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Review article

General intelligence in the age of neuroimaging

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The formal study of intelligence in psychology began with an effort to find students in France who might benefit from assistance in schooling. Binet measured the increase in ability to answer questions that he felt would improve with age and normalized the scores within each age with a mean of 100 as a measure of the student's intelligence quotient [1]. Over the years increasingly sophisticated approaches to intelligence measurement have been developed [2]. However, the basic definition of intelligence remained illusive and it has often been said that intelligence is whatever the intelligence test measures.

The lack of a theoretical definition did not mean that theoretical issues were not important in the psychology of intelligence. An issue central to the discussion of intelligence was whether there might be a single scale of general intelligence (*g*) along which one might, however inexactly, array people according to their score. Against the theory based upon "*g*" was the view that intelligence is domain specific, either limited to a small number like 2 (fluid or crystalized, [3,4]) or 7 [5] or as many as 140 [6] domains.

The idea of multiple intelligences was espoused by Howard Gardner [5], who defined seven intelligences (domains of individual differences) which were supported by brain networks as revealed by brain lesion research. His idea was to consider separate intelligences based upon the following domains: 1. musical-rhythmic, 2. visual-spatial, 3. verbal-linguistic, 4. logical-mathematical, 5. bodily-kinesthetic, 6. interpersonal, and 7. intrapersonal. Gardner's basic idea, of supposing that brain networks underlie individual differences in different domains, remains important in the era of imaging. Gardner did not address the correlation between items, in what, according to his view, were quite different forms of intelligence. However, his theory of multiple intelligences has impact in the field of education, where it spawned new curricula to address different learning styles, but Gardner had much less influence in cognitive psychology and cognitive neuroscience.

With the advent of neuroimaging [7] it became possible to move beyond the lesion studies possible at that time to associate cognitive tasks in many different domains with specific brain networks [8]. In general, this involved performing specific cognitive tasks that could be clustered within a single domain. For example, the Stroop task [9], flanker task [10] and [11], while quite different, were thought to involve the resolution of conflict [12]. Where different tasks were employed within the same domain, they often activated highly overlapping networks, which were seen as central to the domain. Language, number, attention, self regard and negative affect were among the most commonly studied domains.

Early studies investigating the neurobiology of *g* focused on the lateral prefrontal cortex [13,14], motivating an influential theory based on the role of this region in cognitive control functions for intelligent behavior [15]. The later emergence of network-based theories reflected an effort to examine the neurobiology of intelligence through a wider lens, accounting for individual differences in *g* on the basis of broadly distributed networks. For example, the Parietal-Frontal Integration Theory (P-FIT) appeals to the fronto-parietal network to explain individual differences in intelligence [8,16], proposing that *g* reflects the capacity of this network to evaluate and test hypotheses for problem-solving. A central feature of the P-FIT model is an emphasis on the integration of knowledge between frontal and parietal cortex, afforded by white-matter fiber tracks that enable efficient communication among regions. Evidence to support the fronto-parietal network's role in a broad range of problem-solving tasks later motivated the Multiple-Demand (MD) Theory, which proposes that this network underlies attentional control mechanisms for goal-directed problem-solving [17]. Finally, the Process Overlap Theory represents a recent network approach that accounts for individual differences in *g* by appealing to the spatial overlap among specific brain networks, reflecting the shared cognitive processes underlying *g* [18]. Thus, many contemporary theories suggest that individual differences in *g* originate from functionally localized processes within specific brain regions or networks.

Resting state MRI studies found that brain areas were correlated even when the person was not performing a task, but instead was in a resting state [19,20]. These correlations could arise from the high connectivity between brain areas crucial for everyday life as, for example, brain networks related to attention. Functional MRI in the

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resting state supported a fronto-parietal network that in task performance is related to rapid shifts of attention such as would be provided by a cue giving the location of an upcoming target. A cingulo-opercular network was also identified, which in task performance involved slower more strategic switches of attention (as, for example in switching between tasks). In many cases such as attention and language, all people had the network. However, not all people have equal efficiency of networks involved in language or attention. Thus it seems natural to relate individual differences in a domain with the efficiency of the networks involving that domain. These results from neuroimaging would support the idea of multiple brain networks each describing the individual differences within separate domains related to intelligence. This perspective motivates the Network Neuroscience Theory, which proposes that *g* originates from individual differences in the system-wide topology and dynamics of the human brain [21]. According to this view, general intelligence reflects individual differences in network mechanisms for efficient and flexible information processing [21,22].

However, imaging studies could also be used to support a single domain of general intelligence as suggested by Duncan [23]. Duncan used imaging and cellular recording data to argue that, in addition to domain specificity, imaging can provide a single multi-domain network derived from items that load upon a common general intelligence factor (*g*). This multiple domain network includes the lateral areas of the frontal and parietal lobe along with the anterior cingulate and anterior insula and overlaps two of the networks frequently found in studies of attention using fMRI (the fronto-parietal network and the cingulo-opercular network). Crittenden, Mitchell and Duncan [24] recognize the consistency of the fronto-parietal and cingulo-opercular networks with their multiple demand networks and thus with the loading on general intelligence. The existence of a single domain general network could then support the idea that the correlation between various intelligence tests rests upon their common dependence on attention. This view would not necessarily imply that the efficiency of one domain specific network (e.g., for language) was itself correlated with the efficiency of another network (e.g. music), but correlations among their tests depend upon their both using the multi-domain network related to attention.

During development, long connections between remote neural areas increase. These connections gain in efficiency as they become myelinated [25]. Diffusion tensor imaging studies of 1–2 year old children have found that efficiency of major tracts developing in this period are correlated [26], suggesting that common genetic factors are crucial in their development [27]. Efficient connectivity can aid in the development of networks underlying skills in different domains, thus providing a basis for general intelligence (*g*). In fact, measures of cognitive functions are significantly correlated with myelination of major pathways [26].

It is thus possible to suppose that a correlation between brain networks might be induced by a common mechanism for learning new skills regardless of domain. In a recent rodent study it was found that DNA methylation of BDNF influenced the long term memory of newly learned place fields [28]. The role of methylation in the learning and performance of skills also extends to humans.

People with a genetic variation of the MTHFR (methylenetetrahydrofolate reductase) gene that increases the efficiency of methylation show faster learning rate and higher performance in a variety of speed related human skills [29,30]. While these studies dealt with alleles of only one gene it is likely that many individual genes would be involved in conduction speed and reliability [31].

How might improved rate of learning by those with more efficient methylation come about? One possibility is that higher methylation improves the efficiency of synaptic plasticity. Another possible mechanism is that more efficient methylation improves myelination of axons that occur during learning [32]. Myelination would improve the speed and reliability of the long connections between the often remote areas important for orchestrating performance [31]. Some support for this view comes from a human and monkey study in which morphometric similarity networks defined from MRI were used as a proxy for degree of connectivity between neural areas. The authors predicted that individual differences in this measure would correlate with IQ measured in the same human subjects. The outcome supported their conjecture and thus suggests that the efficiency of white matter is related to IQ [33].

There is little question that specific and often mostly non-overlapping brain networks underlie a variety of skills that are constituents of intelligent behavior. At the same time there is also little doubt that a variety of tests of intelligence are correlated across domains. The specific mechanisms that underlie "*g*" still remain to be established. Three prominent possibilities are: (1) system-wide network mechanisms for efficient and flexible information processing, (2) multipurpose brain networks such as those underlying attention and (3) molecular mechanisms that underlie common mechanisms of learning. These are not mutually exclusive and represent mechanisms at multiple levels of granularity (i.e., system-wide, network-based, and molecular-level mechanisms). As we await further investigation of these mechanisms there are insights from both separate brain networks and a common *g* factor that can be applied to foster better achievement in educational settings.

Declaration of Competing Interest

The authors have no conflicts of interest to report.

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Ethical statement

Both authors contributed equally to this paper.

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