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# How neuroscience can inform the study of individual differences in cognitive abilities

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**Abstract:** Theories of human mental abilities should be consistent with what is known in neuroscience. Currently, tests of human mental abilities are modeled by cognitive constructs such as attention, working memory, and speed of information processing. These constructs are in turn related to a single general ability. However, brains are very complex systems and whether most of the variability between the operations of different brains can be ascribed to a single factor is questionable. Research in neuroscience suggests that psychological processes such as perception, attention, decision, and executive control are emergent properties of interacting distributed networks. The modules that make up these networks use similar computational processes that involve multiple forms of neural plasticity, each having different time constants. Accordingly, these networks might best be characterized in terms of the information they process rather than in terms of abstract psychological processes such as working memory and executive control.

**Keywords:** attention; intelligence; mental abilities; networks; speed of information processing; working memory.

## Introduction

Many theorists have asserted that the brain is the ultimate source of individual differences in cognitive abilities. For example, Jensen (2000) stated that psychometric intelligence ( $g$ ) could not be described in psychological terms, but rather was a property of the brain. Colom (2014a) suggested that the most fruitful approach for investigating the basis of human cognitive abilities would be to understand how the brain produces intelligence. Habeck et al. (2015) state that latent cognitive abilities have a neural basis that reflects their tendency to engage common brain areas.

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The Cattell-Horn-Carroll (CHC) model is currently a popular account of human cognitive abilities that postulates a single general factor and several second-order group-level factors (Benson et al., 2010; Ward et al., 2012). Indeed, McGrew (2009) contends that there is a consensus that CHC theory best explains human intelligence. Within the CHC model, a general factor contributes to performance on all cognitive tests whereas the group level factors contribute to performance on specific subsets of tests. These group level factors are identified with cognitive processes such as working memory and speed of information processing. Some researchers hold that the general factor accounts for most of the variance in cognitive test performance and that clinical interpretation should be primarily at the level of general intelligence (Canivez and Watkins, 2010).

Neuroimaging is currently a popular tool for exploring the relationship between brain and human mental abilities. Reviewing these data, Jung and Haier (2007) offered the parieto-frontal integration theory of intelligence (P-FIT), which asserts that individual differences in intelligence are related to variations in a distributed network of brain association cortex. This formulation fits nicely with the concept of general intelligence. Brain-ability relationships may be more complex however. For example, Haier et al. (2009) found that there was limited overlap between the neural correlates of different test batteries. Likewise, in a meta-analysis of studies relating neuroimaging and intelligence, Basten et al. (2015) report that functional and structural results did not show any overlap. Colom (2014b) describes numerous inconsistencies in a review of neuroimaging studies. Such results suggest that an overly simplistic interpretation of neuroimaging data may be inappropriate.

According to Ruz (2006), ‘Oversimplified conceptions of cognitive neuroscience regard the goal of this discipline as the localization of previously discovered and validated cognitive processes.’ Studies relating neuroimaging to abilities often seem to be designed to provide support for existing models of the covariance structure of cognitive test batteries. For example, Glascher et al. (2009) reported distinct patterns of lesion-deficits on Wechsler adult intelligence scale (WAIS) group-level factors. However, in a subsequent report using hierarchical factor analysis on what seems to be the same data, Glascher et al. (2010) found that parceling out the effects of a general factor rendered the

effects of the group-level factors nonsignificant. Karama et al. (2011) also report that parceling out the effects of a general factor eliminated specific group-level patterns of significant effects. As discussed by Glascher et al. (2010), their use of the Schmid-Leiman transform results in a general factor that ‘absorbs’ as much variance as possible from the observed test scores. The loadings for group-level factors are then essentially partial correlations (i.e. all variance that could be attributed to the general factor is removed). However, as illustrated by McFarland (2017), whether to attribute variance to general or group-level factors is ambiguous and requires some assumptions about causality. These neuroimaging studies deal only with correlations. Causal inferences need to be based on additional independent sources of information.

Modern neuroscience spans a variety of subdisciplines. To date, neuroimaging methods, such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG), are common methods for exploring the relationship between brain and mental abilities. However, this molar approach does not provide the same sort of detailed description of the mechanisms of neural information processing as more reductionist approaches. Although neuroimaging studies are concerned with the question of where in the brain information is processed, reductionist approaches are concerned with how information is processed in the brain. Ideally, information from both molar and reductionist approaches can be combined to provide comprehensive views of neural information processing.

Factor analytic studies of human cognitive abilities have evolved from models that emphasize content (Cohen, 1952) to those that emphasize elementary cognitive processes (Benson et al., 2010). Studies of neural information processing are beginning to clarify the nature of attention, memory, and speed of processing; constructs central to many theories of human mental abilities (Schweizer, 2005). In what follows, I will discuss some of the recent findings in neuroscience that relate to these constructs. Neuroscience is a very large field of study, and it is only possible to give a few illustrative examples of recent trends. Nonetheless, these examples suggest that simple conceptualizations of these elementary cognitive processes are not supported by what is known of neural information processing. More recent conceptualizations of neural information processing from network science may be more useful.

## Attention

As noted by Posner (1975), ‘attention is not a single concept but the name of a complex field of study.’ This

topic is concerned with selectivity in performance resulting from ‘forces operating at all psychological levels, from sensation through cognition to response’ (Naatanen, 1992). As such, the term attention refers to many psychological processes. This multifaceted view of attention is supported by psychometric studies. In a review of the early psychometric literature, Stankov (1983) concluded that measures of intelligence correlate with several distinct aspects of attention. Likewise, both Schweizer et al. (2005) and Burns et al. (2009) report that multiple facets best accounted for the relationship of attention and intelligence. Moosbrugger et al. (2006) reported that a collection of tests of attention were best accounted for by a model with a perceptual attention factor common to all of the tests and an executive attention factor restricted to a subset of these tests.

One of the earliest demonstrations of attention in neurophysiology was the report by Hernandez-Peon et al. (1956) that visual attention attenuated the auditory evoked response in the cochlear nucleus of cats. Although this finding was initially considered by many to be due simply to the orientation of the peripheral hearing apparatus, subsequent work identified a complex series of descending pathways that regulate the gain of the auditory afferent pathways (Suga et al., 2000). In addition, mechanisms of attentional selection are also involved in more central neural systems (e.g. Fecteau and Munoz, 2006).

Visual spatial attention involves both the orientation of foveal vision as well as the processing of more peripheral visual features [i.e. covert visual attention (Bisley, 2011)]. Control of visual spatial attention involves multiple distributed neural structures at both cortical and subcortical levels including the frontal eye fields, the lateral intraparietal area, the superior colliculus, as well as thalamic, striatal, and cerebellar structures (Bisley, 2011; Krauzlis et al., 2013). These areas contribute to differing aspects of voluntary and reflexive attention. Attention can also be object-centered and there is evidence that there are separate neural systems for spatial and object-based attention (Schenkluhun et al., 2008).

Modulation of stimulus sensitivity can involve rapid, task-dependent effects on neural receptor gain and tuning. For example, David et al. (2008) report that spatial attention modulates the gain but not tuning of V4 neural units whereas feature-based attention can sharpen tuning in this same area. Task-dependent effects on neural tuning have also been described in the auditory cortex (Atiani et al., 2014) and inferior colliculus (Slee and David, 2015). Sharpening of tuning in the auditory cortex can involve both an increase in the gain of the target frequency as well as a suppression of other frequencies

(O'Connell et al., 2014). In the visual system, rapid activation of areas matched to the spatial scale of targets has been reported (Hopf et al., 2006). Thus, there are multiple ways in which central neural attentive mechanisms can rapidly adapt to enhance information processing.

There are mechanisms in the brain for selectively modulating different populations of neurons representing diverse aspects of the external environment. The environment is represented in the brain by the way in which the receptive fields of cortical neurons are tuned. Receptive field tuning is the result of the interaction between excitatory and inhibitory influences on individual neurons (Isaacson and Scanziani, 2011). The structure of synaptic connectivity gradually increases the complexity of representations as one ascends sensory pathways (Hirsch, 2003). Cortical receptive fields are molded by different subtypes of cortical interneurons that have specific functions such as gain modulation or disinhibition (Hangya et al., 2014). These GABAergic interneurons are in turn modulated by subtype-specific afferents from subcortical nuclei (Bacci et al., 2005).

The central mechanisms of attention are complex. Selective modulation of information processing in distributed forebrain sites involves the action of midbrain and brainstem afferents such as those from cholinergic, adrenergic, dopaminergic, and serotonergic nuclei (Green et al., 2008; Harris and Thiele, 2011). Each of these modulating afferents has unique effects. For example, in rat barrel cortex, cholinergic stimulation abolishes synchronous slow waves and increases tonic firing whereas adrenergic stimulation also abolishes slow waves but decreases firing rates (Castro-Alamancos and Gulati, 2014). Cholinergic afferents activate the visual cortex by facilitating somatostatin-expressing inhibitory interneurons, which in turn inhibit parvalbumin-expressing interneurons (Chen et al., 2015). However, the effects of cholinergic modulation are not the same in all neural circuits. For example, activating cholinergic muscarinic receptors in the auditory lemniscal thalamus produces depolarization and tonic firing. In contrast, activating cholinergic muscarinic receptors results in hyperpolarization in the nonlemniscal auditory thalamus (Mooney et al., 2004).

A major source of forebrain acetylcholine is provided by the basal forebrain, a collection of cholinergic and noncholinergic neurons that span several diverse anatomical regions including the septal nucleus, diagonal band of Broca, magnocellular preoptic nucleus, and the globus pallidus (Saper, 1984). These cells are organized into specific groups that project to multiple cortical targets, the overlap of which reflects their interconnectivity (Zaborszky et al., 2015). Zaborszky et al. (2015)

speculate that basal forebrain projections support coactivation of distinct cortical areas that control a particular behavioral domain. This could explain how networks of cortical areas show correlated fluctuations in resting state activity. That is, distinct basal forebrain cell groups can provide modulatory input to interacting cortical areas. Consistent with this view, Nelson et al. (2005) report that stimulation of prefrontal cortex resulted in acetylcholine release in posterior parietal cortex. Likewise, Rasmusson et al. (2007) found that inactivation of prefrontal cortex inhibited sensory-evoked acetylcholine release in somatosensory cortex. In a meta-analysis of effects on neuroimaging, Sutherland et al. (2015) concluded that nicotinic acetylcholine agonists reduce default mode network activity and enhance executive control network regions. The basal forebrain thus seems to be an important efferent for the cortical regulation of the activity of central networks.

These neural mechanisms of attention are relevant to the study of human individual differences in cognitive abilities because there are individual differences in the kinetics of these neural modulators. For example, cholinergic transmission depends on the number of cells in cholinergic centers, synthesis of the transmitter, sensitivity and density of cholinergic receptors, and inactivation by acetylcholinesterase (Soreq, 2015). There are genetic and environmental factors that interact to modify all aspects of cholinergic transmission. Other neuromodulators have similar complex kinetics.

This brief review of neural mechanisms of attention illustrates the complex nature of the processes included within this topic. Attentional mechanisms vary with the content of the information considered (e.g. sensory or higher-order, object, or spatial). Individual differences in these diverse facets of attention may have multiple genetic and environmental determinants.

## Memory

Measures of working memory (Ackerman et al., 2005; Schmiedek et al., 2009) and long-term memory (Kaufman et al., 2009; Unsworth, 2010) both have a strong association with measures of intelligence. In addition, working memory has been used as a latent factor to model cognitive test performance (Tulsky and Price, 2003; Benson et al., 2010) and represents a central construct in many current accounts of the components of intelligence. In contrast with short-term memory, the construct of working memory implies both a storage and a processing component (Baddeley, 2012). Both storage and

processing components of working memory seem to be related to intelligence (Wongupparaj et al., 2015). A popular account suggests that working memory involves a domain-independent executive component, often associated with processing in the prefrontal cortex, as well as several domain-specific components, associated with storage. However, Levy and Goldman-Rakic (2000) have reviewed evidence that there are at least two domain-specific prefrontal working memory networks that deal with visual-spatial and visual-object information. Storage and processing functions are not anatomically separated in this model (Levy and Goldman-Rakic, 2000).

Early research sought to localize the site of the memory engram without success (Grossman, 1967). Subsequent work suggested that the substrates of different types of learning and memory are located in a variety of distinct brain regions (Thompson, 2005). These include early sensory areas (David et al., 2008), association cortex (Gonzalez-Tapia et al., 2016), subcortical nuclei (Ho et al., 2015), and the spinal cord (Wolpaw, 1997). Thus, plasticity seems to be a general property of all neural tissue.

Neural plasticity is involved in information processing throughout the nervous system of mammals. Although there are a number of potential mechanisms for neural plasticity, changes in synaptic connectivity are the most frequently discussed (Citri and Malenka, 2008). There are multiple forms of synaptic plasticity spanning multiple timescales (Larsen and Sjostrom, 2015). In addition, synaptic plasticity is thought to be an important feature of information processing in neural circuits (Destexhe and Marder, 2004; Chaudhuri and Fiete, 2016). For example, auditory stimulus sequences such as those found in speech vary over time and thus require the integration of information beyond the immediate input. The receptive fields of units in the auditory cortex have spectral-temporal tuning characteristics (Froemke and Schreiner, 2015), making them appropriate for encoding time-varying signals. Thorson et al. (2015) have described how neurons modeled as recursive filters with short-term plasticity are better able to account for sensory tuning properties of auditory neurons than simple linear filters. Thus, short-term plasticity seems to be a mechanism for solving the problem of representing sensory information extended in time.

The mismatch negativity is often regarded as an index of auditory sensory memory (Näätänen et al., 2001). The mismatch negativity is the difference in the evoked potentials produced by frequent and rare stimuli and represents a means by which responses to novel stimuli are enhanced. Novelty detection necessarily requires processing information extended over time. Althen et al. (2013)

suggest that acoustic regularities are encoded at different levels of the auditory system as middle latency potentials are sensitive to mismatches of simpler stimulus features as compared to later potentials that respond to a wider range of more complex mismatch features. Their results suggest that auditory change detection involves a distributed system that is not confined to later time periods and higher cortical centers. Thus, short-term plasticity occurs at multiple sites during the processing of information in the ascending auditory pathways.

One influential view of cortical organization holds that the basic unit of information processing is a canonical microcircuit (Bastos et al., 2012). According to the canonical microcircuit view, the cortex consists of cell assemblies that all process information with the same basic operations (Douglas and Martin, 2004). In this view, cortical areas differ in terms of the content of the information they process, rather than in terms of the nature of the processes they support. Content is then determined by extrinsic connections. Although there are anatomical differences between cortical regions, these may be quantitative rather than qualitative (Barbas, 2015). From this perspective, it is interesting that cultures of dissociated cortical neurons are able to form networks capable of spatiotemporal information processing (Ju et al., 2015). This implies that memory is an intrinsic property of cortical networks rather than the property of a limited number of specific areas.

If plasticity is a general property of neural circuits involved in all forms of information processing, then the distinction between processing and storage may not be useful. This follows from the fact that information processing occurs at each synapse and, as a result, processing occurs at all points along neural pathways (i.e. there is no such thing as pure storage). At the same time, these models imply that there are an unlimited number of slots for working memory storage (Bays, 2015). This view of short-term plasticity as a feature of virtually all central nervous system structures contrasts with the commonly held notion that working memory critically involves the prefrontal cortex (Braver et al., 1997; Gerton et al., 2004). In this regard, it is instructive to consider the kinds of tasks that are typically used to measure the construct of working memory in tests of human cognitive abilities.

Digit span is a component of many cognitive test batteries (McGrew and Woodcock, 2001; Wechsler, 2008) and is often modeled as an index of working memory (Benson et al., 2010; Ward et al., 2012). Successful performance of any cognitive test requires remembering the goal of the task, which may be represented in prefrontal areas (Miller and Cohen, 2001; Duncan et al., 2012). Digit span uses

verbal material (i.e. digits), often presented aurally. Perceptual processing of this verbal material likely involves short-term plasticity in the auditory cortex as discussed previously. In addition, because verbal recall is required, speech-associated motor areas are also involved. Finally, a number of studies have provided support for the notion that attentional mechanisms are important in information maintenance by preventing interference (Kane and Engle, 2002; Fukuda and Vogel, 2009). Like other cortical modules, each of these neural systems uses short-term plasticity as part of the process of executing the task at hand. Although short-term plasticity is ubiquitous, the neural areas critically involved in the digit span task are more localized (Irlbacher et al., 2014). Thus, it may be the content of the information processing that is important for the localization of areas active during digit span performance rather than the elementary cognitive processes employed.

Support for models of working memory, which emphasize the role of the prefrontal cortex, is provided by the observation that monkeys performing delayed response tasks show persistent activity in prefrontal cortex and associated thalamic nuclei during the delay interval (Fuster and Alexander, 1971). However, Sreenivasan et al. (2014) have more recently reviewed evidence that implicates prefrontal persistent activity in attention directed toward representations maintained in sensory cortex. This view provides a more distributed view of the representation of working memory and also emphasizes the importance of attention.

The role of attentional processes in tasks designed to evaluate working memory suggests that these two elementary cognitive processes are not distinct. It is also worth noting that the distinction between working memory and intelligence may not be distinct either (Oberauer et al., 2008). Although this is a controversial issue (Beier and Ackerman, 2005), there does seem to be considerable overlap between the psychometric constructs of working memory and intelligence, particularly when considering the relationship between fluid intelligence and working memory (Kane et al., 2005). Although attention, working memory, and fluid intelligence may show considerable overlap, short-term memory tasks can be disassociated on the basis of content (Cacace et al., 1992; Levy and Goldman-Rakic, 2000; Mackintosh and Bennett, 2003). Thus, constructs such as attention, memory, and intelligence may not be distinct, but short-term retention of material may be readily dissociated based on content.

It is likely that mechanisms of short-term plasticity are not separable at a molar level from other aspects of task-dependent information processing. For example, early

work with lesions of the inferotemporal cortex in primates suggested dissociation between memory and perception (Wilson et al., 1968). This distinction between perception and memory in the ventral visual stream is consistent with notions of the anatomical modularization of function. However, more recent studies suggest that there may be overlap between the areas critical for memory and perception in inferotemporal cortex (Murray and Richmond, 2001). Likewise, the hippocampus, generally regarded as a structure critical for episodic memory, also seems to be involved in the perception of spatially coherent scenes (Maguire et al., 2016). In modeling ventral stream processing, Forwood et al. (2012) suggest that the basic computations carried out might be the same all along the visual pathways with differences being due to different levels of representational complexity. Thus, it may be the nature of the information processed rather than particular elementary cognitive processes that characterize differences in the function of brain areas. As suggested by Bussey and Saksida (2007) ‘rather than trying to map psychological functions onto brain modules, we could benefit by instead attempting to understand the functions of brain regions in terms of the representations they contain and the computations they perform.’ The brain may be modularized according to the type of information processed rather than according to abstract psychological processes.

As is the case with attention, memory is a property of many diverse neural systems. Indeed, memory seems to be a general property of neural systems, rather than a localized function. These distributed memory systems vary in large part in terms of the nature of the information being processed.

## Speed of information processing

Jensen (2000) suggested that the speed of information processing might be the fundamental elementary ability underlying general intelligence. In an early attempt to relate neurophysiology and intelligence, Reed and Jensen (1992) correlated what they assumed to be a measure of nerve conduction velocity with intelligence. Their measure of conduction velocity was the latency of the P100 visual evoked potential. Reed and Jensen (1992) interpreted the positive correlation between P100 latency and scores on Raven’s Advanced Progressive Matrices as due to individual differences in processing speed, which they hypothesized was due to cortical nerve conduction velocity. However, this interpretation of the P100 latency was naïve, as the initial response in human primary visual

cortex occurs at approximately 40 to 50 ms after stimulus presentation (Poghosyan and Ioannides, 2007) and the response at approximately 100 ms probably represents a later resonance between multiple brain areas. This example serves as a warning against overly simplistic interpretations of complex phenomena.

The speed of information processing is included as a latent variable in several current models of intelligence. For example, scores on the symbol search, coding, and cancellation subtests define a speed factor for modeling the covariance structure of the WAIS (Benson et al., 2010; Ward et al., 2012). Scores on rapid naming, retrieval fluency, visual matching, decision speed, and cross out subtests have been used to define a speed factor for modeling the covariance structure of the WJ-III (McGrew and Woodcock, 2001). In addition, a number of abilities researchers study tests of processing speed such as reaction time and inspection time to identify elementary cognitive processes associated with intelligence (Sheppard and Vernon, 2008).

Reaction time and inspection time have been popular elementary cognitive tasks that presumably serve as relatively pure indices of speed of information processing. In a review of research examining the relationship between intelligence and speed of information processing, Sheppard and Vernon (2008) concluded that various measures of mental speed, including reaction time and inspection time, all correlate with intelligence. Johnson and Deary (2011) provide psychometric evidence that these elementary tests measure the same general construct as that measured by tests of speed included in cognitive test batteries. Johnson and Deary (2011) also concluded that the factor measured by elementary cognitive tests ‘likely affects all brain structures and regions.’ Staufer et al. (2012) found that a collection of temporal processing tasks were best described by a hierarchical model with modality-specific auditory and visual factors and a second-order general factor. However, other researchers have found a more complex, nonunitary relationship between measures of information processing speed and intelligence (Danthiir et al., 2012; Tachibana et al., 2014).

Inspection time is an elementary cognitive task that has been considered to be a particularly relevant biomarker for cognitive aging (Deary et al., 2010). The typical visual version of the inspection time task requires individuals to make judgments about the length of two lines presented simultaneously for a brief time, followed by a visual masking stimulus. Auditory versions of the inspection time task have also been proposed that include temporal order discrimination tasks. Sheppard and Vernon (2008) report that these auditory tasks are as valid as

other speed tests. However, Olsson et al. (1998) found judgments of temporal order for loudness to correlate with a measure of intelligence whereas judgments of temporal order for pitch did not. This is not surprising as thresholds for temporal order vary widely between different stimulus features (McFarland et al., 1998). Fink et al. (2006) found that individual differences in temporal order judgments seemed to be determined by both feature-specific processing mechanisms and modality-independent mechanisms. There is thus some inconsistency in the extent to which a single individual difference factor in temporal resolution is expressed across all stimulus features. Interestingly, temporal order discrimination is influenced by attention (Schettino et al., 2016). Likewise, Bourke et al. (2013) provide evidence that attention influences the brain areas activated in preparation for visual search, another test of mental speed. These results suggest that the speed of processing and attention are not entirely independent factors.

Livingstone and Hubel (1988) proposed that the primate visual system is segregated into several subsystems specialized for the analysis of distinct visual features. Their model consisted of a dorsal stream specialized for processing movement with high temporal resolution and a ventral stream, specialized for processing form and color with high spatial resolution. Subsequent investigators have argued that there is a progressive decrease in temporal resolution as one moves toward higher areas along the ventral visual pathway (D’Souza et al., 2011; Gauthier et al., 2012). However, Stigliani et al. (2015) suggested that differences in temporal resolution along the ventral visual pathway are more closely associated with the natural temporal statistics of the features that these areas are specialized for processing. In any case, it seems that temporal resolution varies considerably across brain areas processing different perceptual features. These results show that brains do not seem to be characterized by a unitary temporal resolution. However, these differences occur within individual brains and it has not been demonstrated as a source of individual differences.

Visual search tasks figure prominently in psychometric measures of information processing speed. Neuroimaging studies report activation of frontal-parietal areas during visual search tasks as well as activations in various components of the visual system (Makino et al., 2004; Hayakawa et al., 2006; Wei et al., 2011). Some of the frontal-parietal activations are associated with areas involved in the control of eye movements (Nobre et al., 2002). Habeck et al. (2015) showed that tests of fluid reasoning and processing speed are dissociable both in terms of the correlations between test scores and in terms of the brain areas activated during performance of these tests.

Inspection of the Habeck et al. (2015) results suggests that many of these areas associated with processing speed are components of posterior visual areas.

Verghese et al. (2014) found that visual search performance is correlated with the functional size of the primary visual area, V1. This is of interest given that there are large, correlated size variations between the optic tract, visual thalamus, and V1 in humans (Andrews et al., 1997). Dougherty et al. (2003) report that the sizes of V1, V2, and V3 varied by about a factor of 2.5 across human subjects. Pearce and Bridge (2013) speculate that these correlated variations in the visual system represent an adaptation to lower light conditions in humans living at higher latitudes. Indeed, Halpern et al. (1999) found large individual differences in subjects' ability to discriminate various visual features. These individual differences in visual discrimination are relevant to performance in visual search tasks as Reingold and Glaholt (2014) found that the durations of fixation during visual searches were related to target-distractor discriminability. Thus, some of the variation in visual search performance may be specific to the components of the visual system.

As noted earlier, the speed of information processing has been viewed as a particularly important biomarker of aging effects on cognition (Deary et al., 2010). There have been a number of studies relating white matter integrity to processing speed. For example, Turken et al. (2008) report that digit-symbol performance from the WAIS-III is related to the integrity of white matter in parietal, temporal, and left mid-frontal areas in young individuals. Kuznetsova et al. (2016) found that the change in processing speed with older age was associated with global white matter integrity. Likewise, Arvanitakis et al. (2016) report that the total volume of white matter hyperintensities, indicative of lesions, were negatively related to psychometric measures of perceptual speed but not working memory or visuospatial abilities of older individuals. Gray matter volumes were not related to perceptual speed after correcting for white matter volumes. However, Hong et al. (2015) found that processing speed was related to frontal-striatal tracts in subjects before the age of 70 and gray matter loss in the left putamen and middle occipital gyrus at older ages. Processing speed is also associated with damage to peripheral visual pathways. For example, Scantlebury et al. (2016) found that children irradiated for brain tumors showed a correlation between the right optic radiation and processing speed. Thus, although measures of processing speed seem to be related to white matter integrity, this relationship may be complex. This is due in part to the disparate measures used to assess processing speed. It could also be due in part to the complexity of brain fiber tracts and the areas they connect.

Whether processing speed should be viewed as a single attribute or a differentiated set of abilities remains a contentious problem. Part of the difficulty lies in what should be considered good measures of the construct of processing speed. Considering measures of inspection time, studies in neuroscience show that temporal resolution varies considerably across various cortical modules. Psychometric measures of processing speed such as visual search are related to the characteristics of a number of neural structures, including early visual pathways. This potential heterogeneity in what is measured by various tests of mental speed is consistent with psychometric investigations suggesting that this construct is best modeled with multiple factors (e.g. Danthiir et al., 2005, 2012). Thus, although individual difference theorists often assume that diverse measures of speed of information processing reflect the same underlying psychological construct, specific measures, such as temporal resolution, seem to be specific to the nature of the information being processed.

## Network models of brain function

There is a long history of debate about the extent to which different functions can be localized to specific brain regions (Posner and DiGirolamo, 2000). Proponents of the localization of function assert that cognitive processes can be localized to specific brain areas. In addition to low-level sensory and motor functions, higher-order functions are often associated with domain-general regions within the frontal and parietal cortex (Fedorenko et al., 2013). This hypothesized domain-general region is thought to deal with processes such as executive control and working memory common to all complex cognitive tasks. The notion of domain general cortex is consistent with models of working memory such as that of Baddeley (2012), which place a domain-general process at the top of a hierarchy above domain-specific processes. The notion of a domain-general cortex is also consistent with models of intelligence such as that of Benson et al. (2010), which place a g factor at the top of a hierarchy of domain-specific abilities.

Models postulating highly localized functions in brain centers can be contrasted to network models (Bullmore and Sporns, 2009; Stam and van Straaten, 2012), which have gained popularity within neuroscience in recent years. An early network model was proposed by Rosvold (1972) who described anatomical and functional relationships between prefrontal and subcortical structures. Based on anatomical connections and lesion studies that suggest

similar functions in primates, he described a dorsal and a ventral prefrontal system that were each associated with a different subset of subcortical areas involved in distinct behavioral functions. More recent network models have been based on the analysis of metrics such as the spatial covariance of resting metabolic activity (Fox et al., 2005), gray matter density (Alexander-Bloch et al., 2013), and gene expression (Richiardi et al., 2015).

Network models based on the covariance of brain features across individuals are particularly interesting because they have implications for the basis of individual differences in brain function. A number of studies have related the covariance structure of brain imaging to that of cognitive abilities tests (e.g. Roman et al., 2014). Modeling the covariance structure of brain imaging features typically involves techniques such as regression, principal components, independent components (Li et al., 2009), or structural equation modeling (Colibazzi et al., 2008). These are data reduction techniques that involve linear transformations of the original imaging data. As such, it is important to keep in mind that the resulting latent factors may not map to the actual sources in a one-to-one fashion (McFarland, 2012). This is due in part to the existence of factor indeterminacy, where many linear transformations can account equally for the same covariance matrix (MacCallum et al., 1993). Thus, alternative decompositions provide different views of network structure (Pessoa, 2014).

As discussed earlier, a popular theory of higher mental functions holds that there is a multiple-demand system consisting of a frontal-parietal network (Thompson-Schill et al., 2005; Duncan, 2010). This domain-general frontal-parietal network has been postulated to be the neural substrate of general intelligence, a conjecture known as the P-FIT model (Jung and Haier, 2007). Gray matter clusters identified by this P-FIT model have been associated with the general factor extracted from cognitive tests (Roman et al., 2014).

Although many higher-order cognitive processes are ascribed to the prefrontal cortex, the computational details of these processes are not described so that these models amount to the postulation of a homunculus (Hazy et al., 2007). This might be acceptable when one is dealing with commonsense cognitive concepts, as is frequently done in neuroimaging (Francken and Slors, 2014). However, this leaves much to be desired from the perspective of reductionist approaches to neural information processing that seek to describe specific details of these computations (e.g. Grossberg, 2013). In addition, there is evidence for functional specialization within components of the P-FIT network, such as a dorsolateral prefrontal

cortex, which seems to have an anterior region associated with attention and inhibition, and a posterior region associated with action execution and working memory (Cieslik et al., 2013). Hampshire et al. (2016) used independent components analysis to decompose lateral frontal activations into three separate networks, each with distinct associations with the parietal cortex. They describe these three frontal networks as being involved in different temporal aspects of learning. Using a hierarchical Bayesian model based on the notion that behavioral tasks engage multiple cognitive components, Yeo et al. (2015) identified multiple complex zones of frontal and parietal cortex in a meta-analysis of neuroimaging data. Thus, the P-FIT model, which lumps together many distinct neural structures, may be an oversimplification of the brain's network organization.

Rottschy et al. (2013) dissociated frontal-parietal networks associated with working memory for object location and object identity in a meta-analysis of neuroimaging data. This result is reminiscent of the model of Levy and Goldman-Rakic (2000) discussed earlier. Rottschy et al. (2013) also described the distinct parietal connections of these two frontal areas, which they associate with the motor functions of reaching and grasping. They relate these findings to dorsal and ventral sensory pathways described for vision (Ungerleider and Haxby, 1994) and audition (Rauschecker, 2009), which provide input to action and cognition-related processes (Milner and Goodale, 2008). Thus, frontal-parietal systems do not seem to represent a single unitary system.

The executive control network is often contrasted with the default mode network with which it tends to be anticorrelated. However, the default and executive networks may cooperate during creative cognition (Beaty et al., 2016). Likewise, the default mode network and areas associated with working memory can be coactive during preparation for a working memory task (Koshino et al., 2014). Konishi et al. (2015) suggest that the default mode network is important for cognition that is independent of immediate perceptual input. This latter observation is particularly interesting because most laboratory tasks and items on abilities tests are driven by external stimuli. However, there are numerous intellectual problems that do not fit this format. Thus, although frontal-parietal executive networks may be particularly important for typical laboratory tasks, other networks may be critical for other domains of cognitive performance.

Most studies have emphasized cortical components of networks, due in part to technical difficulties with imaging subcortical structures (Bar et al., 2016). However, there is a substantial involvement of subcortical structures

in cognitive processing as well. These include the basal ganglia, thalamus, basal forebrain, and cerebellum. For example, although the basal ganglia have traditionally been associated with motor functions, there are multiple parallel cortical-basal ganglia loops consisting of segregated anatomical structures and serving distinct behavioral functions (Alexander et al., 1986; Middleton and Strick, 2000). These frontal-striatal loops have recently been detected with network analysis of regional cortical gray matter volumes (Morris et al., 2016) and functional imaging (Soriano-Mas et al., 2013). Helie et al. (2015) have proposed that the basal ganglia serve as a trainer that optimizes cortico-cortico connections based on experience. This would provide a mechanism by which network organization could be dynamically modified on the basis of experience so as to optimize performance.

In addition to the basal ganglia, higher-order thalamic nuclei are important links in cortical networks (Sherman, 2007). The cerebellum also seems to be involved in many aspects of cognition (Caligiore et al., 2017). Likewise, as discussed earlier, the basal forebrain consists of specific cell groups that project to multiple cortical targets, the overlap of which reflects their interconnectedness and seem to be important in regulating network activity (Zaborszky et al., 2015). Bar et al. (2016) found that the serotonergic dorsal raphe and dopaminergic midbrain centers are functionally coupled with the default mode network whereas the remaining serotonergic nuclei and the noradrenergic locus coeruleus are coupled with the executive control network. Thus, multiple subcortical structures represent components of brain networks that are important for regulating their activity.

Generally speaking, more is known about the precise details of neural information processing in the early visual pathways than elsewhere in the primate brain, so they serve as good examples for the details of network information processing. The dorsal and ventral visual processing streams were originally identified by Livingstone and Hubel (1988) in early visual pathways. These two processing streams have their origin at the level of the retina where separate cells are specialized for color, spatial, and temporal resolution. These processing streams continue through the thalamus to primary visual cortex. As suggested by Rottschy et al. (2013) and others, they extend into higher association areas. In contrast to earlier views that conceptualized the early visual system as simply transmitting information (Grossman, 1967), more recent research finds that visual processing occurs along the entire course of these pathways. For example, there are at least 17 types of retinal ganglion cells, each with distinct responses to light and projections to central structures

(Field and Chichilnisky, 2007). Although neurons of the thalamic lateral geniculate nucleus are largely driven by these retinal inputs, they receive extensive feedback projections from the visual cortex to which they project (Sherman, 2007). This recursive arrangement continues into higher-order cortical areas.

These extensive feedback pathways provide a basis for the construction of recursive spatial-temporal filters that can extract different types of information from the visual input depending on their connectivity (Fregnac and Bathellier, 2005). Grossberg (2013) has modeled a number of recursive neural circuits that can account for numerous details of vision as well as other aspects of brain function such as speech and cognition. The applicability of a common recursive model to these diverse brain functions suggests that similar mechanisms might be used for information processing throughout the brain.

The cortical processing of visual information involves a complex interplay between several dozen distinct processing modules, each specialized to some extent for the extraction of specific visual features (Van Essen, 2005). Processing of vision thus involves transformations across the multiple cell layers of retina, visual thalamus, primary visual cortex, and multiple higher-order cortices. This multistep processing model, based on anatomical and physiological data, is in contrast to molar models of visual processing, based on behavioral response latencies, which often conceptualize visual processing as a two-step process (e.g. Buetti et al., 2016).

Gain modulation may be a ubiquitous mechanism of neural computation (Salinas and Theier, 2000). Gain modulation was originally proposed by Andersen et al. (1985) to account for visual-spatial coordinate transformations in the posterior parietal cortex. Gain modulation is a change in the response amplitude of a neuron that is not accompanied by a modification of response selectivity. The transformation of images from a retina-centric to a head-centered representation is difficult using ordinary mathematical operations. Using gain modulation to combine visual sensory representations with extraretinal information, such as eye or head position, the brain can create abstract representations of space (Andersen et al., 1985). Details of the weighting of these inputs can be adjusted by an adaptive neural network using an appropriate error signal. Gain modulation transforms visual information from retinal coordinates to other frames of reference and thus provides a means of stabilizing the visual field in the presence of head and eye movements (Wurtz, 2008).

Brayanov et al. (2012) provide evidence that gain field modulation is also involved in spatial transformations by the motor system for the control of reaching.

Stemmler et al. (2015) describe a model that explains how gain field modulation combines multiple sources of information for navigation in the entorhinal cortex and hippocampus. Finally, Lipinski et al. (2012) used gain modulation to explain how spatial relations in visual scenes can be transformed into spatial language behaviors. These examples show how some of the complex problems faced by nervous systems can be solved by relatively simple recursive networks. In addition, such top-down, bottom-up interactions can occur locally within a network such as the visual system. The brain can use the same basic information processing technique to appropriately combine many different types of information. Along these lines, it is worth noting that cognition and goal-directed choice require the combination of many sources of information such as needs, predicted outcomes, and current sensory input. Gain modulation could provide a means for solving these problems. Thus, as suggested by Pezzulo and Cisek (2016), models of simple motor behavior can be extended to explain higher cognitive skills. Gain modulation may be one of these canonical computation motifs (Turkheimer et al., 2015).

Consideration of visual networks suggest that the nature of their connectivity allows for the sequential processing of information by parallel distributed systems. It is likely that this view applies broadly to neural information processing. Pessoa (2014) has argued that there is a many-to-many mapping of brain structures to function, implying that there are no necessary and sufficient brain systems. Rather, coalitions of regions jointly contribute to behavior. These coalitions may be dynamic in nature (Cocchi et al., 2013), coordinated in part by subcortical structures such as the basal ganglia, basal forebrain, and cerebellum. Stuss (2011) asserts that there is no central executive, but rather numerous distributed domain-general processes. Likewise, Abrahamse et al. (2016) suggest that cognitive control involves a broad range of context-specific functions. Nicolaides et al. (2016) suggest that network organization emerges from the collective interaction of the interconnected components. This view of self-organization in neural networks can be contrasted to models of hierarchical, top-down control. The process of dynamic network configuration seems to be important for optimal task performance (Braun et al., 2015; Alavash et al., 2016).

The concept of cognitive control has been associated with domain-general executive mechanisms that are the basis for general intelligence (Chiappe and MacDonald, 2005) and are localized within the prefrontal cortex (Rougier et al., 2005). However, although broad expanses of frontal-parietal cortex are often implicated in

neuroimaging studies, Scolari et al. (2015) note that these networks can be reliably parceled into 18 subregions that are associated with different attentional control features. These include space-based, feature-based, object-based, and category-based control mechanisms. Furthermore, spatial attentional mechanisms can be further subdivided according to different spatial frames of reference. Along these lines, it is of interest that recent developments in the coordination of large collections of robots have found reconfigurable distributed control to be more viable than hierarchical control (Levy et al., 2014; Li et al., 2015).

To summarize, neuroimaging studies have emphasized the cortex, but numerous subcortical structures are also important for brain function. Neural connectivity is an important aspect of information processing and not simply a mechanism for information transmission. Even seemingly simple perceptual-motor tasks require complex information transformations. These complex transformations may be accomplished by similar canonical processing mechanisms throughout the brain. Control of these distributed processes may be accomplished by a collection of self-organizing networks.

## Sources of individual differences

One approach to evaluating sources of individual differences is to examine the effects associated with genetic polymorphisms. This is not to discount environmental influences (Clemenson and Stark, 2015), but polymorphisms provide an easy way to identify potential differences in brain functions. For example, Berry et al. (2014) found that individuals with a genetic polymorphism limiting the activity of the choline transporter were more vulnerable to distraction. A subsequent study showed that this effect was related to a lack of increased activation of right prefrontal cortex with increasing attentional demands (Berry et al., 2015). Greenwood et al. (2009) report that polymorphisms on both nicotinic and muscarinic receptor genes interact to produce a significant effect on a visual attention task when neither reached significance in isolation. Greenwood et al. (2012) have reviewed evidence suggesting that a polymorphism of the nicotinic acetylcholine receptor affects attention.

As with attention, genetic polymorphisms can serve as one marker for individual differences in working memory performance. Although prior work suggested associations of cholinergic functions with visual-spatial attention and dopaminergic processes with working memory, Stromer et al. (2011) have reviewed evidence that polymorphisms

associated with both of these neurotransmitters are related to both attention and memory. Researchers have also related processing speed to genetic polymorphisms. For example, Schneider et al. (2015) found that a polymorphism for the gene encoding the CHRNA4 cholinergic receptor was related to reaction times on three cognitive tasks. They interpreted this result as an effect of the nicotinic acetylcholine receptor on speed of information processing. At this point, it is worth noting that polymorphisms in genes associated with acetylcholine have been related to all three elementary cognitive processes that we have previously discussed. If one is interested in associating a specific cognitive phenotype such as focused attention with the CHRNA4 polymorphism (e.g. Greenwood et al., 2012) then such results are problematic. However, involvement in all of these abstract cognitive processes would be expected if cholinergic systems regulate the activity of many neural systems in complex ways.

Several studies have reported an association between polymorphisms in the CHRM2 muscarinic receptor and IQ as measured by the Wechsler scales (Comings et al., 2003; Gosso et al., 2006, 2007; Dick et al., 2007). However, Lind et al. (2009) did not find an association between polymorphisms in CHRM2 and *g* factors extracted from an assortment of cognitive tests in three independent samples. Despite problems in replicating the effects of specific genes on behavioral measures (Chabris et al., 2013), methods are beginning to be developed that may account for traits that have previously been shown to be heritable by methods such as twin studies (Vandenberg, 1966). One issue concerns the selection of the appropriate phenotype as combining genetically unrelated measures may obscure results. Another issue concerns the limited effect of single genes on complex biological pathways involving many steps. For example, as discussed by Soreq (2015), cholinergic pathways are regulated by genes coding for receptors and transporters, and for synthesizing and degrading enzymes. Homeostatic mechanisms regulate the activity of these pathways so that single genes are not likely to have a large effect. Consequently, the interaction of several genes (i.e. epistasis) may be necessary to produce significant effects unless studies have extremely large sample sizes. Other neurochemical pathways are likely to have a similar degree of complexity.

Lamb et al. (2015) report that a polymorphism of the brain-derived neurotrophic factor was associated with recall on the faces and family pictures subtests on the Wechsler memory scale (WMS-III). However, recognition was not affected and Lamb et al. (2015) suggest that combining scores as is done with the WMS-III composite might obscure gene effects. This raises the issue of what measure

(i.e. phenotype) should be correlated with genetic polymorphisms. Heck et al. (2014) note that single-marker analyses have limited power and used instead a gene-set-based method to identify an association between working memory and polymorphisms in genes involved in voltage-gated cation channels. Gene-set enrichment analysis uses prior knowledge to combine the effects of multiple genes related to a common biological pathway. Heck et al. (2014) report that an association with a working memory task and nine genes encoding voltage-gated calcium channels were replicated across two samples.

There may also be structural correlates of working memory abilities. For example, Bergmann et al. (2016) report that both gray matter size and volume of the primary visual cortex were related to performance on a visual memory task. Delayed matching of orientation of a single visual stimulus originally presented in an array of three stimuli correlated with the size of V1, but not later visual areas or whole brain thickness and volume. Such results are consistent with the hypothesis that sensory working memory involves early processing centers in addition to prefrontal and parietal areas (Pasternak and Greenlee, 2005). Indeed, the results of Bergmann et al. (2016) suggest that characteristics of early perceptual processing areas may be more of a limiting factor for sensory working memory than characteristics of later areas. Sources of individual differences in regional brain size represent a promising area of investigation.

In a different approach to investigating the relationships of polymorphisms to processing speed, Luciano et al. (2011) performed a genome-wide association study using several measures of processing speed. None of the single gene polymorphisms exceeded the genome-wide significance level. However, a pathway analysis produced significant effects. The pathway analysis considers multiple single-nucleotide polymorphisms (SNPs) related to multiple genes involved in a common biological pathway (Nam and Kim, 2008). Associations with speed of processing in the article by Luciano et al. (2011) included pathways related to cell junction and focal adhesion that are involved in linking cells with the extracellular matrix and serve to relay external signals.

Thus far, we have considered genetic polymorphisms as a source of individual differences in attention, memory, and processing speed. Despite difficulties in relating genetics to human abilities, current technologies do provide objective markers of gene polymorphisms. At the same time, there is ample evidence that environmental experience, such as formal education, affects scores on tests of intelligence (Ceci and Williams, 1997). Unfortunately, environmental effects are not always associated

with simple objective markers. However, individual differences in brain function produced by environmental effects necessarily affect behavior through their effects on the brain.

Environmental influences on the brain include a diverse collection of effects, such as second language learning (Li et al., 2014) and television viewing (Takeuchi et al., 2015). Butz et al. (2009) have reviewed the extensive literature documenting effects on neural structure resulting from learning and sensory experience, and Zatorre et al. (2012) have discussed possible mechanisms for these effects. Environmental influences take other forms in addition to sensory experience, such as the effects of toxins (Needleman, 2004), infection (McFarland et al., 1986), and nutrition (McFarland, 1985; Haas, 1988). Thus, biological substrates of individual differences in cognitive abilities include all possible determinants, both genetic and environmental.

## Conclusions

Theories of human mental abilities should be consistent with what is known in neuroscience. Unfortunately, our understanding of how brains work is currently very limited, although the prospect of eventual theoretical advances is promising (Churchland and Abbot, 2016). Nonetheless, there are a number of generalizations that can be made that have implications for the study of human mental abilities. Current models of nervous systems emphasize networks of interconnected modules rather than localized centers. Processes such as attention and memory are not readily localized into one or a few centers. Indeed, memory seems to be a property of virtually all components of the central nervous system of vertebrates, intimately involved in all forms of information processing (Destexhe and Marder, 2004; Chaudhuri and Fiete, 2016). Properties such as speed of information processing are specific to specialized brain regions rather than a property of the system as a whole. Thus, neuroscience research suggests a much more differentiated model than that which is the current trend in individual difference research.

Current models of human cognitive abilities use constructs that have considerable conceptual overlap. For example, attention is often considered to be an important determinant of working memory performance (Awh et al., 2006; Fukuda and Vogel, 2009) and working memory is thought to guide attention (Downing, 2000; De Fockert et al., 2001). There has been a lively

discussion about whether fluid intelligence and working memory are strongly related (Kane et al., 2005) or less so (Ackerman et al., 2005). These examples point to the fact that these constructs are at times vague and not entirely distinct. Furthermore, as noted by Pezzulo and Cisek (2016), traditional assumptions of cognitive psychology are beginning to conflict with what is becoming known in neuroscience.

At the same time, most experts in the science of mental abilities believe in Spearman's construct of *g* (Reeve and Charles, 2008) despite the fact that it has been known for a long time that the correlation between tests of ability can be accounted for by models based on multiple independent factors (Thompson, 1920; Bartholomew et al., 2009; McFarland, 2012). The popularity of the *g* construct may be due in part to the extensive use of procedures in abilities research, such as principal components analysis, and partly to the appeal of simplicity (Canivez, 2013). However, the nature of principal components insures that the maximum possible covariance will be allocated to the first principal component (McFarland, 2014). As we have seen from the prior discussion, brains are very complex systems. Whether most of the variability between the operations of different human brains can be ascribed to a single factor is questionable.

Neuroscience research suggests that psychological processes such as perception, attention, decision, and executive control are emergent properties of interacting distributed networks. The modules that make up these networks use similar computational processes that involve multiple forms of neural plasticity, each having different time constants. Accordingly, these networks might best be characterized in terms of the information they process rather than in terms of abstract psychological processes such as working memory and executive control. Applied to mental abilities testing, this view suggests that models should focus on content rather than process. Earlier, models of human abilities were based on content-related factors such as verbal and visual-spatial abilities (Silverstein, 1982). More recently, there has been a trend toward models emphasizing cognitive processes such as speed of information processing and working memory (Benson et al., 2010; Ward et al., 2012). Indeed, Primi (2014) advocates the construction of abilities tests based on process-related theory from cognitive psychology. However, the present brief review of findings in neuroscience suggest that models based on content rather than process may be more appropriate.

Not all current models of human intelligence are organized according to psychological processes. For example, Paivio (2014) describes a model that emphasizes

content rather than processes. The main elements of this model are auditory and visual representational elements and referential elements, which are cross-system activations. Paivio (2014) notes that typical cognitive test batteries do not adequately sample a full range of content, such as nonverbal auditory processing. Paivio (2014) also suggests that many tests in typical batteries are multidimensional and obscure factors such as referential processing that might emerge with less complex items. From the perspective of this review, visual systems might also be subdivided into dorsal and ventral visual processing streams that can be further subdivided according to the visual features they represent (Ungerleider and Haxby, 1994). Auditory processing can be similarly divided into dorsal and ventral streams (Rauschecker, 2009). Thus, it should be possible to classify human mental abilities according to a hierarchy of content. The use of less complex cognitive test items, or psychometrically matched tests (Cacace and McFarland, 2013), would facilitate this process.

Kovacs and Conway (2016) present process overlap theory as a model of human cognitive abilities that emphasizes multiple determinants of test performance and  $g$  as a formative factor. As a formative construct,  $g$  is modeled as a composite that emerges from rather than causes multiple subprocesses (MacCallum and Browne, 1993). For Kovacs and Conway (2016), the overlapping processes that are common to cognitive test performance are mainly executive in nature, such as attention and working memory. Again, it should be possible to organize these executive processes according to a hierarchy of content, such as spatial and feature-based attention (Schenkluhun et al., 2008) or working memory for object location and identity (Rottschy et al., 2013). However, although object and spatial processing might represent distinct abilities, it may not be necessary to differentiate between spatial attention and spatial memory (Bussey and Saksida, 2007). The suggestion here is that the organization of content should parallel emerging concepts of brain organization.

Kovacs and Conway (2016) also contrast compensatory models and noncompensatory models of multidimensional accounts of  $g$ . In compensatory models, the different dimensions combine in an additive manner. In contrast, noncompensatory models combine the separate dimensions in a nonlinear manner so that the final outcome is limited by the single lowest component. Noncompensatory models basically hold that a single weak link in a chain of cognitive processes is sufficient to preclude good performance. Detterman et al. (2016) provided a simulation of a noncompensatory model that they contend can account for the positive manifold. Noncompensatory

models thus provide a means of reconciling the frequent dissociations seen in neuroscience with the concept of a general factor.

Abilities theorists such as Kranzer and Jensen (1991), Detterman et al. (2016), and Kovacs and Conway (2016) have advocated models of  $g$  as representing a composite of multiple abilities. This contrasts with the notion of  $g$  as a unitary construct (Carroll, 1991). As discussed by Markus and Borsboom (2013), the issue of item sampling becomes more important with formative constructs. With reflective constructs (i.e. causal latent variables), it is only necessary to sample from a few representative indices of the trait in question. In contrast, formative constructs require a broader representation of the domain in question. As a unitary construct,  $g$  might be associated with some global aspect of brain function, such as myelination (Miller, 1994) or plasticity (Garlick, 2002). Alternatively, cognitive test performance might be determined by multiple partially overlapping abilities (Kovacs and Conway, 2016) associated perhaps with dynamically interacting networks. Thus,  $g$  could potentially be a statistical artifact, a composite of many distinct abilities, or a monolithic determinant of a large portion of mental abilities. To resolve this issue, alternative models of cognitive test performance should be compared in studies of the relationship between neuroimaging and cognitive test performance. In this way, neuroscience and psychometrics can mutually benefit from an exchange of methods and theory.

Researchers and theorists concerned with human mental abilities should consider a broader range of alternatives in modeling mental abilities and correlating these with neurophysiology. Relating the singular construct of general intelligence to the singular frontal-parietal network is currently the most popular approach. As discussed by Goldman-Rakic (2000), the prefrontal cortex is probably best viewed as a heterogeneous structure. The unitary conceptualization of frontal function may be due in part to a lack of precision in descriptions of the precise frontal areas involved in studies dealing with behavioral correlates. Certainly, relating a single behavioral construct to a single network is parsimonious. However, this may not be optimal for understanding the relationship of brain functions to such topics as learning disabilities and psychopathology.

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