RELATIONSHIP OF SPEED OF CORTICAL INTEGRATION AND MEASURES OF INTELLIGENCE

By

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Abstract

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Due to brain modularity, mechanisms of cortical integration are necessary. It is hypothesized here that the accuracy and speed of information integration is reflected as cognitive ability. In order to examine the process of cortical integration, participants perceptually grouped arrays of dots by means of spatial or temporal proximity. Psychophysical measurements were made of the limits of perceptual organization, and of processing time required to discriminate patterns at different levels of stimulus organization. Psychophysical measurements correlated with performance on a battery of tests of cognitive abilities, and different aspects of perceptual measures predicted different cognitive factors. Implications for cognitive enhancement are discussed.

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RELATIONSHIP OF SPEED OF CORTICAL INTEGRATION AND MEASURES OF INTELLIGENCE

This paper addresses questions relating to the brain’s ability to integrate stimuli across cortical areas into the coherent world that we experience. The exploration of this issue begins with a brief overview of the organization of the cortex, focusing on uniformity across the cortex, as well as the modular nature of the brain. Possible mechanisms of cortical integration are then discussed, including evidence for the existence of a distributed neural network mediating cortical integration. This is followed by an overview of perceptual organization, in terms of cortical integration. Inspection time and processing speed are then considered as measures of neural efficiency. Finally, the possibility of these mechanisms in relation to cortical integration is discussed as a measure of intelligence.

Cortical Uniformity

Although cognitive function and ability are seen to vary widely within and across species, it is unlikely that this discrepancy is due to differences in the organization of the cortex. The intrinsic structure of the cortex is uniform within and across species. Research has suggested that basic modules with a constant number of neurons characterize cortical organization (Hofman, 1985). There are identical counts of neuronal cell bodies within different functional areas (i.e., motor, somatosensory, frontal) (Rockel et al., 1980; Manto, 2006). Laminar organization has been shown to be consistent across cortical areas in the cat (Clemo, Keniston, & Meredith, 2003) and, in the adult rat cortex, different functional areas have been shown to have equivalent cell densities (Morin and Beaulieu, 1994). Although the morphology of the cortex may vary from one person to the next, there is general structural covariance within the cortex of each individual (Mechelli, Friston, Frackowiak, & Price, 2005).

Further evidence for cortical uniformity comes from the phenomenon of takeover of function, a common sequelae to congenital or traumatic brain lesions. Functional reorganization of the human brain is well documented, and often is explained in terms of neural plasticity (Chino, Kaas, Smith, Langston, & Chen, 1992). The neural plasticity hypothesis accounts for the ability of the remaining brain areas to assume the function of a damaged area. An example of redistribution of function has been seen in individuals with a cerebral artereovenous malformation (AVM) involving the primary motor cortex. In such cases, reorganization has a distributed function, as measured by specific activation patterns on functional Magnetic Resonance Image (fMRI)[1], to both primary and non-primary motor areas (Alkadhi, Kollias, Crelier, Golay, Hepp-Reymond, & Valavanis, 2000). Similar results have been demonstrated to occur throughout the nervous system. For example, Reiter and Stryker (1988) demonstrated the plasticity of ocular dominance by causing a differential shift in responsiveness of cortical areas to either eye depending on selective inhibition of cortical cell discharge.

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[1] Three patterns of activation were seen: displacement within the affected area, activation within the unaffected area to the moving extremity without activation in the affected area, and corresponding activation in the non-primary areas without activation in the unaffected or affected primary areas.

Although it has been well established that the modular organization of the cortex encompasses many localized functions (see below), originally, the idea of localized functions seemed dubious. This was due to lesion experiments that left the animals with general, rather than specific, residual disabilities (Philips, Zeki, & Barlow, 1984). Since then, it has been established that localization of functions does indeed exist within the cortex (Hansen and Koeppen, 2002). However, there is a great degree of uniformity of function across modules of localized functions (Raizada and Grossberg, 2003). In fact, differences in cytoarchitecture and functions of different modules are attributed to differences in connections (Rockel, Hiorns, & Powell, 1980) and these connections are implicated in multimodal integration (Lewis and Van Essen, 2000).

The Modular Nature of the Brain

Neural architecture is based upon series of modules that are topographically organized (Jung, 2005). This modularity is seen throughout the human brain. For example, anatomically and functionally independent areas mediate visual, auditory, tactile, and motor processing. Research has revealed modularity within each of these subsystems, as well (Amirikian and Georgopoulos, 2003; Seitz, Nickel, & Azari, 2006; Imaizumi, Priebe, Crum, Bedenbaugh, Cheung, & Schreiner, 2004). The visual system provides an example of modularity within a subsystem. Different components of the visual cortex analyze different parts of the visual scene, such as shape, motion, or color (Zeki and Bartels, 1998).

Theories of Cortical Integration

It has been proposed that while simple cognitive functions are organized in a modular fashion (Gisiger and Kerszberg 2006), more complex cognitive functions must involve the integration of these modules (Luna and Sweeney, 2004). The question is, then, what allows the brain to group and organize modules, transforming a collection of values into objects? It seems unlikely that delineated cognitive domains exist in exclusive dedication to specific cognitive functions. Although this modular theory has traditionally been accepted (see Fuster, 2006 for a review), evidence that cognition arises from such demarcated domains is lacking. A network theory of cognition and cortical integration has arisen partly in response to the lack of evidence supporting the modular view of cognitive function. Below, some theories of cortical integration are reviewed.

The Binding Problem: The 'binding' problem refers to the question of how the brain achieves cortical integration. Consider a visual scene that includes more than a single object. The brain must correctly associate features within the visual scene so that objects can be perceived coherently and so that they can be distinguished from the background or other objects. The unification of a visual representation through explicit association of one visual feature with another is called 'binding.' The 'binding problem' applies to many situations across sensory modalities. For example, in the visual system, the 'binding problem' refers to binding information across space, across types of features, and binding neural signals across cortical areas (Roskies, 1999). A binding mechanism of cortical synchronization would require the ability to synchronize and desynchronize groups of cells from one another - a step up from the classical hierarchical scheme of neural coding (combinatorial coding) of Hubel and Wiesel (Hubel and Wiesel, 2004).

In fact, research on cognitive integration has uncovered a wealth of evidence suggesting that dynamic synchronization and desynchronization of selectively distributed and coherent neural populations does occur. As will be reviewed below, empirical support for theoretical models of a binding mechanism can be found from single cell recordings, coherence of cortical field potentials and various neuroimaging research. These models postulate that neural networks give rise to cognitive functions such as intelligence, memory, attention, and perception. These networks consist of widespread distribution of cortical neurons, with neural transactions within and between the networks. These networks are interactive and can overlap with each other, so that a single neuron can belong to multiple networks. Furthermore, and most importantly, these networks are not confined within anatomically related areas (Fuster, 2006). Evidence for the existence of such networks is reviewed below.

<u>Temporal Correlation Theory:</u> It has been proposed that binding occurs via dynamic changes of electrical trajectories in the brain. Neuroimaging research and research utilizing methods of invasive neurophysiology have shown clustering of activity patterns for functionally related brain areas, as well as large scale patterns of interregional connectivity (Costa, Lin, Sotnikova, Cyr, Gainetdinov, Caron, & Nicolelis, 2006). This is the basis behind temporal correlation theory, which postulates that neural oscillations and synchronous signals are used for binding and play a critical role in brain function. The

structural organization of the cortex is characterized by interconnections linking brain areas within and between specific sensory and motor systems across the cortex. The fine structure and morphology of these interconnections are the result of continuous interaction between neural substrate, ongoing neural activity and the embodied interaction of an organism with its environment (Sporns, 2000). These various local networks are integrated with each other, to form a dynamic distributed network that underlies cognition and perception (Costa & Sporns, 2006).

The investigation of cortical functional interactions during audio-visual speech integration (Fingelkurts and Fingelkurts, 2003) has suggested widespread networks of functional interactions between the various brain areas involved in the task and that the components of the networks differed depending on the particular information (i.e., modality) available. Not only does this finding, and others like it, support the notion of a network of cortical integration of a dynamic nature, but evidence from this study and others suggests that the distributed networks have emergent properties; combinations of networks make a percept possible that would be impossible through the linear sum of their individual pieces (Fingelkurts, Fingelkurts, Krause, Mottonen, & Sams, 2003).

Varela, Lachaux, Rodriguez, & Martinerie (2001) describe large scale integration as integration between farther regions of the brain (i.e., temporal to occipital lobes) through feedforward/backward connections. There is no definite distinction between local and global integration, but rather it falls along a continuum. Large scale integration operates in networks with dynamic topography and multiple frequencies. Evidence for the existence of a mechanism for large-scale integration comes from recordings with human subjects during an integration task, where intracortical oscillations showed synchrony between distal brain areas (Rodriguez, George, Lachaux, Mattinerie, Renault, & Varela 1999). Consistent synchrony was found between occipital, parietal and frontal areas during a face recognition task, although this synchrony was absent when faces were presented upside down, making the faces not easily recognized. In addition, a new pattern emerged during an integration task that required a motor response. The authors also reported the occurrence of phase scattering, thought to indicate the uncoupling of dynamic links, and therefore may be related to global integration. They further defined integration as being the interplay of phase locking and phase scattering. Synchronous networks were seen to emerge and disappear in waves that last 100-300 ms (Varela et al. 2001).

The oscillatory activity referred to here is thought to constitute the most basic transfer function in the brain (Basar, 1990). Different functions or tasks resulting in oscillatory activity are represented by several parameters within a given neural population, including enhancement, delay, blocking or desynchronization, prolongation degrees of coherence, and degrees of entropy (Bassar, 2006). A better understanding of what exactly these networks are, how they are organized and how they work come from theories and research done within the field of ‘Science of Complex Systems’.

Theories and Models of Cortical Integration from 'Science of Complex Systems':

Numerous models have been proposed to account for the brain’s ability to integrate information within and across modalities. The majority of network models postulate that cortical connectivity is the result of the widespread distribution of cortical neurons, and that neural transactions within and between these networks give rise to cognition. As evidence has suggested, these network models are interactive, overlapping, and not confined to anatomical boundaries within the cortex (see Fuster, 2006).

Theoretical modelers and researchers within this field generally accept the abundant evidence suggesting a distributed neural integrating system that mediates the complex brain (Dear & Hart, 1999). The question then remains as to how this system works; that is, how is information integrated? A system that would be able to do this would need to satisfy both exogenous and endogenous requirements simultaneously by transiently settling in a globally consistent state. It is known that each cortical area has a unique combination of connections with other areas and that connectivity is reentrant (looped – both influence each other). These interactions, along with direct inputs and subcortical modulation, contribute significantly to local processes. Bressler (2002) determined that the large scale network mediates these connections by supporting “complex patterns of inter-area interactions that promote widespread influences across cortical areas.” Functional brain mapping studies have demonstrated the coactivation of multiple distributed cortical areas during cognitive tasks, indicating not only concurrent activation but interdependence between areas – attributed to reentrant processing (Lamme and Roelfsema, 2000).

Phase synchronization studies have shown specific patterns of interdependence corresponding to various cognitive states. Because all local processes are attached through reentrant connections to larger, global processes, connected areas impose constraining influences on each other. ‘Coordination dynamics’ refers to how interdependence among parts of a system changes with time (science of complex systems). Systems with high degrees of complexity (such as the brain) are said to have ‘metastable’ coordination dynamics, which means that there is a balance of integrating and segregating influences. ‘Intermittency’ refers to the degree of coordination of the metastable system’s component parts changing over time (ex: remaining low, then suddenly increasing). Evidence suggests that the cortex displays intermittency in the coordination of its areas through phase synchronization. Distributed sets of cortical areas remain uncoordinated over a period of time and then change with a rapid increase of phase synchronization when a change in cognitive state occurs – mental flexibility (Bressler, 2002).

Some of these simultaneous constraints are in conflict with each other, while others are in concert, so the brain needs a mechanism to mediate in order to produce unified and coherent cognitive states that are also in harmony with the external environment and the body. This mechanism must produce rapid consensus among various cortical areas and has the ability to support numerous cognitive functions. Bressler theorizes that this mechanism is behind all cognition (Bressler & Kelso, 2001).

Bostrom (2000) proposes various means through which cortical integration may be achieved, and suggests that each of these ways likely contributes to cortical integration to varying degrees. He further claims that his model can account for multifaceted aspects of the binding problem, such as the co-existence of multiple representations in the same ‘territory.’

The first of Bostrom's principles of integration is 'convergence,' which is the convergence of responses of all or many cells within a given cell assembly. It is the convergence of multiple cells that yields a robust enough effect for the information transfer to be meaningful. Similarly, convergence accounts for misfiring or mistaken reactions, as they would be nullified. Therefore, a sustained thought or percept would indicate the continuance of accordant firing of a cell assembly. 'Convolution' refers to recursive connections between different cell assemblies, and 'synchronization' is the temporal coordination of spiking activity. Synchronization within a neuronal population refers to an active representation, and activity levels of the neurons in the population have other representative significance (i.e., intensity of stimulus). Lastly, 'annexation' refers to the brain's tendency to group common representations together in a set. Bostrom proposes that at different levels (i.e., sensory vs. motor processing) these different mechanisms occur to different extents, and that it is the sum of all of them that create unified perception and coherent cognition.

Evidence of Cortical Integration from Neuro-Anatomy: Evidence from neuro-anatomy is consistent with the assertion that percepts are created from the conversion of feature selective individual neurons into groups, as well as the dynamic convergence of these groups (Dear & Hart, 1999). The dynamic and complex nature of these networks have been described as 'small-world topography' (i.e., Sporns and Honey, 2006), which refers to a model of cortical connectivity that supports both modular, specialized processing and distributed processing, through its emphasis on highly dynamic connectivity (Bassett and Bullmore, 2006). In fact, the generalized decline in cognitive functioning seen to occur in Alzheimer's disease has been attributed to the loss of small world network characteristics, as determined from EEG recordings of brain synchronization matrices (Stam, Jones, Nolte, Breakspear, & Scheltens, 2008).

A more neuro-anatomical approach to coordination dynamics addresses the brain's ability to coordinate components into a whole from a neurophysiological perspective. Detailed studies into dendritic and axonal activities have provided insight as to information transport in the brain. Cortical neurons receive axons from many neurons in many different locations (Freeman[a,b], 2003). What are the mechanisms that govern the convergence of multiple inputs from different areas of the brain? Eckhorn, Bauer, Jordan, Brosch, & Reitbock (1988) demonstrated the systematic coordination of gamma activity in multiple cortical areas in correlation with behavior. Freeman, Burke, & Holmes (2003) discovered that cortical neurons, located at great distance from each other, would yield spatiotemporal activity patterns by coordinating the timing of their action potentials. The hypothesis of Freeman et al. (2003) regarding integration is of oscillating pulse densities converged from multiple populations. These oscillations require sustained excitation from internal or external sources and the oscillations are manifested by changes in dendritic currents and participating neurons' firing rates. As mentioned in the previous section, Bostrom (2000) outlines several mechanisms (convergence, convolution, synchronization, and annexation) through which neurons may support cortical integration to varying degrees. Essentially, Bostrom proposes that different processing levels (i.e., sensory vs. motor processing) use different combinations of these mechanisms, and it is the sum of all of them that create unified perception.

Cortical Properties

As indicated in the review of the literature above, cortical integration is a well established and important property of the cerebral cortex (Wang & Merzenich, 1995). Cortical properties responsible for the cortex's ability to integrate are reviewed below.

Physical Organization of the Cortex:

The cortex is formed by neurons in vertical, columnar organization that is further organized into horizontal layers, with columns that combine to form macrocolumns (Hutsler, Lee, & Porter, 2005). Columnar structure is homogenous across a variety of species (Rakic, 2000).

In addition to this columnar organization, the cortex consists of several distinct lamina. The deepest of these layers send and receive projections to and from various subcortical targets, whereas the superficial layers (layers II and III of the traditionally described six layer organization) send and receive projections to and from other cortical areas (both inter- and intrahemispheric cortical connections). The organization of the cortex into columns and layers is consistent across species, although there is variance between species regarding the specifics of organization. However, organization is constant within species (Hutsler et al., 2005).

The nature of the organization of these layers and their projections suggests the presence of networks of primary, secondary and association areas that are responsible for higher-order cognitive function (Fuster, 1995). In primates, the superficial layers of the cortex consist of 46% of total cortical space. This is in comparison with 36% and 19% in carnivore and rodent cortices, respectively. These layers mature last during development (Hutsler et al., 2005).

It has been suggested that differential thickness of the superficial cortical layers might correlate to differential cognitive ability. However, the primarily uniform nature of these layers cast doubt on this theory. If differential thickness of the supergranular cortical layers were indeed indicative of cognitive capability, one would expect to see a much wider range of variation than is observed, both within a given species, and most definitely between a species within an order. Although actual cortical size does vary widely in this regard, the proportion of the superficial layers to cortical size does not, and so it is difficult to attribute cognitive ability or behavior complexity to these layers (Reader and Laland, 2002).

Alternative Integration Mechansims

Cortical Integrating Systems: It is possible that differential cognitive ability might be the result of differences associated with the corticocortical connections (Zhang and Sejnowski, 2000). Research indicates that the different areas of the cerebral cortex are linked through reentrant connections that allow for both parallel and reciprocal processing (Edelman, Reeke Jr., Gall, Tononi, Williams, & Sporn 1992). Extensive research conducted regarding the visual system has yielded distinct patterns of physical connections that communicate between all levels of visual areas. It is possible that this strategy of multi-stage integration might be consistent throughout the cortex, and that these local networks of integration are responsible for the production of complex behavior and cognitive function (Zeki and Shipp, 1988).

Indeed, afferent and efferent connections which may underlie an integrating network have been associated with various cortical areas, such as the superior temporal sulcus (Seltzer and Pandya, 1978), the occipital lobe (Rockland and Pandya, 1979), the premotor area (Barbas and Pandya, 1987), and others. Furthermore, studies have shown that the acquisition of a new skill, or improvement of an old skill, are followed by the strengthening of the connections in those areas without changes in the connections of surrounding areas (Rioult-Pedotti, Friedman, Hess, & Donoghue, 1998). Such evidence may be suggestive of the reliance of cognitive skills and abilities upon localized networks.

However, although the learning or improving of a skill will inevitably require the involvement of certain local areas and not others, it can nonetheless be described as a distributed process. For example, the classical eyeblink conditioning experiment was thought to only involve local processes and relevant encoding was believed to be done only in the cerebellum (McCormick, Lavond, Clark, Kettner, Rising, & Thompson, 1981). However, research within the classical eyeblink conditioning paradigm has suggested the involvement of far more than the relevant local areas in the learned acquisition of an eyeblink in response to a puff of air. Evidence suggests the involvement of extracerebellar (including cortical) processes, and similar evidence has been found regarding other conditioning paradigms, such as trace or discrimination conditioning, all of which had previously been thought to be a subcortical, strictly cerebellar process (Steinmetz, 2000). As such, even classical conditioning can be seen to be the result of the work of a distributed, global network.

Additionally, there are known distributed systems in the brain, such as the ascending reticular activating system, which modulates activity across cortical areas. Differences in arousal levels, a function associated with the ascending reticular activating system, could well be correlated with differences in cognitive ability (Marshall, O’Hara, & Steinberg, 2000). Additionally, attentional modulation by cortical projections is often considered as a means of integration (Buchel and Friston, 1997). Attention is thought to originate in the prefrontal cortex and not as a product of a distributed network with no central control. Evidence for the attention hypothesis of cortical connectivity has been shown in the visual system where increased attention to visual-motion events results in increased connectivity between motion-selective area V5 and the posterior parietal cortex (Buchel and Friston, 1997). Therefore, it is possible that cognitive function in general, as well as differential cognitive abilities may be dependent upon one or more known distributed brain systems.

Cortical Modulating Systems: Distributed systems of modulatory neurotransmitters have been used to explain the basis for cognitive function or dysfunction. Such transmitters are typically synthesized in local midbrain nuclei from which they are distributed to cortical areas, and would therefore implicate subcortical areas in what is traditionally considered to be cortical functioning. For example, the functioning of cholinergic systems has also been associated with cognitive dysfunction, such as in the case of delirium and Alzheimer’s disease (Ross, Peyser, Shapiro, & Folstein 1991).

Acetylcholine is not the only neurotransmitter implicated in various cortical functions. The applications of neurotransmitters, including histamine, norepinephrine and serotonin, increase cortical spiking activity (McCormick and Williamson, 1989). In addition, the synthesis of glutamate, GABA, and acetylcholine in the basal forebrain have all been implicated in cortical modulation and plasticity through afferent connections to the cerebral cortex (Manns, Mainville, & Jones, 2001). Similarly, the dopamine system has been extensively studied regarding its role in schizophrenia[2], as well as its role in reinforcement learning. Changes in the responsiveness of cortical areas to dopamine are associated with changes in behavioral and cognitive functioning (Grace, 1991). However, other research suggests a prominent role of the cortex itself in down-regulating dopamine release (Grace, 1993). Cortical control or influence of integrating systems and modulatory neurotransmitter systems suggests that a global mechanism of cortical integration may not fully be accounted for by either of these two systems.

Regardless of the theoretical perspective, the common theme underlying virtually all research regarding cortical integration is that the global mechanism of cognitive activity relies on several sub-mechanisms, consisting of dynamic neural populations, which act in synergy when stimulated by cognitive input (See Basar 2006 for review).

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[2] Increased dopamine activity in the mesolimbic system, decreased dopamine activity in the prefrontal cortex, and increased dopamine receptor densities have been implicated in schizophrenia (Davis et al., 1991)

Furthermore, these synergetic distributed networks are postulated to have emergent properties, where the combination of networks, or complexity of the system, makes a percept possible that would be impossible through any individual piece.

Implications of Impaired Integration in Neurological/ Neuropsychiatric Disorders

Research on neurological disorders has suggested that deficits with cortical activation and synchronization may be implicated in the cognitive symptoms of certain disease states. Schizophrenia is one such condition, in which hyper-plasticity is implicated in negative and cognitive symptoms, such as disorganization, whereas hypo-plasticity is implicated in positive symptoms, such as hallucinations or delusions (Bullmore, Frangou, & Murray, 1997). Plasticity is defined as “the manner in which the nervous system can modify its organization and ultimately its function” (Kolb, Gibb, & Robinson, 2003), or, as the ability to “reorganize patterns and systems of connections” (Stiles, 2000). Therefore, given the definition for ‘plasticity’ in this context, it is suggested, that the degree of cognitive dysfunction is contingent upon the nervous system’s integrative abilities. Furthermore, the nervous system’s tendency to over-integrate or under-integrate is implicated in the type of ensuing cognitive impairment.

Another example of deficits in synchronization contributing to abnormal cognitive functioning can be seen in autism, which is a condition marked by preserved or enhanced cognitive function in some domains, with deficits in other domains. Studies with autistic individuals have implicated the under-functioning of integrative brain circuitry that results in the deficit of information integration at the neural, and thus cognitive, levels

(Brock, Brown, Boucher, & Rippon, 2002). According to this theory of autism, any psychological or neurological function that is dependent on integration will be compromised. This theory therefore accounts for problems with social interactions that are commonly found in autism, as the large range of stimuli (social and cognitive) and rapidly changing dynamics, among other things, impose a heavy burden on large scale integrative processes. Difficulty in novel cognitive tasks that depend on inter-regional coordination, another common symptom of autism, is explained as well, as it requires the auto-configuration of the brain to the new task. It similarly explains problems with change or shift in strategies as a deficit in ability to shift processing from one area to another (Just, Cherkassky, Keller, & Minshew, 2004). Difficulties with language development and sensory-motor integration are also attributed to integrative deficits (Boucher, 2003).This theory has important implications for the non-autistic population as well, in that it postulates that the coordination or integration of the brain is necessary for any facet of psychological function. These implications will be discussed further in the following section.

Cortical Integration and Intelligence

If, as autism studies imply, cortical integration is necessary for any facet of psychological function, then it is likely that differences in cortical integration would result in differences in psychological function. Indeed, there have been numerous studies that have aimed to determine whether patterns of cortical activation and synchronization might be different for people of differing mental abilities. That the nervous system is able to over- or under-integrate information implies that there is an integrating norm, to which the nervous systems of normal, healthy individuals adhere. A range in such a norm likely corresponds with the known range of normal intelligence levels, such that an individual with a 'high average' rate of integration also has a 'high average' intelligence level, while an individual with a 'low average' rate of integration falls on the low average range of the intelligence distribution.

It has long been suggested that the brain functions cohesively (i.e. Flourens, 1824). Pavlov (1949) described brain functioning to be of an integrative nature, and his conceptualization is still supported today (Detterman, 2000). It follows that intelligence is a global measure of brain function, representing the integration of different cognitive functions (Jung, Haier, Yeo, & Rowland, 2005). Below are reviewed two studies that support this definition of intelligence.

Evidence suggests an association between differences in event-related neural activity patterns in the waking, working brain and differences in general mental ability (see Costa and Sporns, 2006 for a review). Additionally, some sleep-EEG oscillations have recently been connected to wakeful cognitive performances, thereby linking general cortical activity with overall cognitive functioning. Evidence suggests that fast sleep spindle-related oscillatory activity over the frontal cortex, thought to synchronize other sleep rhythms, are correlated with waking cognitive performance, as measured by the Raven's Progressive Matrix (Bodizs, Kis, Lazar, Havran, Rigo, Clemens, & Halasz, 2005). These results were interpreted as a finding for general mental ability being correlated with the effective cortical modulation of some sleep oscillations. It seems that cortical efficiency while one sleeps is implicated in waking intelligence.

In a study conducted in order to determine the extent to which cortical activation differs for differential ability levels, EEGs of artists and non-artists were compared as they were asked to mentally compose a drawing of their choice. The study found differences in functional and anatomical connectivity between the two groups, with greater phase synchrony in gamma and delta bands and less phase synchrony in alpha bands for artists compared t o non-artists (Bhattacharya and Petsche, 2005). This, along with other differences in activation patterns support the role of synchronous signals as an underpinning of cognitive performance. Bhattacharya and Petsche's study indicate the existence of a relationship between level of cortical activation and ability in the context of a specific skill. Other studies (i.e., Costa and Sporns, 2006) have established the existence of this relationship between overall levels of activation and general skill, or ability.

Evidence indicates that any act, cognitive or otherwise, requires the co-activation of multiple cortical areas, as well as the cooperation between the co-activated areas, with cooperation being defined as either synchrony or interdependency between anatomically distinct brain areas. As such, it seems that cortical integration is the driving force behind any cognitive function, and that, differences between individuals on the level of cortical integration likely parallels individual differences in cognitive functioning, including intelligence. Before delving further into the topic of neural or cortical correlates of cognitive functioning, I would like to take the time to explore the topic of intelligence further. Below, I have presented a brief review of the controversial history of intelligence and intelligence testing.

Intelligence

Human interest in disparate mental abilities has long been a staple of scholars and philosophers, boasting an impressive pedigree, having piqued the interest of Plato, Aristotle, Kant and the like (as reviewed by Plucker, 2003). There is no telling when the argument of nature vs. nurture as it pertains to human mental faculties struck its first chord, however, it is generally accepted that the debate entered the realm of psychology circa 1869, with the publishing of Sir Francis Galton's controversial book, *Hereditary Genius.*

Galton espoused that nature accounted for far more in a child's development than did nurture, that human beings differed innately in regards to a variety of things, most notably mental characteristics and mental ability. Galton believed that mental ability was normally distributed among the population, and pointed to his studies of tendencies towards greatness within families, as well as twin studies and corroborating evidence for this assertion. Galton believed mental ability to be the effect of an individual's speed of responses to his or her environment, combined with the refinement of said responses. Galton's tests of mental ability centered on the individual's sensory-motor and perceptual abilities, thereby reflecting his theory (Aiken, 1996).

Galton's sensory motor tests failed to show accurate measurements of mental functioning. However, his controversial work sparked the interest of many, including

Charles Spearman, who set out to define and measure this endowment now termed intelligence. Spearman's mathematical approach to the study of intelligence led to his discovery of evidence for the two factor theory of intelligence, termed 'g' and 's' intelligences, for general and specific intelligence factor, respectively. The 'g' factor is thought to pervade all tasks to different degrees, and therefore measuring an individual's g factor should allow one to predict that person's performance on a range of tasks and tests. The 's' factor performance is not as predictable, as it refers to specific skills, or ability pertaining to a specific task at hand (Spearman, 1904).

Spearman's theory of g was quite prolific. In 1924, L.L. Thurstone, a psychometrician, further investigating the concept of g, provided more evidence for the existence of g, as well as expounding upon the s factors. After exhaustive testing, Thurstone determined the s factors to be word fluency, verbal comprehension, spatial visualization, number facility, associative memory, reasoning, and perceptual speed (Thurstone, 1938)

The quest to define and measure intelligence did not begin, nor end, with Spearman and Thurstone. Many reputable psychologists have attempted to define and measure intelligence, from a decidedly more theoretically relevant perspective. Among the ranks of those interested in quantifying the limits of the human mind were Wundt, James, and Ebbinghaus, as well as many others. While the theories of experimentalists, such as the individuals referenced above, tended to be hierarchical and mathematical in nature, other perspectives of mental ability existed as well. One such consideration is a focus on development. Prominent psychologists, such as Freud and Piaget pontificated on developmental theories, which tend to be stage based. One particular distinction between developmental and hierarchical models of intellectual functioning is the accumulation of intelligence. Whereas hierarchical theories postulate the accumulation of 'more of the same thing' (ability), developmental theories propose a series of discrete, but necessarily sequential steps, each step, or stage, being indispensable. The most prominent of such theories are those of Jean Piaget, who outlined four main stages[3] that loosely correlate (in intervals) with ages ranging from birth to age 12 and beyond (Plucker, 2003).

The focus upon the quantification of intelligence gave way to the now commonplace intelligence testing. Several versions of intelligence tests exist, encompassing slightly different focuses and created for the use of different age ranges or populations. Although many researchers have attempted to measure intelligence and determine where it came from, the type of intelligence testing that we are familiar with and that remains somewhat pervasive today is credited to Alfred Binet, who, in 1904, was commissioned by the French government to identify characteristics of 'good' students. Binet, along with colleague Theodore Simon, took a more pragmatic approach to intelligence testing than did his predecessor, Galton (who often focused on sensory aspects of intelligence), and created the Binet-Simon scale, the first intelligence test on record. The test aimed to measure basic reasoning skills, and test takers were scored by their performance in relation to the average. In 1916, Lewis Terman adapted Binet's test for the English speaking population, and by utilizing a mathematical formula developed by Wilhelm Stern in 1912, Terman calculated what he termed an intelligence quotient, or

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[3] Sensory-motor stage, preoperational stage, concrete operational stage and formal operational stage

IQ. The test now came to be called the Stanford-Binet Intelligence Test (Stanford being the institution at which Terman worked) (Plucker, 2003).

The first foray of the United States into the realm of intelligence testing came in 1917, when the United States entered World War I. The government at the time considered that the field of psychology may have much to offer them, especially in regards to the recruitment and assignment of soldiers. A staff of psychologists (which included Terman) was assembled to develop an intelligence test that would be appropriate for the military's purposes. This resulted in the Army's Alpha and Beta tests, which are still used today. Although the institution of intelligence testing did not actually occur until later on in the war, the involvement of intelligence testing with the military brought attention to its virtues, and its potential utility to the fields of industry, business, and education (Plucker, 2003).

From then on, intelligence testing became an issue of interest for a great number of people. Several researchers, including Spearman, proposed revised versions to the intelligence test. In 1939, David Wechsler designed a test with sub-tests to measure verbal and non-verbal abilities. Wechsler adopted Terman's calculation formula, with its mean of 100, and produced the Wechsler Intelligence Scale for Children (WISC) and the Wechsler Adult Intelligence Scale (WAIS), both of which are widely used today, in revised editions. One common inclusion in modern-day intelligence testing is a focus on information processing. The information processing component is designed to measure how information is processed, as opposed to how much information is known (Hogan, 2003).

Although widely used for a multitude of purposes, intelligence testing was and is not without its critics; theories abound, revolving around concepts such as multiple intelligences that are not measured by these standardized scales. Perhaps the most prominent theory of the sort has been put forth by Howard Gardner (1983). Gardner asserted the existence of multiple intelligences, which include more intuitive categories, such as spatial learning, linguistic, and logical-mathematical, but also includes categories that traditional intelligence theories would consider distinct from intelligence. These categories include musical intelligence, bodily-kinesthetic and spiritual intelligence, among others (Gardner, 1999).

Gardner's theory, (as well as other theories of multiple intelligences), is rather popular within the education community. The existence of multiple, equal intelligences allows for everyone to be good at something, and essentially equates any talent or skill with what is traditionally called intelligence (Hogan, 2003). If the assumptions of theories of multiple intelligences are correct, then tests like the Stanford-Binet or WAIS intelligence test are lacking indeed, as they measure limited components of intelligence. This would be akin to measuring athletic ability by testing a small range of athletic skills, which would obviously offer quite a limited scope of athleticism.

Another area of criticism and controversy surrounding psychometric intelligence regards the unambiguous discrepancy between IQ scores of different ethnic, racial, and cultural groups. Explaining this discrepancy as reflective of actual intellectual differences, as was attempted by Jensen (1969), or Herrnstein & Murray (1994) is largely considered contemptuous. Opponents of such an explanation have asserted that merely exposing group differences does not reveal the cause of the difference, and that even if it does, these difference may change with time (Hogan, 2003). Others have pointed to environmental factors and socio-economic confounds influencing the outcome of such tests (Turkheimer, 1991, Zuckerman, 1990). However, many supporters of psychometric intelligence tests believe that differences do reflect biological differences that are related to g (Nyborg & Jensen, 2000).

Intelligence as an Interaction

By and large, the definition of intelligence as a physical characteristic of the brain was met with much controversy (Reitan and Wolfson, 1992). At the center of the criticism surrounding the measurement of intelligence is the stance that it is impossible to tease out innate ability from environmental, social, and cultural factors (Jones, 1972; Keita, 2001). Hebb (1941, as reviewed by Pascual-Leone and Goodman, 2004) believed that intelligence is composed of two elements, which he termed Intelligence A and Intelligence B. According to his theory, Intelligence A reflected innate ability, while Intelligence B reflected acquired knowledge. However, Intelligence A contributed to Intelligence B; the result of an interaction between innate ability and the environment. In the years since, Intelligence A has been referred to by a variety of different names (e.g. Fluid Intelligence -Cattell, 1987, Biological Intelligence – Halstead, 1949). A survey of the existing literature indicates much empirical support for these two differentiated branches of intelligence, and introduces a possible third: a genetic factor determining the way in which raw ability interacts with environmental factors (Cleveland and Jacobson, 2000).

Hebbian Intelligence B (and its modern-day counterparts) reflects the processes of education and acculturation (Stankov, Danthiir, Williams, Pallier, Roberts, & Gordon, 2006), or learned experiences. Both learning and memory processes have been associated with changes in neurotransmitter and neuropeptide synthesis and release (Gulpmar and Yegen, 2004) and oxidative metabolism (Gonzalez-Pardo, Conego, Arias, Monleon, Vinader-Caerols, & Parra, 2008), and recent neuroimaging studies have supported theories of memories being stored as distributed cell assemblies, or neural networks (i.e. Martin and Chau, 2001). A test measuring ability stemming from these distributed areas does not distinguish between acquired knowledge and innate ability.

Despite the intricate interrelating of learning and ability, it should not be assumed that they are one and the same. The similarity in intelligence seen between identical twins raised apart is taken as evidence for innate cognitive capacity (Jensen, 2003). Similarly, genetic mental retardation, such as Down's Syndrome, which is associated with lower IQ (Simonoff , Bolton, & Rutter, 1996) has also been considered evidence of genes supporting cognitive ability (Plomin and Petrell, 1997). It may be more appropriate to consider innate cognitive capacity as determining learning ability (Antey, 1999), which is in line with the possibility of a genetic factor determining the extent to which exogenous factors contribute to 'total' intelligence (Cleveland and Jacobson, 2000).

Although several subdivisions of psychometric intelligence have been proposed, one theory of subdivided intelligence may be of particular interest to the current study. Horn (1987) proposed a hierarchical description of psychometric human intelligence in which general intelligence (g) is complemented by a series of second order abilities – one of which is termed $g_{s,}$ or broad speediness. This perspective on intelligence is largely influenced by the information processing approach, which was pioneered by Arthur Jensen, among others. Jensen (1969) proposed that a general information processing factor, in conjunction with physical reaction time, influences various information processes, which in turn determines performance on cognitive tasks (Jensen, 1998). The extent to which g, or a general processing factor, might contribute to intelligence will be covered in subsequent sections of this paper.

Social Intelligence

Humans (and other primates) have larger brains (Gibson, 1986) and superior cognitive abilities than other animals (Ruse, 1996). This superior ability is thought to have evolved in response to the physical pressures related to the need to be able to learn and recall where and when food is available, how to use tools effectively (such as in the obtainment of food), or how to navigate through a complex, three-dimensional world (Holekamp, Sakai, & Lundrigan, 2007). The social intelligence hypothesis postulates that social intelligence, a byproduct of enlarged brains, evolved in response to the demands of social complexity, such as the need to anticipate, manipulate, and appropriately respond to the social behavior of our peers. The underlying assumption of such a hypothesis is that social intelligence is different, but not entirely separate from ‘academic’ intelligence. The tradition of viewing social intelligence as a different aspect of intelligence is not new. Thorndike (1920) distinguished social intelligence from abstract and mechanical intelligences.

However, although the determination of the definition and quantification of social intelligence is subject to debate, the fact that such a thing exists is undisputable. Recently, artificial intelligence (AI) research has embarked on a new path in the quest to manually recreate the human mind. Whereas traditional AI models have utilized monolithic processing units, new directions in AI entail a redefined version of human intellect. According to Brooks (1991), the ‘essence’ of human intellect includes social interaction, defined as the ability to manipulate others for our own means, as well as multimodal integration, defined as the maximization of the efficacy of the sensory and motor systems – although the two concepts may not necessarily be distinct.

Cognitive Neuroscience of Human Social Behavior, a new and increasingly important field in the disciplines of psychology and neuroscience, is largely devoted to determining the neurological underpinnings of human social interaction. Recent research (see Adolphs, 1999) has indicated that the processing of social information (and the subsequent usage of it) may not be different than basic human information processing. In fact, social processing can be seen to follow the same course as the processing of any other information:

1. Reappraisal:

Course perceptual processing (superior colliculus) → Detailed perceptual processing (fusiform gyrus, superior temporal gyrus) → Motivational evaluation (amygdala, orbitofrontal cortex, ventral striatum) → Representation of perceived action (left frontal operculum, superior temporal gyrus)

2. Self-regulation:

Emotional response in body (visceral, autonomic, endocrine changes) → Modulation of cognition, such as memory or attention (cingulate cortex, hippocampus, basal forebrain) → Representation of emotional response (somatosensory-related cortices) → Social reasoning (prefrontal cortex)

As with any type of information processing, the flow of social information is multi-directional and recursive. Any given process is implemented by a flexible set of structures, any of which might participate in several different processes at different points in time: dynamic coupling and uncoupling occurs, and is especially evident in the transition from perception to judgment.

Although the implications of the sensory system on social interaction are obvious, the majority of research conducted regarding social processing has focused on the processing of visual social cues. Research by Adolphs, Sears, & Piven. (2001) has indicated that the variable, dynamic characteristics of faces, such as expression or gaze, activate the superior temporal sulcus, while unchanging, static facial features activate the fusiform gyrus. Therefore, in order to make an accurate social judgment, information from those two anatomically distinct visual areas, as well as information from the amygdala pertaining to emotion, must be integrated.

The integrative component in social intelligence has long been known, largely due to deficits associated with autism. Other research has determined that the regulation of social relationships, social cooperativeness, moral behavior, and social aggression are all processes that require integration – the integration of information about other people, oneself, and the relationship between the two (Adolphs, 1999).

Questions still remain as to whether social processing is a distinct system from other information processing, or whether it is a complexity that has arisen from a more basic (information) process. Many researchers maintain that it is a distinct system from that involved in academic intelligence. For example, Weis and Sub (2007) claim that there is a social 'g' factor that underlies what they define as the three major social intelligence processes: 1) Social understanding, 2) Social memory, and 3) Social knowledge. Social understanding has been the core domain of social intelligence research. Social understanding refers to the ability to understand and correctly interpret social stimuli in terms of implications for the person or situation. Social memory includes the conscious storing and recalling of social information, such as episodic and semantic memory that include, but are more complex than, the typically considered memory of names and faces. The third compartment of social intelligence is social knowledge, a concept originally devised by Kihlstrom & Cantor (2000, in Sternberg, 2000) to refer to the social version of procedural or implicit knowledge; social knowledge that can't be taught or recalled explicitly.

Processing Speed and Intelligence

Individual differences in cognitive performance are usually explained in terms of intelligence. Intelligence can often be traced back to measures of processing speed and working memory capacity – which is jointly referred to as the human information processing system (Grabner, Neubaeur, & Stern, 2006). Smarter people are assumed to be able to process faster, allowing them to manipulate more information in a shorter period of time.

Neurophysiological studies have greatly advanced our knowledge regarding the biological bases of intelligence. Brain activation levels observed in different intelligence samples have indicated that the less activation there is, the better that subject is performing. This has been explained as a lot of the activation constituting background noise, or alternatively, as less activation corresponding with less cognitive effort needed (Grabner et al., 2006).

Neural Efficiency

A relatively recent attempt at operationalizing the concept of intelligence has centered around the neural efficiency hypothesis (Neubauer, Fink, & Schrausser, 2002). According to this theory, speed of information processing (SIP) is considered to factor into cognitive capacity threshold, in the sense that the speed or efficiency with which an individual is able to execute, for example, each step of a particular task is thought to have an effect on overall success of performance on that particular task. In fact, SIP, as measured by various reaction time and inspection time measures, correlates with psychometrically defined intelligence. Therefore, it has been suggested that general intelligence (g) is related to how quickly information gets processed (Jensen, 1999). This would apply to the processing of social stimuli, as well. This theory is an alternative to the psychometric approach to intelligence and postulates that the rate of information transmission through the cortex either influences or determines intelligence. Evidence for the theory will be reviewed below.

Evidence for the Neural Efficiency Model of Intelligence

The neural efficiency theory proposes that rate of processing speed determines a person's ability to efficiently react. 'Efficiency' is defined as the maximization of speed while maintaining accuracy (Rabbitt & Goward, 1994).

It has been well established that processing speed and scores on intelligence tests are correlated, although there is disagreement as to the extent of the relationship. Fry and Hale (2000) suggest that the role that processing speed plays in intelligence is in regards to different short term or working memory capacities, in that the quicker information is processed, the less likely that information is to decay in working memory, thus allowing decision making to reach its critical stage. It is also possible that SIP influences the size of working memory, in that the quicker information is processed, the more information can be stored. If the case of any of these possibilities, it necessarily implies that general working memory capacity – how much information can be stored at a time – would also correlate with intelligence and reasoning ability

Electrophysiological studies with the mentally retarded population have provided supporting evidence for a theory of mental speed underlying intelligence. Mental speed is explained in physiological terms as increased nerve conduction velocity in the brain nerve axon. It is this increase in nerve conduction velocity that is defined as the speed of processing. These studies are often conducted by measuring visually evoked potentials (see Reed and Jensen, 1992). Investigating intelligence through these means is centered around the concept that whatever intelligence is, it must start out as nerve impulses moving along cortical nerves (Reed, Vernon, & Johnson, 2004). Studies have shown that the nerve conduction velocity of brain nerve pathways have a positive correlation to overall cognitive ability (Reed and Jensen, 1992, Reed et al., 2004). This implies that the quicker the nervous system is able to function, the higher the degree of cognitive ability. Conversely, a slower nerve conduction velocity, i.e., a slower-running nervous system, correlates with a lower degree of cognitive ability.

It has been argued that virtually any cognitive task is dependent upon SIP (Vernon, 1986), although even the most basic cognitive task is likely to involve multiple processes (Jensen, 1987). A hierarchical factor analysis done by Carroll (1997) of a large battery of tests support the notion that processing speed and processing efficiency are large and important – and not necessarily differentiable – aspects of g.

Genetic Basis of the Relationship Between SIP and IQ

Monozygotic twin studies and multivariate genetic analyses have indicated a positive correlation between processing speed and IQ, and have suggested that this correlation is rooted in genetics. Rijsdijk, Vernon, & Bloomsma (1998) conducted a study investigating the common biological or genetic basis for both SIP and IQ and concluded that there were genetic factors influencing IQ, and that IQ performance revealed a correlation with SIP. The researchers further concluded that biological determinants of IQ may translate into neurophysiological processes in the central nervous system.

IT vs. RT and Intelligence

The concept of reaction time (RT) as a measure of information processing speed and its relationship with IQ have been extensively studied and are fairly well established in the field, however, the extent of the correlation has depended greatly on the type of methodology used. The primary criticism regarding reaction time is that it is not an accurate measure of a mental process, but rather that as a measurement, it accounts for both physical factors and other psychological factors. IT measures of processing speed are typically done by introducing a backwards mask immediately following presentation of the stimulus. The IT measurement does not include actual response time, but rather how long the stimulus must remain on the screen in order for it to be processed.

The relationship between SIP and intelligence is often investigated through the use of IT tasks, due to it providing a good measurement of the speed of intake of the most basic information by utilizing a backwards masking paradigm (i.e., Kurylo, 1997). Correlations between IT and various estimates of g are consistently significant. Vernon and Weese (1993) identified four information processing factors, and the combination of them accounted for general intelligence with a corrected multiple correlations core of .77.

There is a large body of evidence for a relationship between psychometric g and IT. The findings of Bowling and Mackenzie (1996) indicate that IT is more strongly correlated to general intelligence, or g, than it is to any specific ability. Frings and Neubauer (2005) define inspection time as a task used to establish a relationship between processing speed and general cognitive ability.

Furthermore, a stronger relationship between IT and IQ has been found in mentally handicapped individuals, as compared to normal individuals, indicating a possible foundation for IT in the development of IQ (Baumeister and Kellas, 1968). A meta-analysis conducted by Grudnick and Kranzler (2001) of over 90 studies of IT and IQ suggested that the relationship between IT and IQ unequivocally exists, and that it is the same for children and adults. The results also suggested that the measurement of IT is the same across various IT tasks in various modalities; for example, IT tasks in the auditory and visual domains seem to be measuring the same thing. The results of the meta-analysis also supported that the relationship between IT and IQ was a particularly strong one for strategy users vs. non-users (Grudnick and Kranzler, 2001).

Luciano, Posthuma, Wrigth, de Geus, Smith, Geffen, Boomsma, & Martin, (2001) conducted a twin study to investigate the genetic factors behind inspection time (IT), which is used to examine processing speed and is thought to play a significant role in higher level cognition, including intelligence. The study confirmed the association between IT and full scale IQ. The study also determined that a common genetic factor was responsible for a certain degree of variability (36 and 32%, respectively) in IT and IQ. Luciano cautions against attributing intelligence to a single type of processing speed, citing as an example the potential difference between speed of perceptual apprehension and speed of short term memory retrieval, as he indicates that several diverse information processes work in an integrated fashion in order to jointly contribute to the state of higher cognition in any particular individual.

Hansell, Wright, Luciano, Geffen, Geffen, & Martin (2005) conducted another twin study, which used ERPs of cognitive tasks and non-ERP cognitive measurements of information processing speed (reaction time and IT) and working memory performance. Aside from the genetic relationships found between these factors, the analysis indicated that better working memory performance and better IQ were associated with quicker processing speed. Hansell et al. determined that the covariation was likely related to the efficiency of neural processing in evaluating the target information, as defined by IT. Perceptual discrimination also was thought to play a role in the covariation of working memory performance and IQ. Perceptual discrimination and IT are both related to cognitive performance.

Luciano et al. (2005) attempts to define the relationship between processing speed and intelligence. They give two prominent perspectives as to why this relationship might exist. From a ‘reductionist’ or physiological perspective, IT is explained as a reflection of conduction velocity. As such, IT is the direct measurement of nerve conduction velocity, or how quickly the nervous system works. On the other hand, the top down approach postulates the utilization of cognitive strategies affecting IT. From this perspective, decreased IT is the result of more intelligent individuals employing better cognitive strategies.

Although a relationship between processing speed and cognitive ability is supported by data from a broad array of studies, it is unlikely that processing speed is sufficient as a measure of intelligence. Processing speed has been shown to be effected by a number of variables, such as age (Salthouse, 2000) and hormonal imbalances (Ross, Roeltgen, Feuillan, Kushner, & Cutler Jr., 1998). Furthermore, it has been suggested that observed increases in intelligence and working memory are mediated by increases in processing speed, and that this process is normally associated with development (Frye and Hale, 1996). In light of these findings, it seems that processing speed is most useful as a measure of knowledge, rather than as a measure of raw potential, or innate ability.

SIP and Cortical Integration

A faster brain, as defined by decreased inspection time, is a smarter brain, as defined by IQ. EEG studies looking at synchronized activity among neural populations provides further support for this phenomenon. Studies have linked the differences in individual alpha peak frequencies, the dominant rhythmic activity that emerges from EEG measurements, to differences in cognitive performances. This relationship suggests that quicker EEG oscillations indicate a quicker brain, which results in superior performance. Lebedev (1990, 1994) has proposed that the cyclic oscillations determine the capacity and speed of working memory.

It has also been argued that the oscillations represent feedback loops involved in search and encoding. Oscillations are thought to represent neural connectivity, and quicker oscillations mean efficient interconnectivity. Efficient interconnectivity results in a quicker ability to search and code, which would correspond with a higher IQ (Posthuma, Neale, Boomsma, & de Geus, 2001).

Other studies have shown that upper alpha bands are specifically sensitive to processing demands, an that the extent of desynchronization there, as measured by event related desynchronization (ERD), has been shown to reflect better memory performance and intelligence (Doppelmayr, Klimesch, Hodlmoser, Sauseng, & Gruber, 2005). It is generally assumed that alpha ERD represents cortical activation[4]. In the context of the neural efficiency hypothesis, less activation might reflect more efficiency.

Doppelmayr, Klimesch, Stadler, Pollhuber, & Heine (2002) contend that the relationship between alpha power and intelligence varies on two dimensions within any given person: with the task being performed (phasic/event-related changes) as well as with other 'tonic' factors (age, neurological conditions, fatigue). Tonic alpha power increases from childhood to adulthood but then decreases along the advancing lifeline. Good memory performance has been shown to correlate with decreases in phasic changes and increases in tonic changes. Studies measuring tonic changes find a positive correlation with intelligence and studies examining phasic changes find a negative relationship.

EEG studies, such as the ones discussed above, have yielded results suggesting physiological correlates of processing speed, and providing somewhat tangible supporting evidence for the neural efficiency hypothesis. Given what is known about

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[4] During rest, the alpha band is large, but upon presentation and processing of stimuli, or increased cognitive demand, the alpha band becomes suppressed.

both the neural efficiency hypothesis and the cortical integration theory of intelligence, it seems likely that there should be a common bond between the two, and, indeed, there is.

There is compelling evidence for processing speed affecting cortical integration. One study, using an inspection time task, measured grouping threshold by varying the stimulus duration with the presentation of a backwards mask. The results indicated a tradeoff between processing speed, as defined by inspection time, and grouping accuracy, and the extent of this tradeoff differed between individuals (Kurylo, 1997).

Sauseng, Klimesch, Gruber, Doppelmayr, Stadler, & Schabus (2002) conducted a study investigating the functional interrelation of working (WM) and long term memory (LTM). Previous findings have implicated upper alpha bands in LTM and theta oscillations in WM. Therefore, transfer of information from WM into LTM must be reflected by an interaction between the two alpha and theta waves. According to the EEG recordings collected in this study, attempts to retrieve information from LTM evoked theta oscillations that traveled from anterior to posterior recording sites, and upon retrieval of information from LTM, the oscillations reversed direction. The time involved in the direction reversal varied between subjects and was correlated with performance and with the onset of upper alpha desynchronization, implying that these recordings reflect the interaction between memory systems.

As reviewed here, prior research has indicated that both cortical integration and processing speed contribute to intelligence. The obvious question, as brought up by the research of Kurylo and Sauseng, is to what extent do these two phenomena interact, and how does their interaction contribute further to our understanding of intelligence?

Kurylo’s (1997) study explored the first aspect of this question by examining the time course of visual perceptual organization.

Visual perceptual organization may be a particularly useful tool with which to investigate cortical integration. Reasons why and a brief review of visual processing are provided below.

Visual Processing and Cortical Integration

Brain modularity is particularly apparent in the visual system (Arnold and Johnston, 2005), as different components of the visual system are devoted to analyzing features such as orientation, ocular dominance, motion (Polimeni, Granquist-Fraser, Wood, & Schwartz, 2005), and the processing of faces (Gauthier and Curby, 2005). In addition, both mechanisms of attention and spatial representation are organized in a modular manner similar to the visual systems’ submodalities. Cortical integration is particularly relevant to the visual system, which is organized to dissect stimuli into finer and finer modules. Some integrative mechanism must exist to re-constitute these modules into the uniform visual scene that is perceived.

Visual processing begins with the retina, which serves as a source of input from the external world to our visual system. The retina contains no perceptual objects and yet our visual world is so much more than the muddled combination of lights that stimulate photoreceptors. Objects are perceived, integrating spatial location and related features. Unified forms are separated from other objects and from backgrounds, despite spatial or temporal discontinuities. However, as is apparent from our knowledge of the retina (see

Hubel & Wiesel, 2004 for a review), no object can be clearly identified solely by the retinal representation. It is also clear that some internal mechanisms are responsible for organizing and producing perceptual objects from the collection of contours and blobs contained in the distribution of light on the retina (Uhlhaas, Phillips, & Silverstein, 2005). These mechanisms, that process and interpret the retinal image, are poorly understood. It is understood, however, that the visual system must use information provided by perceptual organization. Perceptual organization is the transformation of sensory stimuli into a meaningful cognitive experience. In order to constrain where features are localized and how they should be joined, the visual system utilizes an aspect of perceptual organization known as 'perceptual grouping.' Seventy years ago, Gestalt psychologists came forth with principles of perceptual organization which have been widely accepted as crucial phenomena and are still utilized as means through which to understand perceptual organization today (Chang, Nesbitt, & Wilkins, 2007)

Object recognition is dependent upon perceptual grouping. The magnitude of the role of perceptual grouping in object recognition is made clear when one considers that different objects may produce the same image, and vice versa, depending on viewpoint, lighting, or other factors. While knowledge of the world (memory) is vital in resolving these ambiguities, equally, if not more, important is the brain's ability to take advantage of what information is provided by an image and organize this perceptual input into visual groups.

Information integration, such as what occurs in perceptual organization, is thought to affect speed of processing (Bannich, 1998). The importance of perceptual organization cannot be overvalued, as it plays a huge role in the human visual experience (see Lowe, 1985 for a review). Perceptual organization ability has also been linked to fluid intelligence (McGeorge, Crawford, & Kelly, 1997).

If the brain's integrative capacity affects the brain's cognitive speed, which in turn plays an important role in virtually all cognitive functions, then even slight differences in the brain's integrating abilities would not only affect processing speed but may help account for the functioning of a variety of cognitive faculties.

Proposal

A review of the existing literature yields significant support for a processing speed theory of intelligence; however, it is a field rife with controversy and far from complete (Dreary, Simonotto, Meyer, Marshall, Marshall, Goddard, & Wardlaw, 2004). Numerous studies, described here, have reported findings connecting the speed at which the brain binds information to greater intellectual ability. However, the extent to which education and other socio-economic factors is embroiled within our common definition of intelligence has not been determined. Additionally, the issue of how quickly the brain binds information well has largely been unstudied. Therefore, the present project attempts to address both of these issues, in the hopes that addressing these two variables will yield a more complete picture of the physical nature of cognitive abilities.

The central nervous system is modular in nature, with different areas mediating different aspects of neural functions. The cohesiveness of cognitive function and conscious experience therefore requires a mechanism of cortical integration. The substrate of integration may consist of a neural network that links and coordinates information throughout the brain. The necessity of integration for cortical organization suggests that the efficiency of this network is a fundamental determinant of cognitive abilities, as reflected by measures of general intelligence.

The basic organization of cortical processing is relatively uniform across areas of the brain. It follows that the functioning of an integrating network is also uniform throughout the cortex. Assuming this to be true, a test that monitors the efficiency of integration at any location in the network should provide an index of integration for the entire network.

In order to investigate the relationship between cortical integration and general intelligence, perceptual organization, a basic ability that targets cortical integration, will be compared to several measures of intelligence. Perceptual organization is the manner in which the brain integrates visual representations across cortical areas. Perceptual organization ability will be evaluated with psychophysical measurements that reflect performance thresholds (in terms of stimulus metrics) and speed of processing (in terms of critical stimulus duration). Perceptual tests are designed to minimize the load on top-down (knowledge based) processing, thereby reducing the load on memory, decision making or other non-perceptual cognitive components.

Performance on perceptual tests will then be compared to performance on a comprehensive intelligence test in order to determine whether the integrity of cortical integration, as reflected by perceptual integration, corresponds with intelligence, as commonly assessed by psychologists. Participants will be given a variety of intelligence tasks, including those targeting analytical, social, and language abilities. Tests will be administered to a broad range of the general population, drawn from an undergraduate student body. It is hypothesized that performance threshold and processing speed on perceptual tests will correspond to measures of intelligence.

Additionally, participant performance will be measured on analogous perceptual capacities that do not require integration. It is hypothesized that perceptual abilities that do not place a load on integration will not correlate with measures of intelligence. The use of a non-integrative perceptual task will verify that it is the integrative component of the perceptual task that corresponds to intelligence, and not factors associated with general perceptual processing.

Albert Einstein once said that ‘things should be described as simply as possible.’ This principle put forth by the reputed genius might be the key to understanding how such genius can exist. The fundamental speed of a basic brain mechanism might be the key to understanding not only Einstein, but how and why he differed from other men. The usefulness of being able to measure intelligence in such a quick, efficient, and unbiased manner is obvious and irrefutable, its implications vast. With this goal at the forefront, the efficiency of cortical integration as an underlying factor in general intelligence will be assessed.

Experiment I

Methods

Participants: Participants in this study were 25 college students at Brooklyn College, who participated in order to receive course credit. Mean age was M=24.0 (SD=6.44).

Participants reported having no significant ophthalmologic disorders or history, and were verified to have a best-corrected binocular 14” visual acuity of 20/30 or better (Snellen). It was also verified that participants had no astigmatism, as determined by the radial axis test. The radial axis test for astigmatism consists of a series of black lines radiating from a center point. With monocular viewing, participants fixated on the center point, and indicated if any of the lines seemed to differ in shade. Any perceived difference in line shade would indicate the possibility of astigmatism, which served as an exclusion criterion. No participant showed signs of astigmatism. Visual field restriction and scotoma was tested by means of computer-based perimetry. Participants fixated on a square presented in the center of a computer monitor, and indicated whether they detected flashing squares presented randomly 10 degrees eccentric from fixation at eight locations surrounding the fixation point. The 10 degrees of visual angle extended beyond the size of the stimuli used in psychophysical measurements.

Procedures conformed to the Guidelines for Use of Human Subjects (NIH), and were approved by the Institutional Review Board (IRB) of Brooklyn College. Before participating in the study, participants signed an informed consent statement. Participants were informed that this was an experiment on vision and cognition performed by members of the Psychology Department of Brooklyn College, and the general procedure was explained. In addition, participants were informed that participation was voluntary, that they were able to end their participation at any time without penalty, and that confidentiality would be maintained at all times. Contact information for the experimenter was provided.

Perceptual Organization

General Procedure: Perceptual capacities were measured by having participants indicate the pattern of organization of visual stimuli presented on a computer monitor. Stimuli consisted of an array of dots that could be perceptually organized into either vertical or horizontal lines. Two stimulus features were examined: (1) grouping based upon similarity in luminance and (2) grouping based upon similarity in flicker. For each feature, measurements were made of grouping thresholds, as well as processing times at two levels of organization, for a total of six measurements. In order to minimize possible confounding factors associated with slowed decision making or motor response, reaction time was not a factor, and participants were instructed to maximize accuracy. Additionally, responses were based upon a forced-choice procedure in order to prevent possible response bias that may distinguish participant groups.

Stimuli

Test Stimuli

Test stimuli were briefly presented on a computer monitor. Stimuli were composed of a grid of elements, aligned and spaced at regular intervals along the horizontal and vertical orientations. Stimulus elements were solid squares, 0.35 degrees on a side. Stimulus duration was linked to the display’s vertical synchronization signal. Perceptual grouping was based upon similarity in either luminance or flicker of elements. Each stimulus feature is described below in more detail.

Luminance: For the luminance condition, the horizontal and vertical orientations were distinguished by the pattern of high or low luminance elements each contained. Stimuli could be perceptually grouped into specific patterns based upon similarity of luminance. The same luminance levels were assigned to either the vertical or horizontal orientation, which elicited the perception of a series of either vertical or horizontal lines. Differences in luminance similarity ranged from 100 to 50%, in increments of 2% [Insert figure 1 here]. As such, the 100% stimuli possessed high intrinsic organization, while the 80% stimuli were more ambiguous. The 50% stimuli possessed no intrinsic organization.

Flicker: For the flicker condition, the horizontal and vertical orientations differed in whether the squares flickered or stayed on. Square wave modulation of flickering elements cycled three times at 7.5 Hz. For the vertical condition, every other column flickered. The squares in the alternate columns remained static (Insert Figure 2). The elements in the flickering column were counterbalanced in phase, so that on each frame, half of the elements, distributed randomly along the column, were visible, and the other half became visible on the next frame. Because only half of all possible elements were present in a given frame, element cues based on element proximity or density were not available. The horizontal condition contained alternating rows of flickering and static elements.

Masking Stimulus

For the masking condition, test stimuli were followed by a stimulus mask. The masking stimulus was an 8 x 8 array of crosses (plus signs). The array of crosses contained robust horizontal and vertical co-linearity cues and effectively disrupted perceptual organization of test stimuli.

Grouping Thresholds

For both stimulus features, measurements were made of the least intrinsic organization of stimuli that enabled perceptual grouping. To accomplish this, participants fixated a central target on the monitor. After 500 ms, the test stimulus appeared for 500 ms. Vertical or horizontal conditions were randomly assigned on each trial. Following stimulus presentation, participants indicated whether the stimulus was organized as a series of vertical or horizontal lines. Responses were entered into the computer by the participant.

Thresholds were determined by means of a two-alternative forced-choice staircase procedure. Trial series began with high intrinsic organization of the stimulus, providing a strong grouping cue. Across trials, cue strength was decreased after two consecutive correct responses, and increased after a single incorrect response (reversal levels). Thresholds were based upon the mean of eight reversals, producing a long-run probability of 71% correct responses (Levitt, 1971).

Reaction time was not a factor, and participants were instructed to maximize accuracy, and not the speed, of their response. Before measurements were made, participants were given a demonstration, as well as a series of practice trials, in order to familiarize them with the stimulus and procedure. Following the demonstration and the practice trials, threshold measurements were made. Stimulus generation, data collection, and contingency algorithms were controlled in real time by customized computer software (Bukhari and Kurylo, 2008).

Masking Thresholds

For each of the two stimulus features, two measurements were also made of processing time. One measurement was made at a moderate level of stimulus organization, and a second measurement was made near threshold levels. The level of stimulus organization for each masking measurement was made relative to each participant's grouping threshold. In this way, participants were matched for difficulty level.

A backward pattern mask was used to determine the duration of processing necessary to establish perceptual organization (Kurylo, 1997). The test stimulus was followed by a mask, which served to disrupt processing of the test stimulus. Across trials, stimulus duration was progressively reduced until the organization of the stimulus could no longer be determined. Under these conditions, other stimulus characteristics, such as element shape, are identifiable, but perceptual organization does not occur. In this regard, the mask does not interfere with the detection of the stimulus features, but disrupted processes associated with perceptual organization.

Procedure: Participants fixated a central point for 500 ms, after which the test stimulus appeared. The duration of the test stimulus varied across trials. Immediately following the offset of the test stimulus, the mask appeared for 200 ms (Insert Figure 3). Participants then indicated whether the test stimulus appeared to be organized in the horizontal or vertical orientation. At the beginning of a trial series, the test stimulus duration was 500 ms. Across trials, stimulus duration was progressively reduced in increments of 14.29 ms (70 Hz temporal resolution). As the test stimulus duration was shortened, a threshold was reached in which stimulus elements could be perceived, but the organization of luminance or temporal similarity could no longer be determined, identifying the limit of the perceptual organization process. Durations were adjusted with the 2-down, 1-up algorithm. Thresholds were based upon the mean of eight reversal points from two descending series.

The level of stimulus organization given to a specific participant was determined in the following manner. First, threshold measurements were acquired, as detailed above. Again, thresholds represent the lowest level of stimulus organization that can be perceptually grouped. The first masking measurement was made at a stimulus organization ten percent more organized than their grouping threshold. The second was fifteen percent more organized than their grouping threshold.

Control Conditions

In addition to the threshold and masking measurements, a control condition, containing solid lines in either the vertical or horizontal orientation, was interleaved among the experimental conditions. Control trials occurred randomly. Control trials were included in order to monitor participants' ability to discriminate between vertical or horizontal solid lines, without the necessity of perceptual grouping. Performance on these trials provides an assessment of participants' ability to understand the requirements of the tasks, to perceive and discriminate each pair of stimuli, and to respond appropriately. Accurate performance on control trials indicated that impairment in performance on experimental conditions is likely due to deficits specific to perceptual organization, and not other cognitive factors associated with the testing procedure.

Tests of Intelligence and Scholastic Aptitude

In addition to perceptual grouping measurements, participants were scored on tests of cognitive aptitude. The cognitive battery, to be described below, was administered on a separate day from the perceptual measurements described in the previous section. The reason for the separate sessions was to prevent participant fatigue and better ensure optimal performance on both measures. The second testing session was typically given one to two days following the first session. Participants' scores on the Scholastic Aptitude Test (SAT), which were included in the cognitive battery, were obtained, with participant permission, as described below, from college administrative records. All tests of cognitive aptitude were administered by the principal investigator of this project. The scores of three groups of cognitive tests were used: The Wechsler Abbreviated Scale of Intelligence (WASI), The Diagnostic Analysis of Non-Verbal Accuracy (DANVA 2), and the SAT. Collectively, intelligence and aptitude tests measured cognitive capabilities, either constrained or not constrained by time restrictions. Additionally, both selected-response items and constructed-response items were used in the battery. Selected-response items require that examinees select from one of several predetermined choices (e.g. multiple choice exams), whereas constructed-response items allow examinees to answer questions in their own words, with scoring rubrics used to guide scoring of these items. Selected-response items are associated with, among other things, enhanced reliability, and constructed-response items are associated with enhanced validity (Schaeffer et al. 2002). The cognitive battery included tests of social/emotional intelligence, maximum performance tasks, and vocabulary and mathematical abilities.

(1)WASI: The WASI is the abbreviated version of the Wechsler Adult Intelligence Scale (WAIS), and is considered ideal for research purposes (Hersen, 2004). WASI results correlate with full-scale IQ scores on the WAIS and the Wechsler Intelligence Scale for Children (WISC) (WASI Directions Manual**)** and with other measures of psychometric intelligence, such as the Kaufman Brief Intelligence Scale (Hays et al. 2002), and the Canadian Test of Cognitive Skills (Saklofske et al., 2000). The WASI is divided into a verbal and a performance (non-verbal) component, which has been shown to be insensitive to cultural differences (Razani et al. 2007), a common concern in regards to intelligence testing. Both the verbal and performance components include two subtests: Vocabulary and Similarities, and Block Design and Matrix Reasoning, respectively. The Vocabulary test required participants to define words read aloud by the experimenter. In the Similarities test, the experimenter read aloud two words, which represent common objects or concepts, to the participant, who must then identify the commonality. The Block Design test had the participant viewing a constructed model or design in the Stimulus Book, and then recreating that design with provided red and white blocks. The Block Design test required that recreation of the design occur within a specified time limit (60 -120 seconds). In the Matrix Reasoning test, the participant viewed an incomplete matrix and selected the missing piece from five selected-response items.

The WASI was administered to each participant on an individual basis and took approximately 45 minutes to administer. The WASI was scored in accordance to the guidelines provided in the WASI manual. Administration of the WASI yields raw scores, and the manual provides the corresponding standard scores, which are age adjusted. Only the standardized scores were used in analysis.

(2)DANVA 2: The DANVA 2 is a computerized test that measures individual differences in accuracy in receiving nonverbal social information (Nowicki & Duke, 1994). The DANVA is a clinical task, but has been normed on the general population and has high degree of internal consistency (coefficient alpha = .77 in college students) and test-retest reliabilities (.84 for college students) (Nowicki & Carton, 1993). The construct validity of the DANVA as a measure of adults to receive, process, and decode emotional cues from others is supported by its significant relationships with other indices of social cognition and interpersonal adjustment (Baum & Nowicki, 1998). Although the DANVA consists of four subtests, two were used here. For the Receptive Facial Expressions (Adult Faces) subtest, participants view 24 images of multicultural young adults (both male and female) portraying one of four emotions at high or low intensities: anger, happiness, sadness, or fear. Each image remains on the screen for two seconds. Participants are required to correctly identify the emotion being portrayed. Participants take part in both an audio and visual version of this task; in the Receptive Paralanguage (Adult Voices) subtest, participants listen to the audiotape of young adults saying an emotionally neutral sentence: “I’m going out of the room now and I’ll be back later”. This sentence was repeated in the multicultural voices of young adults (both male and female) with varying prosody for a total of 24 items. After hearing the sentence, participants were required to choose from one of four emotions that they felt were represented by the sentence: anger, happiness, sadness, or fear. The remaining subtests of the DANVA that were not used corresponded to the descriptions provided here, but used children's faces, and a child's voice, respectively. In both the audio and visual components of the task, participants have unlimited time to make their decision following the presentation of the item.

The DANVA was administered to each participant on an individual basis. The DANVA Receptive Facial Expressions subtest took approximately 5-10 minutes to complete. The DANVA Receptive Paralanguage subtest took approximately 15-20 minutes to complete. The DANVA is a computer administered test and provides raw scores in terms of errors made. These raw scores were used in the analysis.

(3)SAT: In addition to an informed consent form, participants signed a waiver allowing the experimenter to access and utilize their SAT scores from the college's computer system. The SAT is commonly utilized by college boards to predict academic performance. The SAT provides three separate indices: an index of verbal aptitude, quantitative ability, and analytical skills. The following descriptions of the SAT subtests are taken from the College Board's SAT website (http://www.collegeboard.com/student/testing/sat/about/SATI.html).

- Critical Reading Section: The index of verbal aptitude, The Critical Reading Section (formerly called the Verbal Section) consists of two measurements: Sentence Completion questions are intended to measure examinees' knowledge of word meanings and their ability to understand the way in which different parts of a sentence fit together. Passage-based Reading is intended to assess examinees' ability to read and think critically about several different passages. This is done through three types of questioning: Vocabulary in Context asks about the meanings of words from their context in the passage. Literal Comprehension tests examinees' understanding of significant information provided in the passage. Extended Reasoning questions measure examinees' ability to synthesize and analyze information, evaluate assumptions implicit in the passage, and recognize techniques (e.g. author's tone) utilized by the author.

- Mathematics: The Mathematics section assesses examinees' mathematical skills and knowledge of topics of varying difficulty, up to a third year college preparatory course (e.g. linear functions, exponential growth, and estimation). The Mathematics section uses both multiple choice (selected-response) and student-produced response (constructed-response) items.
- Writing: The Writing section scores were not used for the purpose of this experiment, as the majority of participants did not have Writing section scores on file. The Writing section asks examinees to generate an original essay that presents and supports a point of view on a given topic. In addition to essay writing, and test skills necessary in the organization and development of paragraphs in a cohesive fashion, as well as testing examinees on their ability to apply the standards of conventional, written English.

Taken together, the two sections of the SAT used here are intended to provide an assessment of critical thinking skills.

Results

Thresholds in the luminance and flicker conditions represent the lowest level of stimulus organization at which patterns could be perceptually grouped. Thresholds are described in terms of relative level of organization. A higher threshold score indicates a greater perceptual capacity, as horizontal and vertical luminance cues or temporal cues are more ambiguous. Table 1 displays the means for the conditions. The correlation between luminance and flicker thresholds was $R=0.528$, $p< 0.05$. The correlation between the luminance threshold values and performance on the performance aspect of the WASI (Block Design, Matrix Reasoning) was marginally significant at $R= 0.456$, $p= 0.057$ (the correlation between the flicker threshold and the performance score was R=0 .343, $p= 0.163$). The correlation between the 10% luminance condition and Block Design was R=.-0.600, $p <0.01$. None of the other correlations between the perceptual organization tasks and the cognitive battery scores were significant. DANVA was not correlated to full scale IQ, performance IQ, or verbal IQ. However, performance on the visual aspect of the DANVA (identification of facial emotion) was correlated to Block Design ($R=-0.056$, $p<0.05$).

Discussion

Lower threshold scores are indicative of a higher degree of intrinsic organization. The values reported above are subtracted from 100 to determine percent of organization. Therefore, a threshold score of 21 indicates that participants were able to group stimuli that had 79% intrinsic organization. A threshold score of 40 indicates grouping at 60% organization.

Upon graphing the acquired data, it was evident that the two processing speed scores in each condition were not measuring equivalent ability levels between people. Prior research has indicated (Kurylo et al. 2009) that perceptual organization ability forms an exponential growth function as the grouping stimuli get increasingly difficult. The attempt to capture critical aspects of this curve by measuring processing speed at five and ten percent of participants' grouping capacity did not yield measurements at equivalent parts of the curve across participants. Therefore these measurements are not comparable, as they are indicative of differences in the grouping function. However, the correlation between Block Design, the speeded element of WASI, and the luminance processing speed score indicated that the hypothesized relationship may very well exist, although, in this case, the variables had not been accurately measured. Thus, in an attempt to accurately capture the perceptual grouping function, the experiment was revised to include a more comprehensive measurement of participant's processing speed abilities. Because of the correlation between the luminance and temporal flicker condition, the ability to group by luminance and by flicker were considered equivalent. This supports the notion of cortical uniformity, as the threshold of integration based upon spatial similarity is correlated with the threshold of integration based upon temporal similarity.

In order to obtain more measurements of the processing speed of perceptual organization, additional luminance processing speed measurements were taken in place of any temporal processing speed measurements. The correlation between the two conditions makes it logical to conclude that any relationship between grouping by luminance and cognitive ability applies to temporal grouping, as well.

Experiment II

Methods

Participants: Participants in this study were 64 students at Brooklyn College, who participated in order to receive course credit. The participants in the second study did not participate in the first study, with the exception of two participants. Mean age was 22.73 (SD=4.78). The inclusion and exclusion criteria applied in Experiment One were utilized here, as well. As before, the procedure conformed to Guidelines for Use of Human Subjects (NIH), and was approved by the Institutional Review Board (IRB) of Brooklyn College. Participants signed an informed consent form prior to beginning the study, which supplied the same information as in Experiment I.

General Procedure

Because results from Experiment I indicated that perceptual measurements of luminance and flicker significantly correlated, only the luminance condition was used. Because all measurements in Experiment II pertain to grouping based upon similarity in luminance, Experiment II was able to more accurately capture the curve function associated with grouping ability for each participant. Measurements were made of grouping thresholds, as well as processing times at five levels of organization, for a total of six measurements. The general procedure for taking these measurements was the same as in Experiment I.

Stimuli

Test Stimuli: Test stimuli were the same as is described in Experiment I. Only the luminance condition was used, in which the horizontal and vertical orientations were distinguished by the pattern of high or low luminance elements that each contained. Details regarding this condition are explained in Experiment I.

Masking Stimulus: As in Experiment I, test stimuli were followed by a stimulus mask, which disrupted perceptual organization of test stimuli. Details regarding the masking stimuli are explained in Experiment I.

Grouping Thresholds

Perceptual capacities were also measured as indicated in Experiment I, by means of participants indicating the pattern of organization of stimuli presented on a computer monitor. Measurements were made of the least amount of stimulus intrinsic organization needed for perceptual grouping.

As before, prior to measurements being made, participants were given a demonstration, as well as a series of practice trials, in order to familiarize them with the stimulus and procedure. Following the demonstration and the practice trials, threshold measurements were made.

Masking Thresholds

Five measurements were made of processing time, each at a different level of stimulus organization. The level of stimulus organization for each masking measurement was made relative to each participant's grouping threshold. In this way, participants were matched for difficulty level. All participants were measured at 100% organization. The other four processing speed measurements were made at 16 (least organized), 12, 8, and 4 (most organized) levels below their grouping threshold (see Table 1). Thresholds represent the lowest level of stimulus organization that can be perceptually grouped.

As detailed in Experiment I, a backward pattern mask was used to determine the duration of processing necessary to establish perceptual organization (Kurylo, 1997). Across trials, stimulus duration was progressively reduced until the organization of the stimulus could no longer be determined.

Procedure: Experiment II followed the same procedure for masking threshold measurements as explained in Experiment I.

Control Conditions

In addition to the threshold and masking measurements, a control condition, containing solid lines in either the vertical or horizontal orientation, were interleaved among the experimental conditions. Further details and reason for inclusion of control conditions are outlined in Experiment I.

Tests of Intelligence and Scholastic Aptitude

The same cognitive battery administered in Experiment I was administered to all participants in Experiment Two. All participants were scored on their performance on the WASI, the DANVA 2, which were administered by the experimenter, and the SAT's, results of which were taken from the college's administrative database.

Results and Analysis

Descriptive Statistics

The means and standard deviations of perceptual and intelligence tests are presented in Table 2. The distribution of full scale IQ (FIQ) scores conformed to the normal population, M= 100.86, SD = 13.360.

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Curve-Fit Analysis

Raw data were used to derive three categories of parameters, outlined below. Additionally, in order to analyze critical inspection time across levels of stimulus organization, inspection time thresholds were used to establish a best fit function. Visual examination of inspection time threshold patterns, and previous work (Kurylo et al. 2008) indicated exponential growth (Figure 4). Inspection time was brief with high intrinsic organization and rose exponentially as stimulus organization decreased, rising to infinity at the level of organization near the participant's grouping threshold. This pattern fit well with a single line, three parameter exponential growth function:

$$y = y_0 + ae^{(bx)}$$

This generated three parameters for each participant, which complemented the other parameters derived from the raw data. Parameters fit into the following categories:

1. Inspection Time with Full Stimulus Organization - In the exponential growth equation, the parameter y0 is the intercept. The intercept (Free Inspection Time) represents inspection time when there is no load on organization processes, which occurs when the stimulus is fully organized. An additional measure of inspection time separate from the demands of perceptual grouping is the initial masking threshold score (100% Condition) taken for each participant. The first masking threshold was taken with 100% stimulus organization.

2. Inspection Time with Load on Organization Processes – In the equation above, the parameters 'a' and 'b' interact to describe the slope, or the way in which inspection time increases as level of organization (represented in the equation as 'x') decreases. Another way to capture this interaction between level of organization and inspection time is by calculating the area under the curve. The area under the curve is defined as the area bounded by the Free Inspection Time score and the X-asymptote. This was computed by taking the integral:

$$\int = ae^{b(x\text{-asymptote})} / b$$

Where e is a constant (2.718) and X-asymptote is held constant (30) in order to standardize the scores.

Correlation Analysis

The full correlation matrix is presented in Table 3. The correlation matrix restricted to relationships between perceptual measurements and cognitive measurements is presented in Table 4.

Factor and Reliability Analyses

An exploratory factor analysis was conducted on the WASI subtests and the SAT subtests. A factor analysis done with Direct Oblimin rotation suggested two components, one on which Vocabulary (.880) and SAT Verbal (SATV) (.908) loaded, with moderate loading of SAT Quantitative (SATQ) (.525), and one on which Block Design (.924), Similarities (.879), and Matrix Reasoning (.920) loaded, with moderate loading of SATQ (.589). The correlation between the two factors was .288. This was confirmed by reliability analysis of the standardized components of the two factors. Factor 1 (Verbal-g) consisted of SATQ, SATV, and Vocabulary with an alpha of .80. Factor 2 (Analytic-g) consisted of SATQ, Block Design, Similarities, and Matrix Reasoning with an alpha of .88 (Insert Figure 5 here).

Linear-Regression and Multiple-Regression Analyses

The extent to which inspection time and grouping threshold served to predict cognitive performance was tested through regression analysis.

Linear Regression:

Threshold: The relationship between Threshold measurements and Analytic-g was highly significant (β= 0.679, p <.000). Threshold measurements can also be used to predict the individual components of Analytic-g; Block Design (β= 0.565, p < .001), Similarities (β=.468, p < .01), Matrix Reasoning (β=0.581, p < .000), and SAT Quantitative (β= 0.523, p < .05). Neither Verbal-g nor any of its component measures were predicted by Grouping Threshold. A marginally significant relationship was found for Threshold and DANVA Facial Recognition (β= 0.332, p = .07). DANVA Language was not related to Grouping Threshold measurements.

Mask-0 (Processing speed independent of threshold): Mask-0 predicted Verbal-g (β= -.0487, p < .01) and Analytic-g (β= -0.561, p < .000). The individual components of Verbal-g, Vocab (β= -0.515, p < .05) and SAT Verbal (β= -0.585, p < .01) were predicted by Mask-0, with the exception of SAT Quantitative. The individual components of Analytic-g, Block Design (β= -0.438, p < .01), Similarities (β= -0.385, p< .05), and Matrix Reasoning (β= -0.488, p < .01) were predicted by Mask-0, also with the exception of SAT Quantitative. Neither DANVA subtest was related to Mask-0.

Integral: The Integral was not significantly related to any cognitive measurements.

y0: y0 was an effective predictor of both Verbal-g (β= -0.457, p< .01) and Analytic-g (β= -0.392, p < .05). Two of the Verbal-g components,Vocab (β = -0.389, p< .05) and SAT Verbal (β = -0.525, p< .05) were also significantly predicted by y0, although SAT Quantitative, the third component of Verbal-g, was not predicted by y0. None of the Analytic-g subcomponents were predicted by y0, although there was evidence for a trend towards significance for Block Design (β = -0.331, p = .052). Neither DANVA subtest was related to y0.

a and b: Neither a nor b predicted any cognitive measurements. There was a trend towards significance for the relationship between b and Block Design (β =0.299, p =.081) and Matrix Reasoning (β = 0.334, p = .066).

Multiple Regression

Threshold, Mask-0 and Threshold x Mask-0: A model that considered both Threshold and Mask-0 and a model that considered the interaction of the two were tested on Verbal-g, Analytic-g, and their respective components. The results were as follows. For Verbal-g, considering Threshold together with Mask-0 did not change the results of the linear regression; Threshold did not predict Verbal-g, the relationship with Mask-0 was significant (β = -0.46, p < .01). The change in R squared was not significant between the two models. A test of Threshold x Mask-0's relationship to Verbal-g was significant ($\beta = -0.488$, $p < .01$), however there was no significant change in R squared when compared to the linear model that tested Mask-0's relationship to Verbal-g.

For Analytic-g, Threshold ($\beta = .442$, $p < .01$) and Mask-0 ($\beta = -0.324$, $p < .05$) considered together yielded significant findings, as did their interaction term ($\beta = -0.504$, $p < .01$). Compared to the model that considered Mask-0's relationship to Analytic-g by itself, considering both Mask-0 and Threshold did have a significant impact on R squared ($R_{original} – R_{new} = -0.342$, $p < .000$). This was not the case, however, when compared to a model that considered Threshold's relationship to Analytic-g by itself. In comparison to that model, a model accounting for both Threshold and Mask-0 failed to yield a significant change in R squared. In both cases, adding the Threshold x Mask-0 interaction term to the models voided the models; nothing was significant.

For all of the cognitive dependent variables, the interaction term did not add to the model. All of the Analytic-g component tests, including SAT Quantitative, followed the results of Analytic-g, in that the addition of a second term into the model was only significant if Threshold was added to Mask-0, but not the other way around. In the case of the Verbal-g component tests, Vocab and SAT Verbal adhered to initial findings of not being related to Threshold, regardless of whether it was considered alone or with Mask-0. Adding Threshold to Mask-0 for these two subtests did not result in a change in R squared. SAT Quantitative also adhered to findings from linear regression analysis, and was not predicted by Mask-0, regardless of whether Mask-0 was considered alone or with Threshold. The addition of Mask-0 to the model did not change R squared.

DANVA Language was not significantly predicted by either Threshold or Mask-0. Models that considered them in either additive or multiplicative terms did not yield significance for any of the terms. For DANVA Face Recognition, the interaction term did not produce significant results whether considered on its own or in addition to either or all of the other variables. However, although results from linear regression did not indicate a significant relationship between DANVA Face Recognition and Threshold, the relationship assumed significance when considered additively with Mask-0: (for Threshold, $\beta = .465$, $p < .05$). In this case, Mask-0's relationship to DANVA Face Recognition showed a trend toward significance ($\beta = .341$, $p < .081$) The R squared change was significant ($R_{original} – R_{new} = -0.158$, $p< .05$).

<u>a, b, and a x b:</u> As indicated above, neither a nor b, considered by themselves, significantly predicted any of the cognitive battery scores. However, a multiple regression analysis in which both were considered simultaneously indicated a different finding. For Analytic-g, a model that accounted for both a and b was significant ($\beta = 0.627$, $p < .01$ and $\beta= 0.624$, $p <. 01$, respectively). This was also the case for Block Design ($\beta = 0.607$, $p < .01$ and $\beta = 0.705$, $p < .001$), Similarities ($\beta = 0.406$, $p = .059$ [marginal] and $\beta = 0.512$, $p < .05$), and Matrix Reasoning ($\beta =0.524$, $p <.05$ and $\beta = 0.678$, $p < .05$), although not for SAT-Quantitative, Verbal-g, or any of its components. For the cognitive measures for which a and b had additive significance, a third model was tested, in which Threshold was added as well. Although Threshold was significant in all of these cases, its

addition to the model had a nullifying effect on the effects of a and b. The interaction of a and b was not significant for prediction of any cognitive measure.

Discussion

The present study used a perceptual task that requires integration of stimulus elements to discriminate stimulus patterns. This task was selected in order to examine differences in integrative functions between individuals with differing cognitive capabilities. Because this task required integration of visual stimuli, all participants were screened for opthalmologic problems. Because of this and the principle of cortical homogeneity discussed previously, deficits in perceptual organization seen here are likely attributable to general integration deficits.

The results indicate that Inspection Time is a strong predictor of the cognitive capacities captured by measurements taken in this study. For Analytic-g abilities, the relationship between Inspection Time and cognitive abilities is stronger when Grouping Threshold is considered, as well. In comparison to Inspection Time, Grouping Threshold is a stronger predictor of the cognitive abilities classified as 'Analytic-g', however Grouping Threshold does not predict the cognitive abilities classified as 'Verbal-g'.

Curve-fit analysis resulted in the calculation of four parameters; y0, a, b, and the integral. Y0 is the theoretical representation of processing speed when there is no load on grouping mechanisms. Y0 was closely related to Inspection Time measurements, which was the actual representation of processing speed with very little load placed on grouping mechanisms. The close relationship between y0 and Inspection Time further establishes the accuracy of the exponential growth equation for the purpose of curve fit analysis with this data. Within the equation, a and b interact non-linearly to define the slope, or rise, of the curve formed by each participant’s five Inspection Time measurements. The non-linear nature of the interaction between these two parameters makes it difficult to completely capture the information that they hold regarding cognitive capacities, however, the data indicate that considering both a and b together will provide significant information regarding participants’ Analytic-g abilities. However, these effects are null when Grouping Threshold measurements are considered as well, indicating some overlap between Grouping Threshold and the interaction of a and b. Again, given the nature of the findings, in which the a and b model was relevant for the same tests that Grouping Threshold predicted, this can be taken as further evidence for the accuracy of the model used to generate the parameter for these data. The integral was intended to capture more information regarding the shape of the curve of each person’s Inspection Time measurements. No significant relationships were established between the integral and any cognitive measurements.

The results of this study have interesting implications for understanding the role of the brain in human intellectual properties. The data reported here support a relationship between efficiency of cortical integration and general intelligence. Efficiency of cortical integration is defined as threshold of integration and speed of integration; how much information is needed for successful integration and how quickly that integration occurs.

Differences in Full Scale IQ and Analytic-g corresponded to differences in grouping thresholds. These thresholds reflect the extent to which a stimulus can be degraded before it can no longer be perceptually grouped. Processing speed was not a factor in grouping threshold measurements, and so requiring higher intrinsic stimulus organization for perceptual grouping reflects a lowered grouping ability. Because the majority of the Full Scale IQ measures are components of Analytic-g, this discussion will be restricted to the implications of the relationship between Grouping Threshold and Analytic-g. The findings here indicate that higher grouping ability, or the need for less intrinsic stimulus organization in order to accurately perceive a stimulus, corresponds with higher scores on Analytic-g and its component subtests. It is likely that general, Full Scale IQ differences are a property of this relationship.

Differences in Inspection Time (IT) measurements reflected differences in all cognitive measures. Participants with lower scores on cognitive measures required more time to correctly discriminate grouping patterns across levels of organization. This was the case regardless of level of organization; even at 100% organization, differences in processing time between individuals of differing cognitive capacities were revealed. However, for Analytic-g measurements, Grouping Threshold was a stronger predictor of performance than IT measurements. This is evident not only from the actual numbers that reflect the strength of the two perceptual measurements relationship to Analytic-g capacities, but from the significantly enhanced predictive value of the model in which Grouping Thresholds measurements are considered with IT, compared to IT alone. The same cannot be said for IT measurements; adding information regarding IT to the model using Threshold measurements to predict Analytic-g does not enhance the model.

The interpretation of the significance of the combined value of using the a and b parameters to predict Analytic-g is unclear. The a and b values associated with the curved function of a participant's IT values are thought to reflect the nature the rise in time required to process the stimuli as the stimuli's intrinsic level of organization decreases. However, a and b are not related to the integral, which is also thought to capture this relationship. Also, the fact that including Threshold measurements with the combined a and b values obviates the effect of that combination indicates that the effect of the combination of a and b are somehow represented by the Grouping Threshold. That the inclusion of the a and b terms in the model using Grouping Threshold to predict Analytic-g does not hinder expression of the Grouping Threshold effect indicates that the relationship between a and b and Grouping Threshold is not reciprocal. The lack of any apparent relationship between a and b and the Grouping Threshold serves to further the confusion.

Relationship of Analytic-g to Innate Abilities and Verbal-g to Exposure Related Factors

Psychometric intelligence tests are intended to discern among levels of raw cognitive ability, although, as discussed previously, this sentiment is rife with controversy in the academic and professional arenas. Dual Process theory accounts for the possibility that general human cognitive ability is best thought of as the combined product of two distinct systems, one formed by learning and context-specific knowledge, and another one that capable of generalization and that supports abstract, hypothetical reasoning (Evans, 2003). This is consistent with numerous studies that have shown no difference in quantitative ability (Rourke and Finlayson, 2005), abstract reasoning and logical thought (Meltzer, 1978), and Performance IQ (Williams and Morgan, 1992) between normal and learning disabled individuals, although significant differences were evident in Verbal IQ. Additionally, studies have shown that deficiencies in quantitative ability are not necessarily related to verbal ability (Rourke and Finlayson, 2005).

WAIS Performance IQ is thought to capture “fluid intelligence”, whereas Verbal IQ is thought to be related to “crystallized intelligence” (Deary, 1993). Fluid intelligence is generally described as abstract reasoning ability (Igarashi and Kashima, 2008) and is not reliant upon acculturated or acquired knowledge, as opposed to Crystallized intelligence is described as exactly that (Bowman et al., 2001).

In the cognitive battery used here, Analytic-g was the result of a conglomerate of subtests, including those that are representative of WAIS Performance IQ (Block Design and Matrix Reasoning). It is important to note that Similarities, a subtest of WAIS Verbal IQ, was seen here to be more closely related to Performance IQ measures. This is thought to be due to the abstract reasoning required by the nature of the task.

The subtests of Analytic-g, all of which were independently linked with Grouping Threshold, are thought to reflect fluid intelligence. Fluid intelligence is thought to describe cognitive capacities that are not strongly influenced by exposure related factors, such as cultural or socioeconomic differences. Genetic mapping studies have indicated that non-environmental factors contributing to individual differences in intelligence are predominantly genetic (Toga and Thompson, 2005), which implies that the Analytic-g measurements taken here have strong genetic underpinnings. The subtests of Verbal-g are thought to represent crystallized intelligence. Crystallized intelligence is thought to be representative of exposure related factors, such as cultural differences and education, and to be much less influenced by genetic factors.

It is important to address the issue of the ambiguous position of SAT Quantitative. Despite a name that seems to explicitly place it in the realm of Analytic-g and fluid intelligence, exploratory factor analysis indicated that SAT Quantitative was equally related to Analytic- and Verbal-g. The relationship to Verbal-g likely reflects the significant portion of word problems presented in the test. Being able to read and understand the lengthy problems taps into a skill that overlaps with those measured through SAT Verbal.

The Functional Anatomy of Speed of Processing (IT) and Cortical Integration (Grouping Threshold)

Prior research has suggested that, unlike reaction time measurements, IT performance in one modality is related to performance in other modalities (Bates, 2005). This is consistent with IT capturing speed of global processing. Global processing speed may be represented anatomically by the topography of event related potentials (ERP) 100-200ms following the offset of the stimulus (Caryl, 1994). Neuroimaging research has indicated that the hemodynamics of distributed brain systems are correlated with the duration of the stimulus, implying that as the critical stimulus duration decreases, cerebral activity increases (Deary et al., 2004). IT measurements here capture the limitations of global potential activity.

While dense synaptic connectivity does account for integration across neurons, effectiveness of this method is low for global integration in an active cortical network and would require synchronization among large groups of presynaptic neurons (Crochet, Chauvette, Boucetta, & Timofeev, 2005). Multisensory integration may be the result of a phenomenon called superadditivity, through which neurons distributed throughout the brain respond to simultaneously occurring stimuli from multiple modalities with more activation than would occur from the sum of the same neuron’s activation to each of the stimuli occurring separately (Rowland, Quessy, Stanford, & Stein, 2007). This account of multisensory integration is consistent with concepts from theoretical neuroanatomy, in which global integration is defined as the emergence of brain states from dynamic interactions within and between different local networks (Sporns and Honey, 2006). This concept of ‘small world’ functional architecture which gives rise to a global whole that is greater than the sum of its parts is referred to in the literature as ‘emergence’ (Bickle 2001). The principle of emergence is believed to be behind the synchronous signals to which cortical integration is attributed (Zorzano and Vazquez, 2003).

Processing speed and cortical integration represent two different measures of neural activity. Processing speed corresponds to the timing of event related potentials in response to detection of a stimulus, whereas cortical integration is the result of dynamic emerging networks. The present study sought to connect the two and measure the speed at which the brain is able to create these dynamic networks. It was expected that this measurement would yield a more complete picture of cognitive ability, which has been linked to both processing speed (e.g. Burns and Nettleback, 2003) and dynamic cortical integration (e.g. Goldman-Rakic, 1987).

Cortical integration, as indicated here by grouping threshold, was related to measures of cognitive ability thought to be indicative of innate ability, but was not related to measures of cognitive ability thought to be indicative of acquired knowledge. Processing speed, as defined by IT measurements, was related to both types of cognitive ability. Cortical integration was a stronger predictor of innate ability, and considering cortical integration in conjunction with processing speed diminished the effectiveness of processing speed as a predictor. This may be due to processing speed being the result of both raw potential and acquired skill; in this context, people with superior cortical integration can be expected to show superior processing speed. However, the reverse relationship would not be expected to occur; acquired knowledge may enhance processing speed but does nothing to improve cortical integration. The following sections will discuss evidence from the literature supporting these statements.

Evidence for Exposure Related Enhancement of Processing Speed and ERPs

The degree and manner of environmental and genetic determinants of brain functioning is of great interest. Numerous studies of late have indicated a significant genetic influence in multiple structural and functional domains (Thompson, Cannon, Narr, van Erp, Poutanen, Huttunen, Lonnqvist, Standerskjold-Nordenstam, Kaprio, Khaledy, Dail, Zoumalan, & Toga, 2001), although other studies have suggested that many structural and functional areas are far less subject to heredity (Biondi, Nogueira, Dormont, Duyme, Hasboun, Zouaoui, Chantome, & Marsault, 1998; Bartley, Jones, & Weinberger, 1997). Different ERP components have been linked to neural and cognitive functioning (Wright, Hansell, Geffen, Geffen, Smith, & Martin, 2001) and results suggest a strong link between timing of P300 ERP components and individual differences in cognitive abilities (Turton, Croft, & Stough, 2003). As mentioned above, ERP components are thought to capture processing speed. Consistent with this theory, the results from the present study show that measures of global processing speed, IT, predicted performance on all aspects of the cognitive battery.

Investigations of the genetic and environmental contributors to individual ERP differences have found substantial amounts of both genetic and environmental influence (e.g., Hansell et al., 2001). This is consistent with the data presented here, which suggest that acquired knowledge is strongly related to increased IT. Further research is needed in order to understand the nature of this relationship.

To be sure, knowledge and skill acquisition have been demonstrated to be strongly subject to education and other environmental influences (Schwann and Riempp, 2004). However, studies that have attempted to improve abstract conceptual knowledge have not met with the same success (Lowe, 1999). Possible explanations for this discrepancy will be discussed in the following sections.

Evidence for the Static Nature of Cortical Integration:

Cortical integration is best understood in the context of the binding problem, which regards the way in which information is combined from various sources (Roskies, 1999). Because of the modular organization of the brain (Jung, 2005) and the specialized functioning of each unit (Hansen and Koeppen, 2002), the binding problem necessarily involves the integration of disparate anatomical areas that are functionally related (Luna and Sweeney, 2004). Perceptual organization provides a striking example of the emergent properties associated with cortical integration (Kubovy and van den Berg, 2008). Evidence suggests that cortical integration may be a vestige of genetic specification within our highly plastic neural systems (Swindale, 1996) and evidence from conceptual models support the hypothesis that internal pattern generation, such as oscillations, and internal organization may account for the integration of different local networks into a coherent system (Bednar and Miikkulainen, 2000). According to this perspective, while the integration of different areas is undeniably the result of early experience, genes determine the nature of the learning and development that occurs (Bednar and Miikkulainen, 2000). This would imply that the findings of the present study may be very different had these same perceptual measurements and (adjusted for age appropriateness) cognitive measurements been collected for children, as opposed to young adults.

Evidence for the Static Nature of Cortical Integration from Cognitive Neuroscience

As discussed previously, neural oscillations are one potential solution to the binding problem of cortical and subcortical integration (Buzsaki, 2006). The study of the genetic underpinnings of neural oscillations have revealed them to be highly heritable traits (Begleiter and Porjesz, 2006), suggesting that the temporal correlation structure of ongoing neural oscillations have robust genetic roots (Linkenkaer-Hansen, Smit, Barkil, Van Beijsterveldt, Brussaard, Boomsma, van Ooyen, & De Geus, 2007). Research has indicated that underlying oscillations may organize a wide range of functions, from the movement of limbs (see Lisman, 2007) to changes in behavioral states (Mohler, 2007). The data presented here suggest that cortical integration corresponds with raw cognitive ability, because of the relationship between tests of fluid intelligence and cortical integration. This is consistent with a model of neural oscillations that are manifested through the expression of genes.

<u>DANVA</u>

Not all elements of the cognitive battery used here were effectively predicted by perceptual measurements. DANVA scores, intended to reflect social intelligence, had a poor relationship with both IT and threshold measurements. One possible explanation for this finding is that the DANVA failed to capture the intended construct. Participant feedback and restriction of scoring range indicate that this may in fact be the case. The DANVA is intended to screen for extreme impairment in a clinical (autistic) population, and may be not sufficiently discriminate in the normal range in individual differences. An alternative explanation is that social intelligence ability was sufficiently captured in these measurements, however, cortical integration abilities and inspection time do not manifest in, or are not strongly associated with, differences in social intellect. This is unlikely, however, due to the integrative manner of social and emotion-related tasks. Further research is required in order to understand the connection between speed of cortical integration and social intelligence, but the findings here suggest that the DANVA is not a sufficient measure of social intelligence for these purposes.

Limitations/Directions for Future Research

Because the environment may act as a determinant for genetic predispositions – such as cortical integrative ability – the present study is limited in its use of college students as participants. By being in college, all of the participants have effectively engaged in the type of environmental factors thought to be conducive to the acquisition of knowledge. Future research may wish to focus on the nature of the relationships observed here in the context of uneducated individuals, people from vastly different cultures, or people that represent disparate socioeconomic statuses.

It is also of great interest to determine the way in which social intelligence fits into this paradigm. Future research may incorporate extensive social and emotional intelligence measures into the cognitive battery. In that same vein, it is worthwhile to consider the expansion of the cognitive battery across all domains.

Finally, in light of the existing literature on the functional neuroanatomy of processing speed and cortical integration, it may be especially revealing to incorporate neuroimaging into the methodology of the present study. Much can be learned from observing the brain's activity as one engages in the perceptual test described here.

Conclusions

Because the brain is modular, most cognitive capacities require integration. The observed relationship between the time course of cortical integration, as measured here by a perceptual task, and cognitive ability, as measured here by the reported cognitive battery, is in line with this assertion. Differences in cortical integration abilities, and differences in the time course in which cortical integration occurs, manifest in differences in cognitive capacities.

Of course, genes often operate through and interact with the environment (Rutter, Silberg, O'Connor, & Simonoff, 1999). The famous "Flynn Effect", the phenomenon of the rising IQ scores in industrialized societies, may be an example of that. Flynn is reported to have explained the interaction of nature and nurture in the context of intelligence as genetic advantages exerting a huge effect on ability later on in life because of the increased likelihood of the genetically advantaged being matched with environments more conducive for the manifestation of that advantage (Restak, 2007). Applying that theory to the context of the current study, individuals who inherited superior cortical integration ability are very likely to be more studious or to engage in other environmental, social, or cultural activities that contribute to greater body of general knowledge. An interesting implication of the present study regards the finding of superior cortical integration predicting spatial, abstract, and complex reasoning abilities (Analytic-g and its components). Although these individuals would be expected to have superior acquired knowledge as well, as indicated here by the relationship of Analytic-g to IT, the same cannot be said for the reverse relationship; we would not expect individuals with superior acquired knowledge to necessarily possess superior spatial, abstract, and complex reasoning abilities, as indicated by the weak correlation between Analytic-g and Verbal-g.

The finding presented here support both the concept of innate ability and the effects of acquired knowledge. As indicated above, threshold measurements reflect the extent of stimulus organization required for accurate perceptual grouping, independent of timing. The relationship of perceptual grouping threshold to Analytic-g is strong, and there is no relationship between this measure and Verbal-g, when the two factors are considered separately (a conglomerate ability score consisting of both factors is associated with threshold ability, likely the result of the contribution of Analytic-g). Analytic-g is also strongly related to processing speed, which is considered here as Inspection Time independent of grouping ability.

The implication of Verbal-g, the component of intelligence thought to reflect acquired knowledge, as a mediating variable for the relationship between Analytic-g, thought to reflect innate ability, and IT, is that while innate ability impacts the knowledge that you will ultimately acquire, it is this knowledge that is driving cortical processing speed and not innate ability. Of course, outside of the lab, processing time is not independent of stimulus organization, and vice versa. This is reflected in the findings regarding the interaction between the a and b parameters, which reflect the rise associated with the interaction of IT measurements and stimulus organization. This interaction reflects a tradeoff between ability to organize increasingly ambiguous stimuli and the time required to do so. This tradeoff exists for everyone, so that as stimuli become increasingly less organized, it takes more time to process the stimuli. This tradeoff was different for people of differing fluid abilities. As stimuli got increasingly less organized it took more time for people with lower Analytic-g scores to process them than for people with higher Analytic-g scores (as indicated by differences in slope). Verbal-g differences were not associated with this tradeoff, implying that acquired knowledge does not totally compensate for inborn ability. To consider processing time independently of integration ability may be useful for basic research purposes, but is largely irrelevant in the context of daily living. Therefore, and based upon the findings presented here, acquired knowledge complements innate ability, but cannot entirely compensate for (lack of) it.

Underlying oscillations make up ERPs (Begleiter and Porjesz, 2006). The application to the present study is that the oscillations themselves are responsible for integration of information across cortical areas, while the timing of the oscillations is related to the quickness of cortical integration. The results presented here suggest a behavioral method of measuring the speed and integrity of cortical integration, and that both of these aspects relate to cognitive ability in different ways. The timing of cortical integration, captured here by IT measurements, is related to general knowledge, whereas the efficiency of integration is related to potential ability.

The data presented here make a strong case for the importance of education, as these findings suggest that acquiring knowledge may speed up cortical integration. In light of the previously discussed findings of neurobiological accounts of cortical integration, these data indicate that acquiring knowledge results in physical changes to the nervous system. The implications of these findings are far reaching, and should be considered in the context of existing studies reporting relationships between level of educational attainment and different medical conditions (Eikemo, Huisman, Bambra, & Kunst, 2008).

Table 1: Descriptive Statistics for Experiment I

	N	Minimum	Maximum	Mean	Std. Deviation
Lum Thresh	25	3	33	21.08	6.80
Lum 90	25	0.08	0.42	0.26	0.09
Lum 80	25	0.04	0.40	0.18	0.11
Flick Thresh	26	9	31	22.92	5.59
Flick 90	26	0.12	0.42	0.24	0.09
Flick 80	26	0.12	0.81	0.26	0.17
Vocabulary	24	36	73	51.54	9.63
Block Design	24	24	67	48.25	10.96
Similarities	24	30	62	51.92	7.83
Matrix	24	25	59	46.33	10.56
DANVA Face	20	3	9	4.80	1.91
DANVA Lang	20	3	11	6.45	2.21

Table 2: Descriptive Statistics for Experiment II

	N	Minimum	Maximum	Mean	Std. Deviation
Threshold	46	15.43	32.57	24.77	3.99
Mask-0	47	28.58	174.79	93.32	36.39
SAT-V	25	280	720	554.80	115.37
SAT-Q	25	320	780	559.60	107.68
Vocabulary	37	24	69	50.03	11.49
Block Design	37	21	67	48.03	10.10
Similarities	37	34	70	53.76	6.96
Matrix	37	10	63	46.14	13.07
FIQ	35	77	124	100.86	13.36
VIQ	35	80	128	103.49	11.72
PiQ	35	67	120	97.06	13.63
DANVA- Face	33	2	14	5.94	2.63
DANVA - Lang	33	0	9	4.85	1.99

Table 3: Full Correlation Matrix

zSAT-V	1.00																
zSAT-Q	.76**	1.00															
zDANVA-L	0.09	-0.16	1.00														
zDANVA-F	0.11	0.26	0.08	1.00													
zVOCAB	.59**	0.24	-.49**	-0.11	1.00												
zBLOCK	0.12	.58**	-26	0.34	0.16	1.00											
zSIMILAR	0.23	.52**	-.41*	0.04	0.20	.60**	1.00										
zMATRIX	0.25	.55*	-0.33	0.03	0.29	.77**	.76**	1.00									
VERBAL-g	.92**	.74**	-.41*	0.04	.86**	0.30	.41*	.41*	1.00								
ANALYTIC-g	.49**	.77**	-.44*	0.29	.38*	.82**	.78**	.91**	.64**	1.00							
THRESH	0.35	.52*	-0.14	0.33	0.02	.57**	.47**	.58**	0.23	0.69	1.00						
MASK-0	-.59**	-0.27	0.19	0.16	-.51**	-.44**	-.38*	-.49**	-.49**	-.44**	-.37*	1.00					
Y	-.53**	-0.36	0.17	0.12	-.39*	-.33*	-0.25	-0.28	-.46**	-.39**	-0.16	.61*	1.00				
A	0.25	0.25	-0.12	-0.02	0.14	0.17	0.09	0.07	0.21	.23*	-0.05	0.01	.78**	1.00			
B	-0.10	-0.23	-0.04	0.13	0.10	0.30	0.25	.34*	0.02	0.22	0.19	-0.18	.37**	-.57**	1.00		
AxB	0.01	0.07	-0.08	-0.03	0.04	-0.16	-0.24	-0.25	0.14	0.05	-0.10	0.19	.50**	.78**	-.65**	1.00	
INTEGRAL	-0.23	-0.22	-0.11	-0.30	-0.06	0.05	0.16	0.12	-0.17	0.03	0.00	-0.01	0.09	-0.11	0.14	-0.08	1.00
	zSAT-V	**zSAT-Q**	**zDANVA-L**	**zDANVA-F**	**zVOCAB**	**zBLOCK**	**zSIMILAR**	**zMATRIX**	**VERBAL-g**	**ANALYTIC-g**	**THRESH**	**MASK-0**	**Y**	**A**	**B**	**AxB**	**INTEGRAL**

Table 4 – Correlation Matrix: Perceptual and Cognitive Measures

Correlations										
	ZSATV	ZSATQ	ZVOCAB	ZBLOCK	ZSIMILAR	ZMATRIX	VERBALG	ANALYTCG	THRESH	MASK0
ZSATV	1									
ZSATQ	0.76**	1								
ZVOCAB	0.59**	0.24	1							
ZBLOCK	0.12	0.58**	0.16	1						
ZSIMILAR	0.23	0.52*	0.2	0.60**	1					
ZMATRIX	0.25	0.55*	0.29	0.77**	0.76**	1				
VERBALG	0.92**	0.74**	0.86**	0.3	0.41*	0.41*	1			
ANALYTCG	0.49*	0.77**	0.38*	0.82**	0.78**	0.91**	0.64**	1		
THRESH	0.35	0.52*	0.02	0.57**	0.47**	0.58**	0.23	0.69**	1	
MASK0	-0.59**	-0.27	-0.51**	-0.44**	-0.38*	-0.49**	-0.49**	-0.44**	-0.37*	1

Figure 1 – Example of Luminance Stimulus Across Levels of Organization

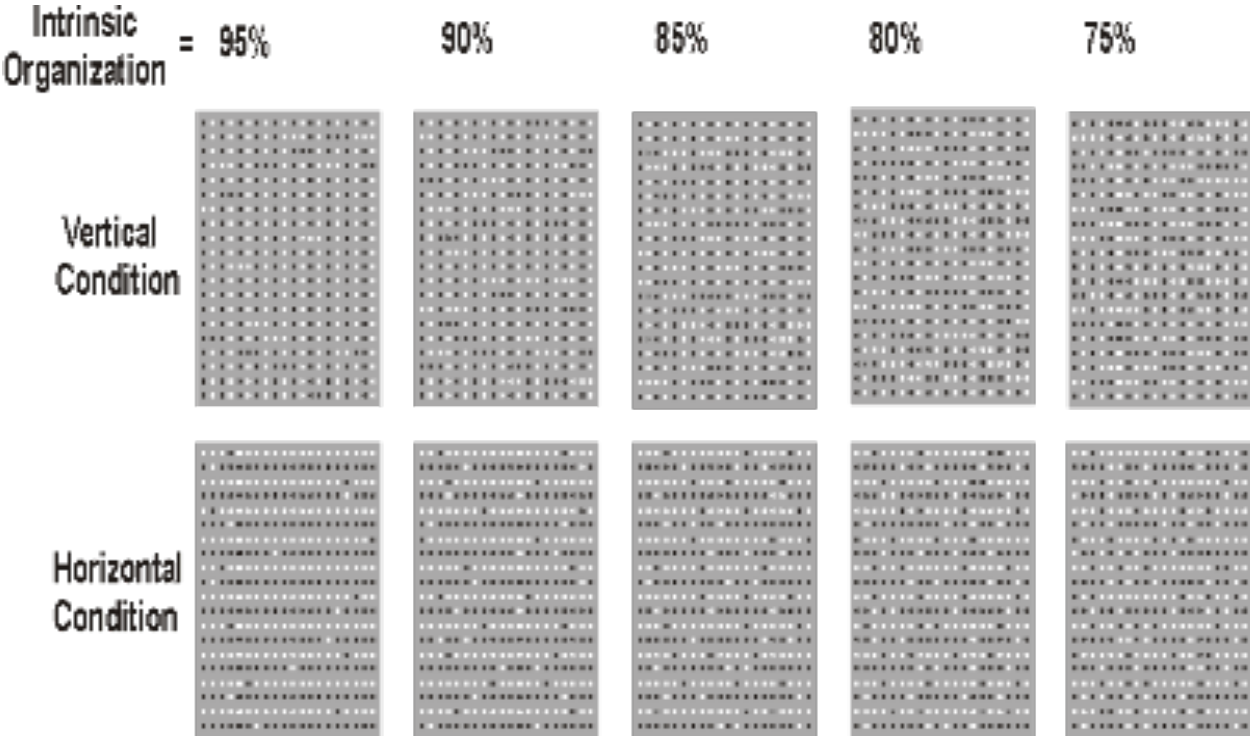
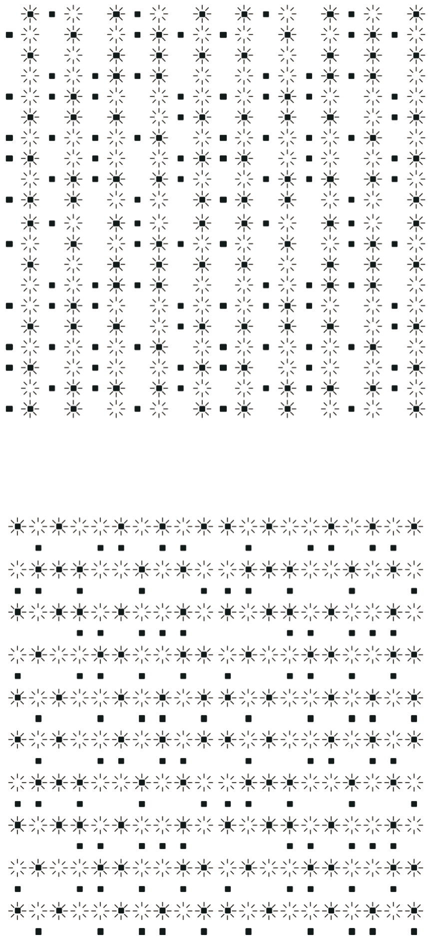
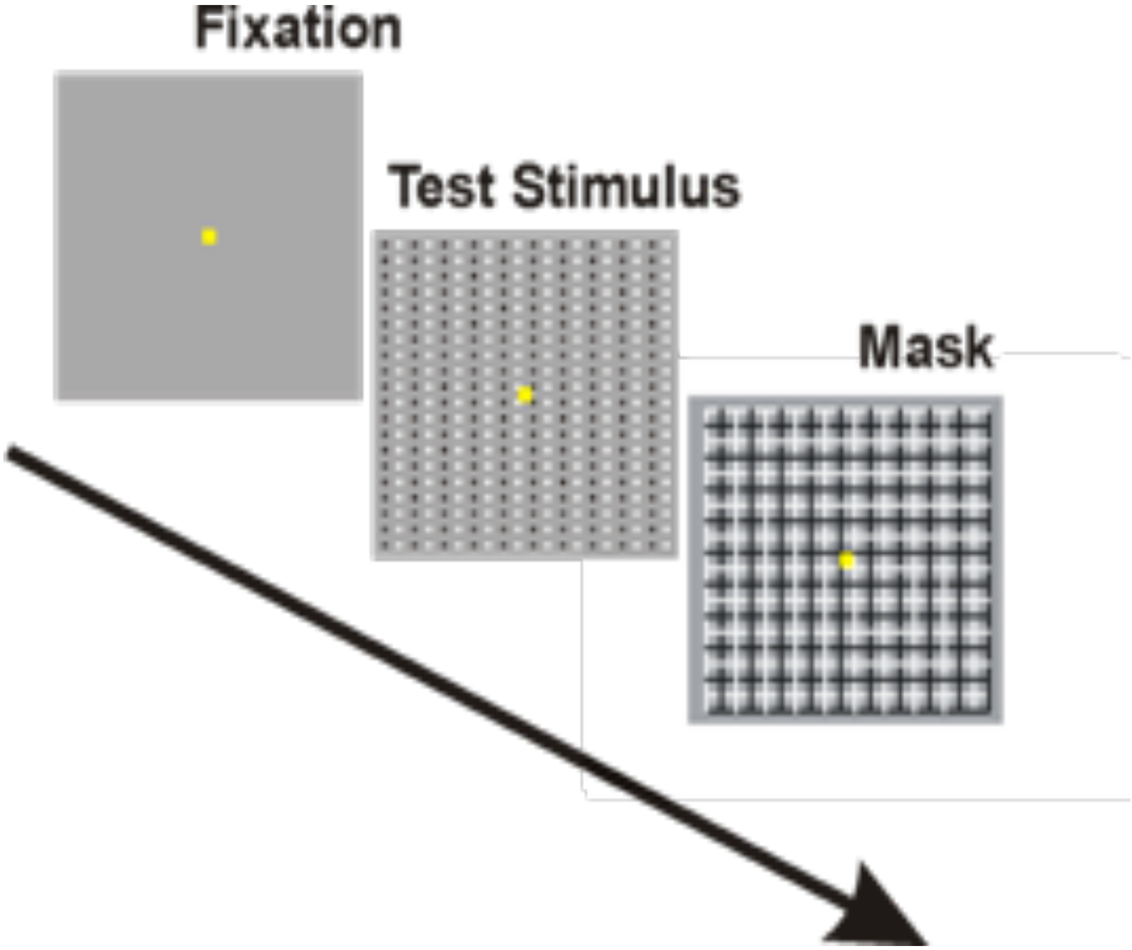


Figure 2 – Example of Flicker Stimulus



Stimulus elements flickered on and off in a pattern corresponding to either vertical (top) or horizontal (bottom) orientation.

Figure 3 – Masking Threshold Procedure



Critical Stimulus Duration (CSD) was captured using an Inspection Time task. Participants fixated on the yellow square in the center of the screen. 500 ms later, the stimulus appeared, immediately followed by the backwards mask. Length of stimulus duration varied between trials, and the average duration at which a given participant was no longer able to perceive the stimulus was the CSD.

Figure 4 – Example of Exponential Growth Curve – Participant response curve to increasingly less organized stimuli

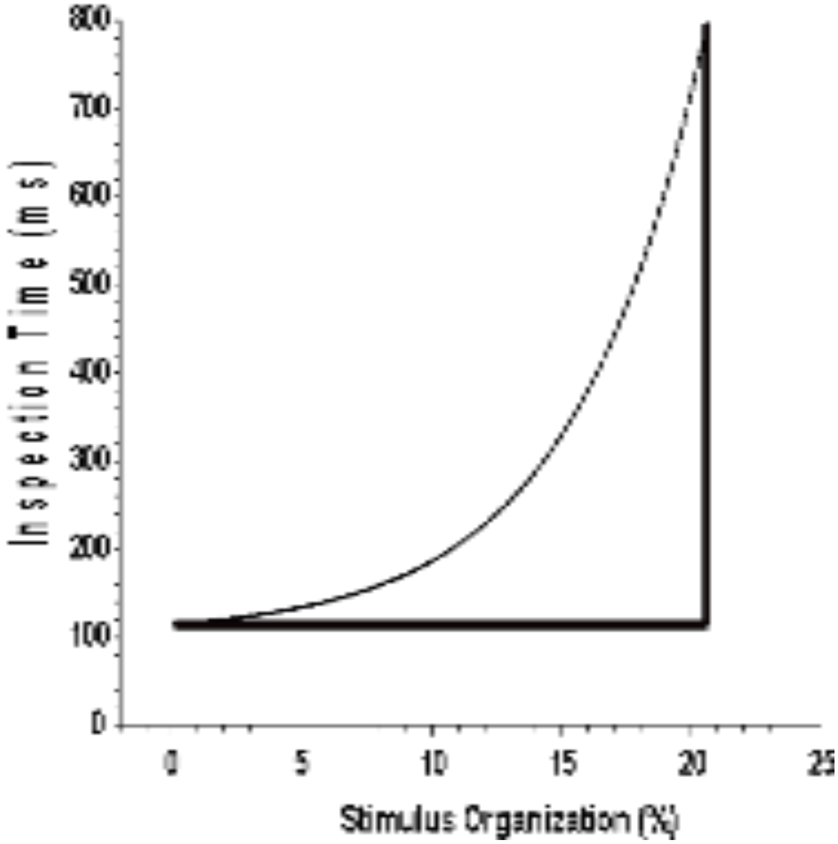
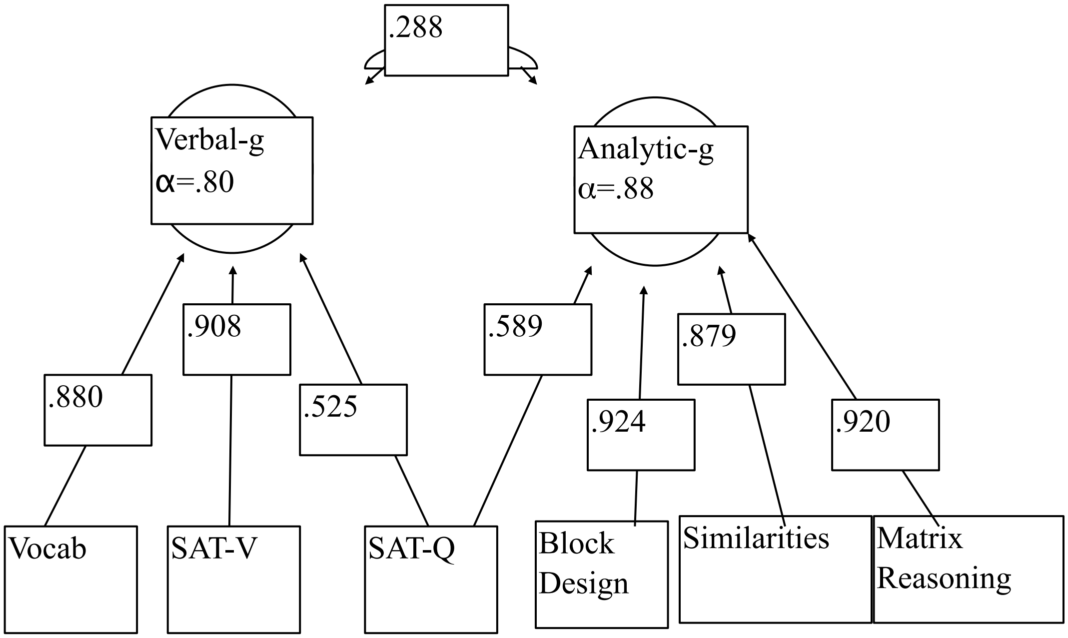


Figure 5 – Factor Analysis



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