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Three individual difference constructs, one converging concept: adaptive problem solving in the human brain

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The study of human individual differences has matured significantly, in the last decade or so owing, in part, to the notable advances in neuroimaging techniques. There are three major domains of inquiry within individual differences research: personality, creativity, and intelligence. Each has a discrete, testable definition (a new definition for intelligence is offered: *rapid and accurate problem solving*), and each has been associated with distinct brain regions and interactive networks. Here, we outline commonalities between these constructs, which appear to conform to two major axes: exploratory behavior and restraint. These axes, in turn, conform largely to two major brain networks dedicated to novelty generation (i.e. default mode network — DMN), and refinement of ideas (i.e. cognitive control network — CCN). Thus, human individual differences represent the expression of adaptive behaviors leading to exploratory and/or restrained action arising from brain structure and function.

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Introduction

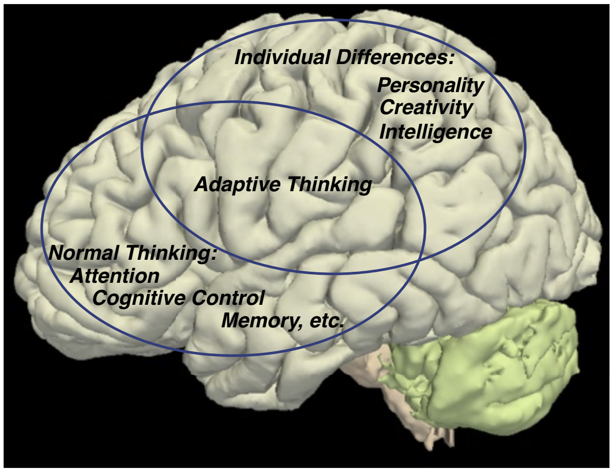
The study of human individual differences has entered a renaissance period in the last decade, particularly with the incorporation of neuroimaging techniques designed to explore discrete cortical networks involved in the manifestation of personality, creativity, and intelligence [1–3]. There will be those rare souls who ceaselessly lament the lack of progress in these endeavors [4], like an idée fixe [5–7]; however, the scope and pace of advancement are beyond doubt to even the most cursory review (see this issue of Current Opinions, as well as Ref. [8]). Let us be clear: no one in the field believes or has posited that personality, creativity, or intelligence is some special construct, somehow separate from other adaptive or normal brain processes (Figure 1). As with any scientific endeavor, the variable of interest is isolated from other variables, as much as possible, with knowledge that interactions and congruence (or anomalies) will emerge from individual studies over time, leading to 'revolutionary science' [9••].

There now exist major theories regarding how personality, creativity, and intelligence are manifested in the human brain: each has been tested empirically over time, and each has been supported to varying degrees [10,11••12]. These constructs have been subdivided into more tractable parts amenable to cognitive inquiries: for example, creativity has been explored from cognitive domains including memory, attention, and cognitive control [13•]. Finally, each has explicit definitions which provide a basis, from which empirical, falsifiable, research can proceed. The purpose of this review is to point out an emerging similarity between the constructs, which might serve as a basis to integrate these within cognitive and brain sciences. This review focuses on cortical networks; thus, we explicitly do not discuss white matter and/or cortico-basal ganglia circuits that constrain exploratory and restraint behaviors, although such subcortical influences have been well researched, and most certainly interact with our theoretical framework [14].

Personality and the brain

There exists universal acceptance that humans possess "relatively enduring styles of thinking, feeling, and acting" comprising the construct of personality. Further, personality is broadly accepted as being comprised of five main factors, including Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (OCEAN), which fold into two metatraits via factor analysis: Plasticity and Stability [15]. The metatrait of plasticity includes Openness/Intellect and Extraversion, and "has been hypothesized to relate to an individual's basic need to incorporate novel information from the environment." (page 1086). This capacity has been theoretically linked to the dopaminergic system, although evidence to support this supposition is scant [16,17]. On the other axis is the metatrait of stability, which includes Neuroticism (reversed), Agreeableness, and Conscientiousness. This meta-trait is described as "the need to maintain a stable organization of behavioral and psychological function" (page 1086), and is hypothesized to be modulated by serotonergic inhibition upon mood, behavior, and cognition [18]. For a detailed review of the 'Big Two' of personality see this issue [19].

Figure 1



Conceptual diagram showing the overlapping relationship between individual difference variables, (i.e. personality, creativity, and intelligence within the larger context of well-established cognitive domains within the neurosciences (e.g. attention, cognitive control, memory). The intersection of individual differences, cognitive domains, and brain structure and function, would be within the realm of adaptive human thinking.

The relationship between Big Five personality variables and brain structure/function have been relatively underexplored in normal human subjects, with the exception of the Openness/Intellect facet. As we, and others, have described in detail, these facets of the Openness factor must be separated [20], which is accomplished with the Big Five Aspect Scale [21]. Once Openness is properly distinguished from Intellect, researchers find that: 1) intellect is associated with working memory performance and posteriomedial prefrontal cortex activation (pMPFC) [22], 2) Openness is positively correlated with right posteromedial temporal gyrus (pMTG) volume, and negatively correlated with orbitofrontal cortex (OFC) volume [23], 3) Openness is related to network efficiency within the Default Mode Network (DMN) [24], and 4) most recently [25], Openness (but not Intellect) is associated with cortical thinning in regions associated with cognitive flexibility [26], conceptual expansion [27], and various creativity tasks [28–30].

No one has studied the metatraits of Plasticity and Stability in normal humans using neuroimaging techniques (although see [31] for subcortical correlates of the analogs 'novelty seeking' and 'harm avoidance'). What we believe the data will show, is that personality traits fall upon two major axes – Plasticity and Stability – and that their brain correlates also comprise two major axes: Plasticity overlapping significantly with the DMN, and Stability with the Cognitive (or Executive) Control Network (CCN). This hypothesis is supported by data from Openness/Intellect showing associations between Openness and regions within the DMN (e.g. pMTG, DMN connectivity), and Intellect with regions within the CCN (e.g. pMPFC). There are also data, albeit less consistent, supporting associations among Neuroticism, Conscientiousness, and Agreeableness and topological characteristics of the CCN [10,32–34].

Creativity and the brain

Creativity has been defined as the production of something both novel and useful [35••]. This definition holds great appeal, as it creates a dynamic tension between the production of novel ideas, critically dependent upon exploratory behavior, and the refinement of these into useful ideas that are adaptive within ones environment, critically dependent upon behavioral restraint. There are numerous tools to assess creative cognition, which have extended well beyond the cliché that it is measured only by divergent thinking. These tasks include such tools as diverse as: divergent/convergent thinking [36], creative achievement [37], remote associates [38], imagination [39], verb generation [40], analogical reasoning [41], and insight [42], tapping cognitive domains including internally focused attention, achievement, verbal fluency, verbal association, response inhibition, semantic/episodic memory, reasoning, and broad components of executive functioning, including updating and shifting (see Refs. [13•,43] for recent reviews).

We first became suspicious that creative cognition overlapped significantly with major brain networks, namely the default mode network (DMN) and cognitive control network (CCN), when reviewing structural neuroimaging studies of creative cognition [2]. In that review, we posited several hypotheses: 1) that creativity represents 'blind variation and selective retention' (BVSR) (a notion hotly debated, but virtually untested within the empirical literature), 2) that divergent thinking represents an approximation of 'blind variation' in that it generates novel ideas, 3) that structural studies possess the requisite reliability necessary to provide validation regarding brain-behavioral relationships underlying creative cognition, and 4) that morphological studies showed a 'striking' congruence with both increased and decreased cortical thickness/volume "across a broad network of brain regions," "within and overlapping the default mode network." (page 7). Finally, we note:

> "Thus, the DMN appears to have been co-opted (or co-evolved) for the purpose of BVSR, with other hubs pulled in as task demands dictate. The production of something "novel and useful" appears to depend, at least in part, on disinhibitory neuronal processes within this core network, while excitatory processes (i.e., more refinement of ideas or *selective retention*) would appear to depend on the CCN. This

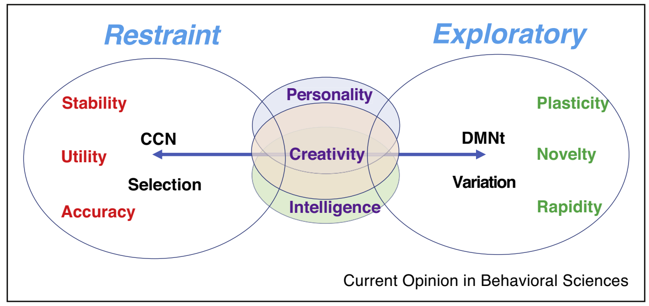
> would be a plausible allocation of cognitive resources with DMN devoted to the innovation and blind variation mechanisms associated with the "constructing of dynamic mental simulations," while the CCN would be engaged to test retained innovations within the framework of the external environment." (page 9).

Subsequent research has universally supported the association of creative cognition with both structure and function of the DMN [42,44,45,46•,47,48], with an increasing number of studies demonstrating dynamic interplay between DMN and CCN [49–58]. This notion has supported by lesion studies, with damage to specific nodes within the DMN and CCN (e.g. right medial prefrontal region; rostrolateral prefrontal region) being associated with impaired ability to generate and combine remote ideas respectively [59••]. Given the dozens of studies over hundreds of normal subjects, utilizing multiple measures of creativity, there can be little doubt that creative cognition represents a dynamic interplay of the DMN (involved in novelty generation/variation), and the CCN (involved in utility/selection). Readers are also directed to [31] for subcortical relationships between the analogues 'novelty seeking' and 'harm avoidance,' and verbal creativity, all of which intersect with the current theoretical framework.

Intelligence and the brain

The definition of intelligence is as variegated and far flung as the Task Force of academics that created it: "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought." Unfortunately, this definition lacks critical falsifiability in its breadth of scope. We propose a more succinct version of this definition that will be as familiar to anyone who has taken an IQ test as it is to someone trying to solve a nettlesome problem at work: *Intelligence is rapid and accurate problem solving.* Thus, all biological life can be intelligent: it is a matter of degree, with rapid/accurate problem solving being 'rewarded' with high genetic penetrance into future generations. Indeed, all IQ tests also have components that are judged by a combination of rapid and accurate performance (e.g. Block Design), and nearly all reliable and valid tests of intelligence are timed (e.g. Ravens Matrices). Finally, in our model, accuracy of performance would be associated with 'restraint', while speed would be associated with 'exploratory' behavior (Figure 2).

Figure 2



Diagrammatic overview of the theory linking restraint and exploratory adaptive behaviors. Individual differences have characteristics of both restraint (e.g. personality – stability; creativity – utility; intelligence – accuracy) and exploratory (e.g. personality – plasticity; creativity – novelty; intelligence – rapidity) behaviors. Exploratory behaviors are predominantly associated with structure and function within the Default Mode Network (DMN), and evolutionary characteristics of Variation. Restraint behaviors are predominantly associated with structure and function of the Cognitive Control Network (CCN), and evolutionary characteristics of Selection. This unifying theory links evolution (variation/selection), brain (DMN/CCN) and behavior (exploratory/restraint) on two major axes amenable to empirical research.

We formulated the Parieto-Frontal Integration Theory (P-FIT) over 10 years ago, which showed a striking correspondence of various brain correlates of intelligence and reasoning within a network that, unbeknownst to us at the time, mapped well on to the CCN or 'task positive' network (TPN) [3]. This theory was 'revolutionary' at the time, in that it ran counter to the prevailing lore, namely that intelligence was a human capacity that resided within our massively overdeveloped frontal lobes [60,61]. We did not expect to discover that intelligence was associated with structural and functional brain correlates distributed throughout the brain: however, that is what we found, and that is what we reported. There are now some inklings (i. e. 'anomalies') that the CCN, executive control network (ECN), or task positive network (TPN), is not exclusively related to intellectual ability. Let me be the first to tell you that this does not disappoint me: indeed, it is the natural order of scientific 'revolution' [9••].

In any event, some clever researchers, bringing to bear increasingly sophisticated neuroimaging techniques, have begun to develop further these 'anomalies' within the prevailing theory provided by the P-FIT. The first notion that intelligence was related to both TPN and the Task Negative Network (TNN) – also known as the DMN – found that neural effort when performing the Raven's matrices was positively associated with TPN and negatively with TNN, and that more intelligent subjects displayed lower efficiency in the TPN and increased efficiency in the TNN [62]. This same group, in a quantitative meta-analysis, added the posterior cingulate cortex (a critical node of the DMN/TNN), to the structures relevant to the expression of intelligence [63••]. An independent group found 'striking' similarities between connectivity of the fluid intelligence (gf) network and the dorsal attention and right fronto-parietal control networks (i.e. TPN), and negative correlations with medial prefrontal structures of the DMN [64]. Finally, researchers found that subjects with higher cognitive ability had lower brain responses to task demands during an N-back task, "suggesting that expansion of the TPN or TNN is associated with greater cognitive ability" [65]. Processing speed tasks, such as the symbol digit modalities test (SDMT), also show positive activations within the TPN and negative activations within the TNN, further supporting the 'speed/accuracy' tradeoff involving both TPN and TNN networks [66].

Not everyone finds significant relationships between the TPN and reasoning, however. In a very large sample ($N = 1336$), very weak (non-significant) relationships (e.g. betas around 0.1) were found between distributed regional gray matter volumes and measures of complex cognitive abilities (CCA), including non-verbal reasoning, implying that great caution should be exercised in interpreting any individual study which might be reporting real effects, although of low power, distributed across multiple cortical regions [67]. Interestingly, this same study did find that simple processing speed was significantly associated with regional gray matter within a region limited to the precuneus, controlling for age, sex, and total gray matter volume, supporting the current theoretical framework. It is evident that these are early days in better understanding the full implications of moving 'beyond P-FIT' in grasping the emerging interplay between exploratory and restraint behavior underlying intelligence, TPN, and TNN

Conclusions

What we (hope we) have demonstrated above is the congruence of various studies of individual differences – including personality, creativity, and intelligence – reflecting a nesting of two major adaptive processes within brain structure and function. These two axes are flexibility, novelty, and rapid problem solving on the one hand (i.e. 'exploratory'), and consistency, utility, and accuracy on the other (i.e. 'restraint') Figure 2. We invite your empirical work to support or challenge this theoretical framework, which attempts to weave several frayed threads into one garment.

Conflict of interest statement

Nothing declared.

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