Menon, 2003; Raichle et al., 2001) were related to higher intelligence scores (Langeslag et al., 2013; Sherman et al., 2014; Song et al., 2008). Graph-theoretical investigations of intrinsic connectivity broadened the focus to the consideration of whole-brain characteristics. The pioneering finding that higher intelligence was linked to a globally more efficient network organization (van den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009) was not replicated in more recent work (Hilger, Ekman, Fiebach, & Basten, 2017a; Kruschwitz, Waller, Daedelow, Walter, & Veer, 2018; Pamplona, Santos Neto, Rosset, Rogers, & Salmon, 2015) and the global level of network modularity (level of segregation between distinct brain networks) did not show a significant association with individual differences in intelligence (Hilger, Ekman, Fiebach, & Basten, 2017b). In contrast, region-specific associations between connectivity characteristics (i.e., how a specific brain region is embedded within the whole brain network) and intelligence have been reported in multiple studies and highlighted the role of brain regions belonging to the fronto-parietal network, to the dorsal and ventral attention networks and to the task-negative default-mode network (van den Heuvel et al., 2009; Hilger et al., 2017a, 2017b; Fraenz et al., 2021; Pamplona et al., 2015; for reviews about intelligence-related aspects in functional connectivity see Cohen, & D' Esposito, M., 2021; Dizaji et al., 2021; Hilger & Sporns, 2021).

Finally, a large number of recent studies applied machine learning-based predictive modelling approaches to demonstrate that significant prediction of intelligence scores is possible on the basis of functional connectivity assessed during resting state (e.g., Cai et al., 2021; Dadi et al., 2021; Dryburgh, McKenna, & Rekik, 2020; Dubois, Galdi, Paul, & Adolphs, 2018; Ferguson, Anderson, & Spreng, 2017; Finn et al., 2015; He et al., 2020; Jiang et al., 2020; Lin et al., 2020; Hebling Vieira, Dubois, Calhoun, & Garrido Salmon, 2021; Wei, Jing, & Li, 2020; Zhang et al., 2019), during tasks (Gao, Greene, Constable, & Scheinost, 2019; Greene, Gao, Scheinost, & Constable, 2018; Jiang et al., 2020), or both (Elliott et al., 2019a,b). One pioneering study also succeeded to predict intelligence from dynamic (time-varying) brain connectivity (Fan, Su, Qin, Hu, & Shen, 2020). In most of these studies the mean absolute prediction error remained quite high (~10 IQ points, ~0.66 SD), and the size of correlations between predicted and observed IQ scores varied between $r = .24$ (Ferguson et al., 2017) and $r = .50$ (Finn et al., 2015; for an overview see Dizaji et al., 2021). Nevertheless, such research endeavors support the assumption that it is important for the explanation of individual differences in intelligence to consider the interaction between different brain regions – both during rest and during active cognition. Of note, the interplay between the task-positive networks (dorsal and ventral attention networks; fronto-parietal control network) and the task-negative default-mode networks seemed to play a particularly critical role for the prediction of individual intelligence test scores (Dubois et al., 2018; Jiang et al., 2020).

To conclude, while an overall higher integrity of structural connectivity can be interpreted against the background of advantages in information processing speed, findings from functional connectivity studies highlight the role of attention networks, the executive control network, and the default mode network for individual differences in intelligence. These findings provide indirect support (Poldrack, 2008, 2011) for the assumption that cognitive processes related to working memory and attentional control are involved in intelligence test performance.

3.4. Open questions and future directions

Beyond the introduction of machine learning-based predictive modelling approaches to the neuroscientific study of intelligence, another important point to enhance the reproducibility of research findings is to increase sample sizes since correlations between neuroimaging measures and phenotypical variables such as intelligence stabilize only in sufficiently large samples (Marek et al., 2020; Sui, Jiang, Bustillo, & Calhoun, 2020). Data sharing initiatives like the Human Connectome Project (van Essen et al., 2012) or the Enhanced Rockland Sample (Nooner et al., 2012) that provide not only neuroimaging data from more than thousands of people but also implemented psychometric assessments may therefore play an increasingly important role in future neuroimaging-based studies of intelligence (Laird, 2021). With respect to methodological advances in network neuroscience, the further analysis of dynamic (time-varying) brain connectivity (Ashrafi & Soltanian-Zadeh, 2020; Fan et al., 2020; Hilger, Fukushima, Sporns, & Fiebach, 2020b; Sen & Parhi, 2021), the consideration of metrics from network control theory (Ashrafi & Soltanian-Zadeh, 2020; Kenett et al., 2018; Sen & Parhi, 2021), and a closer study of the interplay between resting-state and task-related connectivity present promising future directions (Girn, Mills, & Christoff, 2019; Ramirez-Mahaluf et al., 2020; Shine et al., 2019). For example, two studies suggested less rest-task brain network reconfiguration in more intelligent individuals, a finding that can be interpreted against the background of neural efficacy (Schultz & Cole, 2016; Thiele, Faskowitz, Sporns, & Hilger, 2022). Moreover, the investigation of structural-functional brain network coupling with methods combining (f)MRI with DTI data (Levakov, Faskowitz, Avidan, & Sporns, 2021; Zimmermann, Griffiths, & McIntosh, 2018) may represent promising ways to gain additional insights from neuroimaging into the neurobiological basis of intelligence.

4. Genetics

4.1. Quantitative genetics

The question whether and to which extent intelligence is heritable has not only provided cause for controversial discussions but has also facilitated various scientific endeavors. Results from twin and family studies show that genetic differences between individuals are associated with individual differences in intelligence, accounting for approximately 50% of the variance when studies across all age groups are combined (Deary et al., 2021). A recent meta-analysis of the heritability of 17,804 human traits from 2,748 publications over fifty years of twin studies revealed that for a majority of these traits, twin resemblance was solely due to additive genetic influence, which explained 49% of the phenotypic variance across all traits (Polderman et al., 2015). In line with Turkheimer's (2000) three laws of behavior genetics, the effect of being raised in the same family (shared environment) was much smaller than the effect of genes. Furthermore, a substantial portion of the variation was neither accounted for by the effects of genes nor by the effects of families – rather, it was a non-shared environmental effect that made the strongest contribution.

Intelligence differs from the above results in so far as it shows a differentiated etiological pattern. Specifically, substantial shared environmental influences were observed in early childhood but those declined across the school years up to only modest influences in young adulthood and negligible influences in later adulthood (Briley & Tucker-Drob, 2013). In line with this, it has also been shown that the heritability of intelligence increases from childhood to adolescence, reaching 60% or more in later adulthood (Haworth et al., 2010). This effect of increasing heritability in the face of genetic stability has been called "genetic amplification" (Knopik, Neiderhiser, DeFries, & Plomin, 2017). More specifically, this effect reflects the concept of active genotype-environment correlation: Small genetic differences are magnified when growing-up individuals select, modify, and create environments in accordance with their genetic propensities. At the level of twin correlations, the change in heritability over time was shown to be mainly caused by decreasing similarity in dizygotic twins. In sum, the observation that less genetically similar individuals become more different in the face of environmental diversity suggests that it takes a highly similar genetic make-up to retain high phenotypic similarity in intelligence over the life course. At the same time, it is noteworthy that the pronounced stability of intelligence found when large samples of individuals are tested repeatedly in a longitudinal design can largely be attributed to genetic factors (Deary, 2012).

Two additional findings from decades of quantitative genetic research on intelligence warrant attention: First, intelligence appears to capture genetic effects on diverse cognitive and learning abilities, which correlate only modestly at the phenotypic but substantially at the genetic level – an observation which suggests the existence of a genetic *g* factor of intelligence (Plomin & Spinath, 2002). Second, assortative mating or phenotypic similarity between spouses is greater for intelligence than for most other behavioral traits, which might contribute critically to the high narrow heritability (a predominance of additive genetic effects) of general intelligence. Both of these above outlined findings facilitate molecular genetic research strategies that benefit from the absence of major gene x gene and gene x environment interactions as they are in their essence exploratory and do not incorporate assumptions about interactive effects (Plomin & Deary, 2015).

4.2. Molecular genetics

For almost twenty years, candidate gene or genome-wide association studies (GWAS) for intelligence yielded disappointing results, as no replicable associations were found (Chabris et al., 2012; Plomin & von Stumm, 2018). Key issues with these early-stage failures were insufficient sample sizes combined with very low effect sizes of 0.05% or even less.

In 2018, three studies (Davies et al., 2018; Hill et al., 2019; Savage et al., 2018) with samples of 200,000-300,000 individuals reported several hundred significant associations with intelligence (see Deary et al., 2021, for a review). All three studies calculated polygenic scores (PGS), i.e., an individual-level aggregate composed of large numbers of single-nucleotide polymorphisms (SNPs), which are combined using a weighted sum of allele dosages multiplied by their corresponding effect sizes. These PGS studies succeeded to significantly explain 4-7% variance in individual intelligence scores.

Respective investigations tied in with a series of GWAS focused on years of education (Lee et al., 2018; Okbay et al., 2016, 2022; Rietveld et al., 2013), which could increase the size of study samples further and identified an increasing number of significant genetic loci. Those studies explained an increasing amount of variance in educational attainment, and, to a lesser extent, intelligence. The largest GWAS on educational attainment to date (Okbay et al., 2022) investigated a sample of ~3M individuals from 71 cohorts and found 3,952 independent SNP associations of genome-wide significance. This study succeeded to explain 12-16% variance in educational attainment on the basis of PGSs. In addition, Lee et al. (2018) conducted a joint analysis of educational attainment and cognitive phenotypes (intelligence). Using data from 1.1M subjects, PGSs explained 11-13% of the variance in educational attainment and 7-10% of variance in cognitive performance. Finally, Malanchini et al. (2021) used PGSs to explain 12% of variance in a newly developed gamified but not yet extensively validated measure of intelligence.

4.3. Open questions and future directions

One line of current genetic research aims at boosting the predictive validity of PGS further by using multi-trait genomic methods (e.g., Allegrini et al., 2019) or by combining genomic and phenotypic measures (e.g., SES) in the prediction of complex outcomes (Allegrini et al., 2020; von Stumm et al., 2020). These investigations foster a deeper understanding of the mechanistic consequences of significant genetic loci and a comprehensive investigation of this issue is only beginning to emerge.

GWAS data sets on intelligence have found associations between SNP variation and tissue-specific gene expression across many of the cortical regions of the brain (Davies et al., 2018; Hill et al., 2019; Savage et al., 2018). SNP variation associated with intelligence has been linked to tissue-specific gene expression in specific classes of neurons, including pyramidal neurons of the somatosensory cortex, the CA1 region of the hippocampus, midbrain embryonic GABAergic neurons (Coleman et al., 2019), and medium spiny neurons (Savage et al., 2018). In addition, tissue-specific analyses found the largest number of significant associations with intelligence for genes that are expressed in the frontal cortex. In their recent review, Deary et al. (2021) identified synapse and post-synaptic density as promising biological systems, because respective SNPs showed the strongest association with intelligence in GWAS. Nevertheless, the authors also warned that “the variance accounted for by the intelligence-associated SNPs found in these biologically plausible tissues is probably very small” (p.8).

Second, the need for large samples in GWAS has resulted in the predominant use of short and narrow intelligence measures instead of more comprehensive test batteries, which makes it difficult to differentiate the predictive power of PGS in different areas of cognitive functioning (but see Genç et al., 2021, for a good example). Thus, future studies may include selected, yet more diverse cognitive tests to close this knowledge gap.

Finally, the promotion of PGS as indicators of genetic propensity that may be used prospectively to tailor personalized medicine (McCarthy & Mahajan, 2018) or education (Plomin, 2018) must be evaluated against the background of their poor accuracy at the individual level (Morris, Davies, & Davey Smith, 2020).

5. Future directions of biological research on intelligence

Our overview of benchmark findings from electrophysiological, neuroimaging, and genetic research on intelligence identified a number of common issues and open questions for future research. Below, we discuss four issues that we conceive of as particularly central for further advances in the field as well as for an integration with other scientific perspectives on intelligence.

5.1. Improving the robustness of neuroscientific research on intelligence

A common problem of neuroscientific research on intelligence is that small sample sizes and the use of unreliable measures with questionable validity limit the replicability and generalizability of promising findings. Small sample sizes result in low statistical power, which often yields exaggerated estimates of effect sizes even in the absence of publication biases (Button et al., 2013). This problem has so far only been systematically tackled by genetic research on intelligence, where researchers have long been aware of the large sample sizes required to robustly test tiny effects. Moreover, we usually know little about the reliability, stability, consistency, and validity of neuroscientific measures in comparison to what we know about the psychometric properties of intelligence tests. Because neuroscientific measures are typically not developed to investigate individual differences, their psychometric properties need to be carefully assessed. Low reliabilities and consistencies are a common problem with various resting-state and task-evoked neuroscientific measures (e.g., Bennett & Miller, 2010; Cassidy, Robertson, & O`Connell, 2012; Colclough et al., 2016; Hardmeier et al., 2014; Lew, Fitzgerald, Ott, Penhale, & Wilson, 2021; Neuper, Grabner, Fink, & Neubauer, 2005; Schubert et al., 2017; Shehzad et al., 2009), but less so with structural measures (Boekel, Forstmann, & Keuken, 2017; Fox et al., 2012). Thus, researchers may limit the robustness of their findings when not accounting for low reliabilities and consistencies (e.g., by using latent estimates). Together, these three issues – low sample sizes, low reliabilities, and low consistencies – threaten the robustness of findings in neuroscientific research on intelligence.

To make matters worse, independent replications of important findings are scarce[1], because access to technical equipment, methodological expertise, and financial resources are limited. This is not only a problem of neuroscientific intelligence research, but of cognitive neuroscience as a whole (Button et al., 2013; Cwiek et al., 2022; Poldrack et al., 2017; Schäfer & Schwarz, 2019). The field of cognitive neuroscience has only recently begun to address this issue by coordinating systematic replication attempts from different laboratories in so-called “many-labs” studies (Botvinik-Nezer et al., 2019; Klein et al., 2014; Pavlov et al., 2021). The launch of such many-lab projects in intelligence research and systematic meta-analyses of published findings are needed to assess the robustness of relations between neuroscientific measures and intelligence. In addition, researchers should attempt to recruit large and heterogeneous samples or use publicly available datasets (exemplary samples including an intelligence assessement: NKI Rockland sample; Nooner et al., 2012; Amsterdam Open MRI Collection, Snoek et al., 2021; Human Connectome Project, Van Essen et al., 2013) to generate the most robust estimate of a given effect possible. However, an overreliance on specific data sets (e.g., the Human Connectome Project data) may also limit the generalizability of findings to other samples and measures. Finally, systematic in-sample and, if possible, out-of-sample cross-validation should become a standard for empirical investigations to avoid overfitting and to increase the generalizability of research findings on neural correlates of intelligence. In the case of in-sample cross-validation this implies that models are first fine-tuned in one part of the sample (training sample) and tested afterwards for their ability to predict intelligence in the other, withheld part of the sample (test sample). The even harder test of external (out-of-sample cross validation) requires an additional sample with neuroscientific data and respective phenotypical assessments (i.e., IQ scores), but represents the optimal way to establish reliable, robust, and generalizable relations between neuroscientific measures and intelligence (for further discussion and an impressive illustration of how cross validation can decrease effect sizes see Cwiek et al., 2022).

5.2. Relating neural parameters to cognitive processes

Another important requirement for future research on the biological correlates of intelligence is a closer connection to cognitive processes and mechanisms – based not only on conceptual ideas but also on empirical results obtained with behavioral measures. Here, we call for a more rigorous inclusion of behavioral measures of the targeted cognitive processes when their underlying neural circuitry is investigated and related to intelligence. To be clear, many studies have implemented behavioral measures, but it is still not the gold standard. Including

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[1] One historical exception is the debunking of the hypothesis that string-length, a measure of ERP signal complexity, is positively related with intelligence (see Hendrickson, 1982; Robinson, 1993).

behavioral measures helps validating the interpretation of neural correlates of intelligence. This might also solve some of the problems discussed under the keyword of "reverse inference" (Nathan & Del Pinal, 2017; Poldrack, 2015). The reverse inference problem refers to the fact that most brain areas and electrophysiological measures are associated not only with one but with several different cognitive processes. Thus, if intelligence is related to the activation of a specific brain area, a brain network, the latency or amplitude of an ERP component and so on, this relation cannot be unambiguously attributed to one specific cognitive process, in particular when this interpretation is generalized to tasks different from those used to formally establish a valid reverse inference (Hutzler, 2014). Including behavioral measures of the cognitive process of interest (e.g., performance parameters of a working memory task) can improve the convergent validity of the interpretation of biological correlates. The inclusion of behavioral measures of other cognitive functions (e.g., processing speed) would enable to determine divergent validity. This might also be informative in studies on the genetic basis of intelligence.

However, even at the behavioral level, the reliable and unambiguous assessment of specific cognitive processes is challenging given that not only one single cognitive function underlies the behavioral measures in a cognitive task (c.f., Frischkorn et al., submitted), which are, therefore, referred to as "impure" measures (Schweizer, 2007). As mentioned above, experimental manipulations of the demands on targeted cognitive processes might be especially helpful, allowing to relate changes in behavior (RTs, errors, hit rates, or mathematical model parameters) to changes in brain activity, because those changes on the behavioral and the brain level can be attributed to the experimentally induced demands on the targeted cognitive process (Wagner, Rammsayer, Schweizer, & Troche, 2015). This will also facilitate the interpretation of the obtained changes when related to individual differences in intelligence (Jungeblut et al., 2021). When using this approach, difference scores should be avoided as they are well-known to be prone to low reliabilities and may therefore contribute to an underestimation of the relationship between experimentally induced changes in neurocognitive parameters and intelligence. This problem can be overcome by latent-change (McArdle, 2009) or fixed-links modeling (Schweizer, 2009).

Finally, the measurement of biological correlates of intelligence often requires a high number of trials. In a given task with many trials, more intelligent individuals may automatize their task processing faster than less intelligent individuals. This could lead to individual differences in brain activity because brain areas associated with controlled processing are no longer required for an automatized processing of the task in more intelligent individuals but still in less intelligent individuals. This difference in brain activity may, however, be misinterpreted to reflect individual differences in controlled processes, while they actually reflect temporal differences in the relative deactivation of those controlled processes. Thus, more attention to temporal changes in the biological processes and mechanisms during task course might be insightful to disentangle quantitative and qualitative differences in the psychophysiology of individuals with different levels of intelligence.

5.3. *Methodological developments*

Beyond the above-mentioned methodological issues specific to a certain research modality (i.e., EEG, neuroimaging, genetics) or a certain type of study design (task-based vs. resting state), three aspects that refer to studies across modalities might be worth mentioning. First, all of the above outlined research was focused on identifying biological correlates of intelligence. These correlates, however, do not allow for any conclusion about directionality of effects and causality. Does a more efficiently connected attention network contribute to higher intelligence or does it rather represent the results of a brain organization with higher functionality? Experimental study designs probing the effects of certain cognitive interventions or applying non-invasive neurostimulation techniques are required to address those questions systematically. For instance, Curtin et al. (2019) combined cognitive training with transcranial magnetic stimulation to the left dorsolateral prefrontal cortex (DLPFC) to show causal effects of DLPFC functioning on the performance in speed of processing tasks. Other studies used transcranial direct current stimulation (tDCS) alone (Sellers et al., 2015) or in conjunction with cognitive training (Brem et al., 2018) to directly modulate performance during an intelligence test (see also Santarnecchi et al., 2015, 2016, 2019). However, large heterogeneity in study protocols, stimulation sides, small sample sizes, and the lack of replication limit comprehensive conclusions, but also suggest room for improvement in future investigations.

Second, a different consideration refers to partially contradictory findings from EEG vs. fMRI research (e.g., in some studies that focus on neural efficiency). To rule out that such contradictory results can be attributed to circumstantial factors (e.g., sample compositions, measurement characteristics, …), the simultaneous assessment of neural activity with EEG and fMRI is warranted. Respective methodologies are available today (e.g., Huster, Debener, Eichele, & Herrmann, 2012; Rosenkranz & Lemieux, 2010), however, to the best of our knowledge, those have not yet been applied to the study of intelligence.

Last, in EEG as well as in fMRI research a broad variety of methods have been developed to address different aspects of brain signal variability. Microstate analyses (e.g., Liu et al., 2020; Santarnecchi et al., 2017b), the analyses of signal complexity and entropy measures (Dreszer et al., 2020; Kaur, Weiss, Zhou, Fischer, & Hildebrandt, 2021; Stankova & Myshkin, 2016; Ueno et al., 2015), as well as the identification of specific moments of brain-wide cofluctuations (Esfahlani et al., 2020) represent some examples of advanced methodological approaches that have only started to get used in the field of intelligence research but may allow for promising insights into the temporal dynamics of intelligence.

5.4. *Building bridges across measurement levels*

To understand *how* genetic variability contributes to variability in intelligence, it is necessary to develop and test theoretical models how genetic effects exert their influence on intelligence through neurocognitive endophenotypes (for first attempts see Deary et al., 2021). This ambitious goal involves at least two steps: Advancing theory development and broadening the scope of empirical research.

In psychological science, there is an ongoing debate about valuing and improving theory development (Proulx & Morey, 2021). Instead of only testing and replicating "effects-bounded hypotheses" (Proulx & Morey, 2021, p. 675) – a practice that is common in many fields of psychology –, intelligence research is a field with a rich history of theory development and continues testing influential theories as well as to develop new ones (e.g., Geary, 2018; Kievit et al., 2016; Kovacs & Conway, 2016; Van Der Maas et al., 2006). Two recently proposed theories already attempted to mechanistically bridge the long and winding path from gene expression to reasoning ability (Geary, 2018; Kievit et al., 2016). This focus on theories as well as empirical findings is an important trajectory the field of intelligence research should stay on. Most importantly, agreeing on important theoretical concepts and key hypotheses will allow pooling resources to develop measures and study protocols to test those hypotheses across different labs.

Testing theories becomes more complicated if those theories make causal or mechanistic predictions that span multiple measurement levels (e.g., genetic variability, brain structure, cognitive process parameters, and fluid intelligence). Therefore, we believe that future research on biological correlates of intelligence could profit from interdisciplinary collaborations. Ideally, labs researching intelligence should consist of researchers with backgrounds in cognitive psychology, cognitive neuroscience, genetics, data analysis, and psychometrics. Moreover, intelligence researchers should make concerted efforts to conduct large-scale longitudinal projects spanning multiple measurement levels or identify elements of an important theory they can test in clearly defined smaller-scale projects. Once the field has agreed upon key hypotheses, it could be very promising to coordinate many-labs studies testing those hypotheses or to generate a large, publicly available dataset designed to test central theories of human intelligence. Nevertheless, there would also be great value in smaller individual studies aimed to cleverly test key predictions of those hypotheses. For example, former empirical studies revealed structural and functional brain properties to mediate the link between single polymorphisms and intelligence (e.g., Green, Kraemer, DeYoung, Fossella, & Gray, 2013) or analyzed shared genetic correlations to gain insights into potentially mediating factors (e.g., Posthuma et al., 2002), while more recent research demonstrated that even the link between PGS and variations in intelligence is mediated by specific neural features, both on a whole brain level (e.g., brain volume, Elliott et al., 2019a,b) as well as at the level of single brain regions (e.g., structural connectivity: Genç et al., 2022; cortical surface: Lett et al., 2020; Mitchell et al., 2020). More research of this kind is essentially required to advance the development of a theoretical framework for the biological basis of intelligence.

6. Conclusion

This article provides a focused overview of key benchmark findings on biological correlates of intelligence (see Fig. 1 for a summary). Electrophysiological studies have been revealing candidate components of the ERP and characteristics of the alpha frequency band that are associated with intelligence, while neuroimaging research has been providing insights into how different brain regions and their functional and structural connections relate to individual differences in intelligence. Finally, genetic research has been suggesting that intelligence is highly heritable, with polygenetic scores of GWAS accounting for up to 10 percent of variance in intelligence today. However, common to all research modalities is the problem of much heterogeneity in methodological choices, which limits systematic cross-study comparison and meta-analytic summaries. In fact, much about the current state of biological research on intelligence is reminiscent of the famous “chaos in the brickyard” metaphor established by Bernard K. Forscher (Forscher, 1963), who warned that assembling bricks (i.e., generating new findings, developing new methods) cannot replace the building of edifices (i.e., the development and testing of theories). The aim of this paper was to assemble the most important and robust bricks in the field of biological research on intelligence, to put them into the hands of researchers in the field, and thus contribute to theory testing and future theory development.

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