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Individual variation in EEG spectral power enhancement and intelligence

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INDIVIDUAL VARIATION IN EEG SPECTRAL POWER ENHANCEMENT AND INTELLIGENCE

BY

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DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

Psychology

The University of New Mexico
Albuquerque, New Mexico

July, 2010

DEDICATION

This dissertation is dedicated to my parents, Bryan and Annie Euler, who taught me how to persist on difficult obstacles and gave me the confidence to know I could.

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ABSTRACT

This study tested the relationship between short-term neuroplasticity and individual differences in intelligence. Twenty-two participants completed cognitive testing and a visual EEG experiment involving exposures to repeated and novel stimuli. Time-frequency analyses of phase-locked (evoked) and non-phase-locked (induced) power showed a small effect of decreasing evoked/induced theta (4-8 Hz) ratios over stimulus exposures, irrespective of condition. Hypotheses that intelligence would relate to an increase in this ratio over exposures were not supported. However, the magnitude of the ratio positively correlated with intelligence; while the amount of induced gamma (30-50 Hz) activation pre- to post-stimulus was highly inversely related to *g*. Results suggest that transient changes in neural network phase strongly relate to intelligence in physiological measurements acquired over brief intervals.

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Introduction

Intelligence is one of the most useful and most widely researched concepts in psychology. One widely accepted view of intelligence is that it is one's "ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, [and] to overcome obstacles by taking thought (Neisser et al. 1996)." Individual differences in intelligent behavior (or latent intellectual capacity) result from differences in the underlying neurophysiology which gives rise to that behavior. Attempts to understand this neurophysiological basis of intelligence has preoccupied physiological psychologists for many decades. Yet, despite considerable advances linking variation in intellectual capacity to its underlying neurobiology, especially since the widespread use of magnetic resonance imaging (MRI) technology (Gray & Thompson, 2004), much is still unknown about the mechanisms which enable one individual to consistently reason, learn, and adapt more effectively to their environment than another. Research on the physiological basis of intelligence not only aims to clarify one of the central constructs of psychology, but will also enhance our understanding of the mechanisms underlying developmental and acquired disorders of learning and adaptive behavior, including schizophrenia, ADHD, and Alzheimer's disease (Whalley, Starr, Athawes, Hunter, Pattie, & Deary, 2000).

One important concept pertinent to many theories of intelligence is the notion of *g*, or the general psychometric factor reflecting the positive covariation in cognitive tests (Jensen, 1998). Early on in mental ability research, it was found that whenever a sufficiently large sample of individuals was administered a sufficiently large and diverse battery of cognitive tests, a higher-order factor comprising the positive covariation between test scores reliably emerges upon factor analysis (Spearman, 1904). Common examples of such tests might include verbal repetition of aurally presented digit strings, speeded symbol coding tasks, tests of vocabulary definitions, and multiple choice tests of figural matching and reasoning (Wechsler, 1997). Not only do mental ability tests consistently exhibit positive covariation across diverse test batteries, but factor analysis methods consistently reveal that a single higher order factor- *g*, accounts for the majority of their shared variance (e.g. 50%; Carroll, 1993). Restating this, whenever a large and diverse battery of ability tests is administered to enough individuals, it is consistently observed that not only do the test scores always positively correlate, but a single factor accounts for much of their shared variation.

This general factor has also been consistently and strongly related to performance on tests designed to measure overall intellectual ability. For example, *g* accounts for 52% of variance in Wechsler Adult Intelligence Scale (WAIS) performance (Deary, 2000). This finding is so consistent that it has been frequently argued that what *g* actually measures is an individual’s overall amount of cognitive ability or their *general intelligence* (Jensen, 1998). This implies that when some people are said to be more or less “intelligent” than others, what they actually differ on is this level of overall cognitive ability. The extent to which a given ability test correlates with *g* is understood as its *g*-loading. Thus, those tests with the highest *g*-loadings are in turn thought to best measure an individual’s overall intellectual ability. Whether a single, latent general intelligence variable best accounts for the emergence of the psychometric *g* factor is controversial (see van Der Maas et al., 2006). Yet, the statistical reality of the *g* factor remains, and its utility for exploring the neurobiological basis of intelligence is attested by numerous findings relating it to biologically meaningful characteristics.

For example, it has been consistently shown that the general intelligence factor demonstrates high heritability (Plomin & Spinath, 2004), and that its heritability increases over an individual's lifespan while environmental variance in intellectual abilities diminishes (Jensen, 1998). The high heritability of *g* is likely related to the numerous adaptive outcomes associated with higher intelligence (Gottfredson, 2004). Among these are one's desirability as a mate in laboratory settings (Prokosch, Coss, Scheib, & Blozis, 2008), academic and job success (Neisser et al., 1996; Schmidt & Hunter, 1998), risk of developing a psychiatric illness (Batty, Mortenson, & Osler, 2005), risk of developing late onset dementia (Whalley et al., 2000), and longevity and hospital admissions (Deary, Whalley, & Starr, 2003). Since *g* strongly relates to so many biologically meaningful outcome indices, it represents an optimal psychological index from which to explore the underlying neurobiology of intelligence. By then relating the most highly *g*-loaded tests to various neural characteristics of interest, researchers are able to evaluate candidate variables which may account for variation in intelligence.

Candidate Neural Variables Underlying Intelligence

As research on the neural basis of intelligence has proceeded, numerous theories have been advanced that advocate variables which might be most fruitfully studied. Among the most frequently cited candidates are the size, efficiency, and plasticity of either particular brain regions, or the brain as a whole. One recent proposal adopts these candidates in the forms of the "availability, reconfigurability, and customizability" of cortical modules to explain variation in "cognitive plasticity" (i.e., intelligence and learning ability) both within and across species (Mercado, 2008). In this framework an organism's ability to discriminate stimulus representations (including private stimuli) is the critical determinant of what and how quickly it can learn. These three characteristics are hypothesized to be necessary for the creation, maintenance and switching of those stimulus representations. In order, they refer to the number and diversity of cortical modules, the brain's capacity to develop new configurations of those modules, and the extent to which those modules can be modified or reallocated to resolve new stimulus representations. Although speculative, this framework provides a basis from which to explore the empirical data on neural correlates of intelligence. Moreover, this framework roughly corresponds to the various neuroimaging techniques which have been used to study intelligence. For example, availability can be construed as a static or structural property of brains which is investigable using structural and metabolic MRI technologies. Reconfigurability refers to the way in which existing functional aspects can be dynamically combined, such as in resting state data or non-task dependent research, or with methods which emphasize spatial relationships and the role of particular structures. Customizability lends itself most readily to neuroimaging studies which attempt to measure rapidly shifting neural dynamics or neural network change in real time.

Neural Availability

Brain size and related indices of neural availability have been posited as determining factors for intelligent and adaptive behavior. In the framework above, availability refers to the amount and type of neural material available for resolving stimulus adaptations (Mercado, 2008). A widely replicated example of the significance of availability is the finding that psychometric intelligence consistently shows modest albeit positive correlations with brain volume in humans, especially when body size is controlled for (Wickett, Vernon, & Lee, 2000; McDaniel, 2005). The same is true of its counterpart constructs when measured across species in non-human animals (Reader & Laland, 2002). Moreover microcephaly, a condition in which people are born with undersized heads and brains, is associated with severe intellectual impairment and disrupted learning (Woods, Bond, & Enard, 2005). Also, in support of availability as a necessary feature of intellectual capacity, is the evidence that non-human animals lack the necessary architecture for determining the stimulus relationships necessary to develop language (Boysen, Bernsten, Hannan, & Cacioppo, 1996). By extension, their ability to solve certain types of problems is constrained by the number and types of neural modules they possess. Thus there is good evidence to suggest that the sheer volume of and type of neural material one possesses is a limiting determinant of intellectual ability.

A recent review of the structural neuroimaging literature of intelligence speaks directly to the importance of the size of particular cortical regions for intelligence. Specifically, Jung and Haier (2007) have recently proposed that that a predominantly parieto-frontal network which integrates input from temporal and lateral occipital structures primarily underlies variation in intelligence (Parieto-Frontal Integration Theory, P-FIT). In support of this model, the authors cite volumetric data from several studies which have consistently demonstrated positive correlations between IQ measures and Brodmann areas comprising P-FIT structures. For example, one report examined the correlation between the *g*-loadings of Wechsler subtests and gray matter volume (Colom, Jung, & Haier, 2006). Results demonstrated that the most highly *g*-loaded tests were associated with the greatest number of gray matter voxels, and that as *g*-loadings increased the significance of gray matter/IQ correlations also increased. In support of the model, the most highly *g*-loaded tests were correlated with gray matter in discrete regions corresponding to Brodmann areas in superior, lateral, and medial frontal areas; inferior and superior parietal lobules; inferior, middle, and superior temporal regions; and lateral occipital sites..

Similarly, findings obtained from diffusion tensor imaging have supported the positive relationships between occipito-parietal and frontal white matter integrity and IQ in children (Schmithorst et al., 2005), while magnetic resonance spectroscopy has demonstrated an association between left parieto-occipital metabolite concentrations and verbal and performance IQ measures (Jung et al., 1999). Hence, data from structural and metabolic studies support robust IQ effects for specific regions within the P-FIT model (Jung, & Haier, 2007).

At the same time, it seems fundamental that adequate neural material and metabolic functioning is a necessary feature underlying the development of complex or intelligent behavioral repertoires. So although availability represents a necessary aspect of cognitive plasticity and intelligence, it alone is unable to address aspects of functional neuroplasticity which are likely related to intelligence. Taking the associations between amount and capacity as granted, the more explicitly functional variables in this model, *i.e.* reconfigurability and customizability, suggest other interesting avenues for examining differences underlying intellectual variation.

Neural Reconfigurability

In this model reconfigurability refers to an organism's ability to maintain and control cognitive representations through the flexible development of configurations of neural modules, or through rapid temporal switching between modules or networks (Mercado, 2008). Examples of this might include the neural processes involved in momentary set switching, or manipulation of sensory elements (stimulus representations) in working memory. This capacity is posited to rely substantially on the action of the prefrontal cortex in particular to modulate or bias responses from other neural modules (e.g. sensory, motor and limbic regions) into new configurations, or to enable switching between configurations to enable stimulus representation and responding. In a sense then, reconfigurability is the capacity of a network to effectively combine its existing architecture into new functional units to solve problems. The importance of flexible utilization of cortical modules for intelligence has been demonstrated in several ways. One particularly well-studied example is the relation between working memory, reasoning, lateral frontal function, and *g*.

For instance, one PET study adapted stimuli from multiple choice reasoning tests for use in the scanner (Duncan et al., 2000). The authors rationally selected visual stimuli for verbal and spatial tasks which utilized nearly equivalent content, but which varied according to difficulty. Preliminary behavioral data indicated that the low and high difficulty stimuli exhibited low and high *g*-loadings, respectively, when tested in large samples. They then designed experimental conditions which compared neural responses during performance of multiple choice reasoning tasks which varied on *g*-loading. Cerebral blood flow measures obtained during PET scanning indicated that high versus low-*g* comparisons across spatial and verbal tasks were primarily associated with lateral frontal activation. Since content-dissimilar verbal and spatial tasks elicited common frontal activation, the authors argued that *g*-loaded tasks primarily recruit frontal regions as opposed to activating diffuse neural regions.

Similar research has utilized fMRI to examine neural correlates of intelligence during task performance. As described in Jung & Haier's recent review (2007) numerous studies have implicated the role of frontal and parietal structures in functional neuroimaging research on intelligence. Diverse working memory and reasoning tasks such as visual analytic reasoning, n-back paradigms, relational reasoning and inference, and chess problems have implicated parieto-frontal networks with occipital and temporal contributions (Prabhakaran, 1997; Gray, 2003; Ruff et al, 2003; Atherton et al., 2003). Additionally, the role of lateral frontal cortex in performance of working memory and reasoning tasks has been well supported (Levy & Goldman-Rakic, 2000), as have the covariation between working memory and reasoning tasks and *g* (Oberauer, Schulz, Wilhelm, & Süβ, 2005; Jarrold, & Towse, 2006).

Overall, the structural and functional imaging literature has made numerous contributions to our understanding of the neural basis of intelligence. However, these methods can be enhanced and augmented by information from electrophysiological sources. Although PET and especially fMRI technologies provide excellent spatial resolution regarding locations of increased or decreased activation related to intelligence or task performance, they are currently unable to resolve neural dynamics at the millisecond scale at which the brain operates. Thus it is necessary to utilize electroencephalography (EEG) and magnetoencephalography (MEG) in order to more fully understand the real-time neural dynamics underlying individual differences in intelligence. In particular, resting EEG/MEG data provide excellent opportunities to examine the baseline properties relating to the interdependence of neural modules and the flexibility of their temporal configurations.

Overview of EEG/MEG Techniques

Briefly, human electrophysiological research has been primarily conducted using two data-processing methods. Classic EEG research on intelligence utilized the cognitive event-related potential (ERP, and its sensory correlate the evoked response- ER) as a proximal means to quantify neural plasticity. The ERP/ER is obtained by repeatedly presenting a stimulus to a subject and averaging the neural responses recorded in their EEG over trials relative to the same time-point in each trial. This procedure results in an average evoked response. More recent work utilizing EEG/MEG technology to examine the neurophysiological basis of intelligence has employed frequency-domain measures which are becoming more widely adopted in electrophysiological research. Unlike ERP measures which quantify the amplitude and latencies of features in ERPs, these other techniques convert data to the frequency domain through the use of Fourier-based or wavelet transforms (Makeig, Debener, Onton, & Delorme, 2004). This data transformation gives the benefit of an additional dimension on which to characterize electrophysiological responses; specifically, latency, magnitude (in the form of power), and frequency itself. Moreover, by using these transformations to preserve a balance of time and frequency resolution, researchers are able to also quantify significant changes and effects of signal phase. As a result, time-frequency analyses permit investigations of power in either conventional time-locked (evoked), as well as in non-phase-locked locked activity known as induced power. Thus, time-frequency analyses permit quantification of the variability in neural responses across trials, through evoked and induced power analyses, and through direct investigations of signal phase dynamics. One useful application of EEG time-frequency measures is the study of ongoing neural dynamics observed during resting periods.

In general, resting EEG studies of time-frequency data have typically demonstrated positive relationships between EEG power, especially alpha band (8-12 Hz) power, and intelligence (Doppelmayr, Klimesch, Stadler, Pollhuber, & Heine, 2002; Klimesch, 1999). One rather comprehensive EEG study which utilized frequency-domain measures investigated the intelligence relationships with resting EEG power, coherence, and phase in a sample of over four hundred people between the ages of 5 and 52 (Thatcher, North, & Biver, 2005). Participants' EEGs were recorded during two five-minute periods of eyes-closed rest, before or after which the Wechsler Intelligence Scale for Children IQ (WISC-R) or WAIS-R subtests were administered. The data were divided into two-second epochs and absolute power as well as pair-wise EEG coherence and phase delay were obtained for frequencies from 1-30 Hz. First, the authors performed factor and discriminant analyses to determine if EEG measures could differentiate between high and low IQ individuals. An extreme groups design was implemented where participants were divided into high and low IQ groups and t-tests were performed on all EEG measures. Significant variables were then subjected to factor analyses for discriminant analysis between groups. Discriminant analyses revealed excellent classification, which included overall classification accuracy, sensitivity, and specificity from 92% and greater for full-scale, verbal, and performance IQs (FSIQ, VIQ, PIQ). Multiple regression analyses revealed that individual subject's discriminant scores significantly predicted IQ variables.

Parsing these relationships, subsequent correlation analyses performed with the EEG measures across IQ groups revealed that EEG coherence was consistently inversely related to IQ while absolute power was consistently positively related to IQ. As coherence measures signal correlation, these results indicate that mere increased association (positive or negative) between electrode sites is inversely related to intelligence. Results with respect to phase delays were split, which is consistent with the fact that coherence reflects both negative and positive phase-locking. In general, decreased short distance frontal phase delays in the delta (1-3.5 Hz) and beta bands (12.5-25 Hz) were associated with higher IQ, while the converse was found for delta and beta short distance phase delays over posterior regions. Overall, coherence and phase delay measures exhibited the strongest correlation with IQ. Summarizing their complex findings, the authors suggested that the generally similar associations between EEG measures and VIQ, PIQ, and FSIQ indices indicated that these EEG measures were tapping a general intelligence factor as opposed to specific intellectual domains. They argued that as energy and intelligence are “necessarily” linked, the association between absolute power and intelligence was not unexpected. In light of the observed phase relationships they further hypothesized that general intelligence is associated with more rapid processing in frontal regions and more integrated processing in posterior and temporal areas.

Given the robust association between measures of phase coupling and IQ found in the prior report, a later report utilized two aspects of pair-wise phase resetting: phase-shift duration (i.e. time between the onset and offset of phase-shift) and phase-lock duration (duration of synchrony), to quantify neural correlates of intelligence in the same sample (Thatcher, North, & Biver, 2008). Using one to two minutes of each participant’s resting data, the authors obtained ongoing phase information and calculated pair-wise phase-shifts and phase-locks on the time-frequency transformed data. The phase measures from all 171 pair-wise electrode combinations were used to predict IQ in multivariate regression analyses. Overall, combined values across frequency bands yielded multiple R = .75 for FSIQ and phase-shift and R = .61 for FSIQ and phase-locking. Together phase measures accounted for 68% of the variance in IQ in the sample. Pair-wise phase-shift duration (mean duration ~ 50 ms) was generally positively related to IQ while phase-locking (mean duration ~250 ms) was negatively correlated with IQ. Additionally, the highest correlations with phase measures were obtained in the 6 cm distance range compared to longer inter-electrode distances. For both phase-shift and phase-locking, the authors used observed group differences to develop models which related optimal durations of each to IQ. Based on other theoretical and empirical work, the authors hypothesized a model where sufficiently long phase-shift durations facilitate recruitment and allocation of neural resources for subsequent phase-locking, while phase-locking duration must balance information processing needs against network flexibility. On the basis of this model they argued that obtained values for phase reset measures in the high IQ group are indicative of optimized durations which facilitate rapid and efficient neural processing.

Overall this research program demonstrates that reconfigurability or dynamical flexibility in the form of reduced resting EEG coherence and phase-locking is associated with higher IQ performance. This increased spatial differentiation among higher IQ participants may indicate more flexible neural networks which are more able to be rapidly integrated into continuously evolving combinations of processing units. Simultaneously, findings that increased resting phase-locking is inversely related to IQ imply that neural reconfigurability may specifically relate how well the brain is able to balance the apparently competing needs of regional integration and differentiation (Thatcher, North, & Biver, 2008). Thus when taken with PET and fMRI research, resting EEG data suggest specific dynamical mechanisms underlying the fronto-parietal interactions necessary for intelligent behavior.

Neural Efficiency

Another important idea within intelligence research is the notion that one’s intelligence is a function of one’s neural efficiency. Specifically, the “neural efficiency hypothesis” inversely relates intellectual performance to neural activation, and has received substantial empirical support for nearly two decades. In one of the first studies to provide data on neural efficiency and intelligence, researchers collected PET data on male participants' cerebral glucose metabolization while they performed one of three tasks: the Raven's Advanced Progressive Matrices (RAPM; Raven 2000), a vigilance task, and a visual control task (Haier et al., 1988). The most important finding of this report was an inverse association between brain glucose utilization and performance on the RAPM. That is, more intelligent participants actually required less metabolic exertion than lower IQ participants to complete a cognitively challenging task. This result led to the formulation of the neural efficiency hypothesis, wherein the underlying neural differences between less and more intelligent individuals is the efficiency with which their brains process information (Haier et al, 1998).

A particular strength of perceptual and cognitive electrophysiological studies of intelligence is that their temporal resolution affords precise tests of neural efficiency. Indeed, several studies utilizing traditional ERPs have reliably shown inverse relationships between neural response latency and IQ (Burns, Nettelbeck, & Cooper, 2000; Bazana, & Stelmack, 2002). This relationship has been demonstrated in children as well as adults. For example, an early study of more than 500 randomly-sampled Canadian children enrolled in grades 2-8 demonstrated an inverse-relationship ranging from $r = -.18 - -.33$ between visual evoked-potential component latencies and WISC IQ scores (Ertl & Schafer, 1969). This relationship has been replicated in cognitive studies as well. A more recent study compared ERP-IQ relationships in average and gifted children during performance of simple and complex choice reaction time tasks. Consistent with the larger literature, gifted children exhibited shorter ERP latencies than their average IQ counterparts across conditions (Zhang, Shi, Lou, Liu, Yang, & Shen, 2007).

A general examination of the frequency-domain EEG literature on neural efficiency indicates that although resting EEG alpha power is generally positively correlated with intelligence, event-related alpha activity is more often inversely related to intelligence (Neubauer, Freudenthaler, & Pfurtscheller, 1995; Klimesch, 1999), though exceptions have been observed (e.g., Jausovec, & Jausovec, 2001a). With respect to resting data, one study replicated the positive relationship between IQ and resting alpha power in children and additionally observed an inverse correlation between delta (0.5-5 Hz) power and intelligence (Schmid, Tirsch, & Shirb, 2002). One large study examined the heritability of individual peak alpha band *frequency* and its association with IQ (Posthuma, Neale, Boomsma, & de Geus, 2001). However, results generally showed no associations with the exception of a small positive correlation (r = .15) between alpha frequency and the WAIS-III working memory index in middle-aged adults despite high heritabilities of both peak frequency and IQ.

Generally however, reports utilizing event-related EEG power or source localization methods have found support for the neural efficiency hypothesis. In one source-localization study, a mixed-gender sample of high and low IQ groups exhibited differential cortical activation patterns to correctly identified visual and auditory targets during oddball tasks (Jausovec, & Jausovec, 2001b). Times of onset and peak amplitude for the P200 and P300 ERPs were examined for their association with IQ. Results demonstrated that high IQ individuals exhibited lower reaction times across tasks relative to the lower IQ group. There were no group differences for signal to noise ratio or maximal current strength. Conversely, source analyses revealed significant interactions where higher IQ individuals exhibited larger spatial activation at P300 onset which decreased relative to the low IQ group at the time of peak P300 amplitude in both modalities. Lower IQ individuals exhibited an opposite pattern of increasing spatial activation over time. With respect to current density estimates, a similar IQ-activation interaction was observed for the auditory task only, where higher IQ individuals had increasing current densities over time from P300 onset to peak amplitude, while the lower IQ group exhibited no change. There were no significant effects of P200 onset or peak amplitude. These findings were interpreted as indicating more efficient processing of stimuli in more intelligent individuals a source analyses suggested use of fewer and more specific neural resources in those individuals.

Another group investigated potential interactions of sex and neural efficiency in two reports and observed similar effects (Neubauer, Fink, & Schrausser, 2002; Neubauer, Grabner, Fink, & Neuper, 2005). In the latter report the authors measured alpha event-related desynchronization (ERD) while male and female participants completed verbal and spatial reasoning tasks. Importantly, although ERD signifies desynchronization, since alpha power decreases during cognitive processing versus during rest, lower ERD is interpreted as indicating lower cortical activation (Pfurtscheller & Lopes da Silva, 1999). In turn, event-related synchronization (ERS) is hypothesized to reflect cortical activation. In the study, the authors examined correlations between sexes separately and distinguished between verbal and nonverbal IQ performance without examining general intelligence. Behavioral data indicated that there were no overall IQ differences between males and females. Similarly there were no sex differences with respect to verbal task performance, although males exhibited greater solution rates and lower reaction times relative to women on the spatial reasoning task. Overall it was observed that ERD during the verbal task was inversely related to verbal IQ in the female group only with males demonstrating non-significant trends in the opposite direction. Conversely, males showed an inverse relationship between alpha ERD during visuospatial task performance and nonverbal IQ while females exhibited trends in the opposite direction. As these results were largely consistent with their previous findings, the authors interpreted the results as indicating that neural efficiency is greatest for each sex on those tasks for which the two sexes generally perform better

Another study examined the effect of task difficulty on neural efficiency in an attempt to reconcile conflicting findings (Doppelmayr et al., 2005). In that report the authors adapted high and low difficulty RAPM items for use in an EEG experiment. Alpha and theta ERD/ERS were examined across average and superior IQ groups. Analyses of correct trials indicated that high IQ subjects exhibited greater theta ERS across task conditions, potentially reflecting greater working memory involvement in that group (Klimesch, 1999). With respect to alpha ERD, and contrary to the neural efficiency hypothesis, high IQ subjects exhibited significantly increasing ERD as task difficulty increased. However when groups were compared across the low-difficulty condition, the high IQ group exhibited significantly less ERD relative to the average IQ group. ERD did not significantly differ across task conditions in the average IQ group. The authors suggested that their data implied a qualification of the neural efficiency hypothesis wherein high IQ subjects make use of existing strategies during easy tasks thereby relying on less cortical activation, while unlike average performers they are able to increase cortical activation in response to more challenging tasks.

Finally, one EEG study examined the boundaries of neural efficiency by investigating the relationship between IQ and EEG measures during performance of an over-learned task

(Grabner, Stern, & Neubauer, 2003). There, the authors examined potential interactions between intelligence and cortical activation during performance of a task in which both high and low IQ participants were already experts. Participants completed an expertise task where they were asked about common taxi routes in Graz, Austria where they were employed as taxi-drivers, and an intelligence task in which they studied fictitious route maps and decided if a subsequently presented point on the map passed through the fictitious route. Alpha ERD was analyzed during task performance in relation to IQ. Behaviorally, performance on the intelligence task was correlated with RAPM scores while performance on the expertise task was not. As hypothesized, analyses of alpha ERD showed that higher IQ participants demonstrated less ERD during intelligence task performance than lower IQ participants while there were no group differences on the expertise task. When the results were further analyzed by electrode region, high IQ subjects exhibited a region effect where they showed highest ERD at parietal sites and lowest ERD in over frontal areas. The results were interpreted as generally supporting the neural efficiency hypothesis. However, they also suggested that when higher and lower IQ participants are both tested on tasks involving prior learning, more intelligent individuals do not exhibit greater neural efficiency. The authors suggested that their results indicate that intelligence no longer impacts achievement on well-learned tasks or neural activation during task performance. Notably, this finding suggests that some neural differences underlying intelligence may be most related to processes involved in new learning and solving novel problems.

Despite some inconsistent findings, the overall trend within the neural efficiency literature supports an inverse relationship between the latency or extent of neural activation and differences in intelligence. At the same time, it is necessary to clarify effects of task difficulty and expertise on cortical activation in more intelligent individuals. Elaborations of this literature might include determinations of whether greater neural speed or specificity between connections underlies the inverse IQ-efficiency relationship, and how reliably this relationship is observed in novel or challenging versus less demanding contexts. In light of conflicting EEG findings, more data are needed to better develop well-specified tests of neural efficiency in intelligence.

Neural Customizability

While the efficient allocation of neural resources has been supported as a part of intelligence, it fails to account for basic research findings regarding neural mechanisms of learning and behavioral adaptation. For example, even if potential differences in neural transmission underlying neural efficiency were confirmed, neural efficiency still would not account for data relating individual synaptic change to an organism's ability to learn and retain information (Garlick, 2003). As adaptation to one's environment (i.e. learning), and the ability to solve novel problems have typically been included in definitions of intelligence (Carroll, 1993), efficient processing within existing networks seems insufficient as a lone neural mechanism underlying intelligent behavior. Hence, the final aspect of this model relates to the customizability or plasticity of individual cortical modules in resolving stimulus representations. Here "representational resolution" is understood as an organism's ability to detect or differentiate between stimuli, which is in turn necessary for adaptive responding (Mercado, 2008). This capacity to tune neural networks has been featured in isolation in some theories of individual variation in intelligence.

For example, Garlick (2003) hypothesized that individual variation in the brain's ability to adapt to the environment may underlie individual variation in intelligence. He notes that individuals whose neural connections rapidly change in response to stimuli would be expected to more effectively process information relative to individuals with more slowly adapting neural connections. In turn, more rapidly adapting neural connections would facilitate more rapid and/or effective problem solving. Just as the development of cognitive skills from infancy to adulthood is coincident with the development and elaboration of neural connections, it is plausible that ongoing plasticity in existing connections would mediate new learning and intelligent behavior throughout the lifespan. Moreover, this account provides a neural mechanism underlying variation in *g* where individual differences in brain-wide neuroplasticity could account for the fact that individuals with highly developed cognitive abilities in one domain are also highly developed in another (Garlick, 2003).

The notion that neural plasticity is critical to learning and adaptive behavior is of course not new. Rather, these ideas trace back to iconic figures in the fields of neuroscience and neuropsychology (Ramon y Cajal, 1904; Hebb, 1949). The above framework of customizability is even explicitly acknowledged to be an extension of Hebb’s initial hypothesis which related synaptic plasticity to learning (Mercado, 2008). Hebb’s classic theory of cell assembly formation provides a basis by which neurons increase their efficiency as a functional unit. It postulated that when one neuron consistently causes another to fire, its efficiency in exciting the second cell increases. Thus, the two cells comprising the “network” exhibit plasticity and become a more efficient unit through repeated co-activation. Clearly, this model was an apt predecessor to contemporary models in which synaptic plasticity via long-term potentiation (LTP) is hypothesized to be a primary neural mechanisms underlying learning (Morris, Anderson, Lynch, & Baudry, 1986). As this and other mechanisms (e.g. hippocampal neurogenesis) have been related to learning (Gould, Beylin, Tanapat, Reeves, &

Shors, 1999), it follows that the neural processes underlying experience-dependent plasticity might also underlie individual variation in intelligence.

Electrophysiological techniques possess natural advantages for studying neuroplasticity within the constraints of most human psychology experiments. Through the use of EEG or MEG, researchers can potentially measure subtle changes in neural dynamics over time or stimulus exposure as they occur within the organism. Due to their superior temporal resolution, it is possible to quantify electrophysiological indices of neural plasticity in single experimental sessions, such as change in trial-to-trial response variability. As such they provide excellent tools for examining the relation between neural plasticity and intelligence.

Early EEG research programs which shed light on the relationship between neural plasticity and intelligence utilized the ERP as a proximal means to quantify neural plasticity. Although newer methods are increasingly supplementing ERP research, some of the most compelling data on this topic were originally obtained using relatively simple methodology

In one notable study, Schafer (1982) studied groups of adults with mental retardation and healthy adults with IQs ranging from average to very superior. The author obtained participants' average auditory evoked response to a series of fifty auditory clicks under three different stimulation conditions. First, they employed a control condition in which the clicks were delivered at regular two-second intervals in order to obtain each participant's average amplitude. In the second condition the subjects used a button press to "randomly" self-administer a click every several seconds. This second series was recorded and then played back for the third condition which was intended to represent a random presentation condition. The self-administered series was hypothesized to elicit an expectancy effect since the subjects were themselves controlling the administration of the clicks. The author examined the difference in evoked response amplitude across the three conditions and observed that normal adults exhibited larger than average amplitudes to clicks during the random condition and smaller than average amplitudes during the expectancy condition. This effect was not observed in individuals with mental retardation. The finding that healthy adults exhibit greater than average evoked responses to unexpected stimuli but smaller than average responses to expected stimuli suggests that their brains marshal greater resources to deal with unexpected stimuli, while they conserve resources when stimuli are predictable.

Next the author calculated the ratio of the evoked response amplitudes from the random condition over the expectancy condition to obtain a measure of “neural adaptability” in the healthy adults. When the relationship between neural adaptability and IQ was investigated it revealed a correlation of r = .66 in the healthy sample; a result which increased to r =.82 when corrected for the attenuated IQ range in the sample. Thus, healthy adults exhibit an expectancy effect whereby the strength of their neural responses decrease in amplitude to expected relative to unexpected stimuli. In addition, those subjects with the greatest evoked response amplitude discrepancies between expected and unexpected stimuli obtained the highest IQ scores.

The same author also developed a second, conceptually related measure which was intended to quantify habituation of the ERP (Schafer, 1985). Again, he had subjects relax in a chair and listen to auditory clicks while their EEG was recorded. Like the neural adaptability effect, he observed an attenuation of the ERP amplitude to repeated clicks. Unlike the previous study however, in this experiment auditory clicks were delivered at regular two second intervals. The percent difference between the average amplitude of the “N1-P2-N2 excursion” between the first and second blocks of 25 trials was calculated as the habituation index of the ERP. An examination of the relationship between the habituation index and performance on the WAIS revealed a positive correlation of r = .59, which rose to r = .73 when corrected for attenuation due to restricted range. In addition, when the method of correlated vectors was applied to the vector comprising the *g*-loadings of the WAIS subtests and the vector comprising their correlations with the habituation index, it was found that the two vectors correlated r = .80, while the rank order correlation between the vectors was r = .77. In other words, the more *g*-loaded each subtest was, the stronger its correlation with evoked potential habituation. This indicates that differences in neuroplasticity in the form of the habituation index are strongly related to differences in measured intelligence.

Basic research examining cortical experience-dependent plasticity also supports the view that experience modifies evoked responses. One study compared evoked responses between adult rats raised in standard laboratory cages versus those temporarily moved to naturalistic environments (Polley, Kvasnak, & Frostig, 2004). The authors observed a 46% reduction in single-whisker somatosensory evoked response amplitude as well as a 46% spatial contraction of cortical receptive fields in rats moved to naturalistic environments, compared to control animals. It was found that individual receptor fields no longer functionally overlapped, and the authors argued that the reduction of the evoked response resulted from the spatial differentiation of the whisker’s receptive field. These findings suggest that electrophysiological responses exhibit plasticity in the form of amplitude attenuation and increased spatial specificity following novel stimulus exposure.

Further pursuing the link between experience and change in electrophysiological measures in humans, one study investigated change in alpha ERD before and after training and its association with IQ. In that report twenty-seven adult males with IQ scores ranging from low average to very superior completed parallel forms of a multiple choice figural reasoning task while their EEG was recorded over two experimental sessions (Neubauer, Grabner, Freudenthaler, Beckmann, & Guthke, 2004). Item complexity was manipulated during the experimental tasks. During the interval between EEG sessions, participants were trained on a similar figural task during which they were given feedback for correct and incorrect responses. As they mastered the task, the difficulty of subsequent items was increased. The authors observed that during session one the higher IQ group exhibited non-significantly greater ERD relative to their lower IQ counterparts. Conversely, during session two more intelligent participants showed generally decreased alpha ERD which was significant over frontal regions. Tests of item solution rates indicated that complexity had been manipulated successfully, while EEG results showed that item complexity interacted with region such that increasing complexity resulted in greater ERD at posterior but not frontal sites. Difference measures between sessions showed that more intelligent individuals exhibited greater ERD decreases from session one to session two, which was interpreted as signifying that more intelligent individuals received greater benefit from training than their lower IQ counterparts. Overall, the authors argued that their results supported the neural efficiency hypothesis in that after training higher IQ subjects exhibited relatively less cortical activation during task performance.

Last, work on neuroplasticity has also been done relating neurofeedback training to change in electrophysiological responses and cognitive performance (Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005a). The EEG experiment involved alternating sessions of mental rotation task performance and individualized alpha and theta band neurofeedback training. In the experimental sessions, participants performed a modified version of a German intelligence scale subtest which requires mental rotation and comparison of target and probe dice. Neurofeedback training involved viewing an array of six colored squares corresponding to frontal and parietal EEG electrodes. Participants were informed that the squares colors changed according to their brain activity and were instructed to try and modulate the squares' colors, which variously corresponded to increases in alpha or theta activity. Based on their ability to modulate their ongoing EEG alpha and theta power, participants were then classified as responders or non-responders to neurofeedback training. The effect of neurofeedback on task performance was then analyzed for alpha and theta responders and non-responders separately

Results indicated that baseline cognitive performance and EEG power did not differ between alpha or theta responders or non-responders. However, it was observed that only successful alpha neurofeedback responders exhibited performance improvements on the mental rotation task, and that these performance increases were associated with increased pre-stimulus alpha power during the mental rotation task. Ratings of successful alpha neurofeedback training were correlated with improved task performance across all subjects, although significant performance improvements were not observed for the other groups. Thus, only those individuals who were most able to modulate their ongoing neural responses exhibited performance improvements. While this finding is confounded with differences in response to neurofeedback training, it nonetheless suggests a positive relationship between real-time EEG neuroplasticity and cognitive performance. Although a full assessment of intellectual ability was not performed, the results suggest the hypothesis that the greater neuroplasticity exhibited by alpha responders underlies not only their improved performance but also higher IQs in those same individuals.

Overall, the electrophysiological literature demonstrates that indices of neuroplasticity such as expectancy-related amplitude suppression, ERP habituation, training-related ERD reduction, and neurofeedback-related power increases are all associated with greater intelligence or improved task performance. Thus, there is compelling evidence to suggest a relationship between electrophysiological measures of neuroplasticity and intellectual ability. In light of the behavioral adaptability included in many conceptions of intelligence, it is appropriate to more fully examine this relationship. Also, recent advances in electrophysiology such as time-frequency analyses enable examination of more complex phenomena such as trial-to-trial response variability and phase relationships. These techniques provide more sophisticated ways examine neural dynamics, and can point to specific neural mechanisms which can be addressed in basic research. At the same time, an examination of the literature reviewed above indicates a relative dearth of this type of neuroplasticity research on human intelligence. While numerous studies have been conducted which examine structural brain correlates of intelligence, fMRI and PET techniques have difficulty resolving the trial-to-trial neural dynamics which may underlie rapid neuroplasticity (Romero, McFarland, Faust, Farrell, & Cacace, 2008). Thus, given the gaps in our current knowledge and recent technological advances, electrophysiological studies of neuroplasticity and intelligence represent a promising and new direction for intelligence research.

Current Study

Preliminary data collected at the MIND Research Network revealed noteworthy patterns of neural plasticity in human subjects across distinct experimental tasks (Weisend et al. unpublished data). First, it was found that when individuals were repeatedly exposed to a visual stimulus in an experimental session, the relative portions of the evoked and induced activity in their MEG data appeared to change systematically. Specifically, in four subjects evoked activity between the alpha and gamma frequency bands (here 8-40 Hz) was found to increase following repeated exposures to the stimulus while the induced activity in the same frequency range decreased. Moreover, this effect occurred not only in a single experimental session as described above, but also occurred across days in the alpha band in eight subjects. Currently, the specific mechanisms underlying such neuroplasticity in evoked and induced activity are controversial (Conrad, Giabbicioni, Muller, & Gruber, 2007).

For example, visual repetition priming studies using meaningful and scrambled pictures have observed respective increases and decreases of parieto-occipital induced gamma power to repeatedly presented scrambled -“unfamiliar” versus meaningful stimuli (Gruber, & Muller, 2005). The authors argue that the reduction of induced activity to meaningful stimuli signifies sharpening of the “conceptual” network which processes a meaningful versus meaningless stimulus; whereas the increasing induced response to the scrambled stimuli signifies the formation of a qualitatively different network for processing unfamiliar material. Hence they claim these findings signify the existence of conceptual networks for processing familiar stimuli versus other networks for processing unfamiliar stimuli.

One alternative to this view is the suggestion that although unique combinations of synapses and cells within "unfamiliar stimulus networks" may initially create increasing induced activity; ultimately, sufficient repetitions of the stimulus should result in the sharpening of that network as well. Thus, rather than the unfamiliar network exhibiting a linear increase and plateau in induced activity, that network should ultimately begin to exhibit decreasing induced (and increasing evoked) activity to repeated stimulus presentations.

With respect to the current study, the systematic increase in evoked activity and concomitant decrease in induced activity is nonetheless indicative of some type of experience-related change in neural networks, regardless of whether the change in evoked and induced activity is mediated by one or two distinct neural networks. A change in the ratio of evoked to induced activity over time might still be considered a measure of neuroplasticity at the electrophysiological level even if the cellular mechanisms are yet undetermined. Notably, the finding that the reliable phase-locked responding of the brain generally increased across stimulus exposures, while the non-phase-locked response components decreased is evocative of previous work on ERP habituation. A similar effect has also been observed in right-hemisphere theta band (4-8 Hz) activity during performance of a transverse patterning task in other preliminary data (Weisend et al., unpublished data).

The early work on ERs indicates that EEG habituation to simple stimuli is positively correlated with IQ. Moreover, this work demonstrated that the vector of each test's correlation with habituation is correlated with the vector of their *g*-loadings, implying a robust relationship with the neural variables most directly responsible for general intelligence. The preliminary MEG data described above suggest that both repeated exposure to a simple visual stimulus and performance of a transverse patterning task results in a relative enhancement of evoked power or activity (EA) relative to induced power (IA) over time. Following from these data then, it is hypothesized that individual variation in the rate of enhancement in the EA/IA ratio over repeated stimulus exposure or task performance is correlated with variation in intelligence. More specifically, it is hypothesized that differences in individual neuroplasticity observable during the course of an EEG experiment relate to an organism's capacity to develop intelligent behavioral repertoires as manifested in observed differences in IQ scores.

Also, in his account of the hypothesized relationship between neuroplasticity and intelligence, Mercado (2008) notes that the relationship is difficult to test due to the lack of a straightforward way to quantify neuroplasticity across individuals. It is hoped that quantification of change in the EA/IA ratio across trials will provide such a measure. The current study endeavors to extend prior work on EEG habituation and IQ by testing the IQ relationship of the EA/IA enhancement effect, and provide clues as to the mechanisms underlying it.

Methods

Participants

Study participants were recruited from an existing database of individuals who had participated in prior studies of intelligence and creativity (Jung et al., 2010a, Jung et al., 2010b), and from an advertisement placed on an internet classified website. All study procedures were reviewed and approved by the University of New Mexico Health Sciences Center Human Research Protections Office. Participants were screened for significant prior neurological or psychiatric illnesses, and to ensure they had normal or corrected to normal vision. Participants were compensated $15 per hour for their time. The total time for all experimental procedures was between 3 and 5.5 hours, depending on whether participants had completed cognitive testing during the prior study.

Stimuli

Stimuli consisted of 411 unique centrally presented line drawings taken from the larger set of 520 stimuli developed by the Center of Research on Languages International Picture Naming Project (Bates et al., 2003). The stimuli consist of black line drawings on a white background. Subsets of these stimuli have been widely utilized in fMRI research (Stark & Squire, 2000) and EEG research on stimulus repetition (Gruber, & Muller 2005). The complete set has been used in several fMRI studies to date (e.g. Saccuman et al., 2006). The specific subset was selected on the basis of comparable visual complexity as assessed by digital file size, and comparable naming reaction times (Szekeley et al., 2004). Each participant was exposed to a total of 361 stimuli from the subset of 411. A psuedo-random number generator was utilized to select a unique stimulus set for each participant.

Experimental Session and Tasks

Each subject was seated in a sound and light attenuated room for EEG acquisition. The black and white line-drawings comprising the stimuli were presented on a larger gray background on a 45.6 cm monitor located 150 cm in front of subjects. The gray background was implemented to reduce eye fatigue. Stimuli comprised 3.2 by 3.0 degrees of visual angle top to bottom and left to right, respectively. The experimental condition consisted of a four-minute period of eyes-closed rest, followed by three experimental conditions which lasted between 11-18 minutes each, in turn followed by a four minute eyes-open rest period, resulting in approximately 50 minutes for EEG data collection. The order of conditions was counterbalanced across participants in an ABC and BAC design.

Visual Tasks

Condition A- Repeated Stimulus.

Condition A was a "visual oddball" task consisting of 240 trials of presentation of the same visual stimulus ("Repeated" stimulus), and 48 trials of visually comparable novel stimuli in a single experimental session. Particular experimental stimuli for the repeated stimulus conditions were chosen by a random number generator. All but two participants were tested using different repeated stimuli, which occurred due to an error. Individual trials were separated by a variable inter-stimulus interval lasting between 1000 and 2500 milliseconds.

Subjects were instructed to fixate on a central cross on the screen in order to minimize eye movements. Stimuli were exposed for 1000 milliseconds on each trial. Another 48 novel stimuli of comparable visual complexity representing the "oddball" stimuli were used to ensure participants visual attention to all study stimuli. Thus, repeated and novel stimuli were presented at an 80/20 ratio. Prior to the session, participants were instructed to press a response button as quickly as possible to each novel stimulus. At the end of each 50-trial block participants were given an opportunity to rest their eyes prior to continuing at the time of their choosing, which they indicated with a button press.

Condition B-Once-Viewed Stimuli.

The second counterbalanced condition consisted of 240 trials of novel visual stimuli derived from the larger stimulus set and 48 presentations of the repeated visual stimulus from Condition A. These stimuli and the novel stimuli from Condition A are henceforth termed "Once" (e.g. once-viewed stimuli) for clarity. Prior to scanning in this condition, participants were instructed to press a button as quickly as possible when they saw the Repeated stimulus. Due to counterbalancing, all participants were briefly shown their particular repeated stimulus prior to beginning either counterbalanced condition. Condition B contained the same inter-stimulus intervals, stimulus exposures, response trials, and rest opportunities as the prior condition.

Condition C-Novel, Once-Viewed, and Repeated Stimuli.

A third condition was included to facilitate follow-up tests of behavioral repetition priming effects. This condition was comprised of 120 presentations of the original Repeated stimulus from Condition A, 120 trials of previously seen Once stimuli (seen only once across either Conditions A and B), and an additional 120 Novel stimuli randomly intermixed. Participants were instructed to press one of three buttons as quickly as possible indicating whether they have seen each stimulus once, more than once, or never. As in prior conditions, Condition C utilized the same inter-stimulus intervals, and rest opportunities; however, stimulus exposures were increased to 1500ms to allow participants sufficient time to determine and make their response.

Cognitive Testing

Following EEG data collection, participants without prior testing (n = 15) were administered the Picture Completion, Vocabulary, Digit-Symbol Coding, Similarities, Block Design, Information, Arithmetic, Digit Span, Symbol Search, , Letter-Number Sequencing, and Object Assembly subtests of the Wechsler Adult Intelligence Scale-III (Wechsler, 1997). Two participants underwent cognitive testing prior to EEG data collection due to scheduling considerations. All participants were administered the Picture Arrangement subtest from the WAIS-III, as well as the Judgment of Line Orientation and Hooper Visual Organization tests. One participant did not complete the Object Assembly subtest, though was ultimately excluded due to excessive blink artifacts. Scaled scores on the Comprehension subtest were estimated based on the average scaled scores of the Vocabulary, Similarities, and Information subtests. Individual estimates of intellectual ability based on FSIQ were obtained from the resulting scaled scores. All WAIS-III subtest scaled scores were also entered into a principal components analysis (without rotation) in order to obtain the first principal component as an index of general intelligence (Jensen, 1998). Individual subtest-factor loadings with this component were retained for use in correlated vectors analysis.

Electrophysiological Recordings

Individual EEG data was obtained for each participant using the 128-Channel Biosemi Active-Two amplifier System (Metting van Rijn, Peper, & Grimbergen, 1990), located at the Mind Research Network Imaging Center at the University of New Mexico Health Sciences Center Campus. The nose-tip was chosen as the offline reference. Data were sampled on-line at 1024 Hz with a 0.16-100Hz bandpass filter. Vertical and horizontal eye movements, as well as EKG were monitored via 6 additional channels respectively placed above and below the left eye, at the external canthi of each eye, and superior to the clavicles bilaterally.

EEG Data Reduction and Analysis

Study data were processed using a combination of EEGLAB processing routines (Delorme and Makeig, 2004) running in MATLAB 7.8.0 (R2009a, Natick, MA), and MATLAB routines developed by our group and for the study specifically. EEG data were loaded into EEGLAB referenced to the nose-tip channel and down sampled to 512 Hz to speed further processing. Data were bandpass filtered 1-50Hz to correct for low-frequency artifacts and 60 Hz line noise. Continuous data was divided into epochs time-locked to stimulus presentation. Repeated and Once-viewed stimuli in their respective visual (i.e. non-response) conditions were divided into 2 second epochs from -1000 to 1000 seconds post stimulus presentation. Response trials (i.e. 'targets' in the oddball nomenclature) were epoched from -1000 to 1500 milliseconds post-stimulus for trials containing correct responses.

Artifact Rejection

Individual epochs of all trial types were normalized to an average baseline period of -1000 ms pre-stimulus for purposes of artifact rejection. Preliminary visual inspection of the VEOG data indicated large numbers of ocular artifacts due to blinks, especially in the period after 500 milliseconds post-stimulus in several subjects. In order to minimize the number of epochs lost due to contamination by blinks, trials were rejected based first on whether the VEOG channels contained high-amplitude artifacts in the period from 1000ms pre-stimulus to 500ms post-stimulus. The subsequent 500ms post-stimulus period was not utilized for further analysis. This analysis epoch is comparable to similar studies of visual priming (e.g. Gruber and Muller, 2002). The absolute value of the baseline-corrected trials was then taken, and trials containing amplitudes exceeding 60 microvolts between -1000 and 500ms post-stimulus were rejected via an automated script. Individual EEG channel data epochs were similarly subjected to threshold-based rejection if they contained values exceeding 100 microvolts in the entire epoch. Individuals channels were rejected if the absolute value of the average sample contained therein exceeded three times the standard deviation of all 128 channels across each individual subject. This procedure resulted in rejection of a single channel in a single participant from among 10-posterior channels utilized to derive a ten-channel average (Oz, Pz, and 8 channels corresponding to or variously approximating O1, O2, P3, and P4 in the International 10-20 system). This participant's data was ultimately removed from further analyses due to excessive blink artifacts. Following completion of the artifact rejection stream, the identified set of artifact-free EEG data was saved prior to baseline-correction and subjected to time-frequency analysis.

Time-Frequency Analysis

The artifact-free epochs were baseline corrected via the frequency-specific uniform windowing (FSUW) technique developed by M. P. Weisend et al. (personal communication, October, 2008), using a uniform window of 240 ms. Like conventional rectangular baseline-interval correction, FSUW utilizes a uniform pre-stimulus epoch length for deriving average baseline activity for each frequency bin present in the data. This technique differs from the conventional approach in that the baseline interval is scaled via a function of half each frequency's wavelet length, thereby minimizing smearing of signal into the pre-stimulus period, which can occur when rectangular baseline intervals are utilized for time-frequency analysis. This permits sufficient resolution to adequately baseline-correct low frequencies (e.g. 4 Hz).

Time-frequency analyses of evoked and induced activity were obtained via wavelet transformation (specifically, S-transform; Stockwell, 1996) implemented by Weisend and colleagues at The Mind Research Network. The S-transform represents an extension of the continuous wavelet transform. These methods permit extraction of the time-varying magnitude of the EEG signal at each frequency present in the data, which can subsequently be depicted as a joint time-frequency representation. This is accomplished by convolving the single trial data (or ERP) with a family of wavelets whose width varies as a function of the convolved frequency. This process results in an approximation of the instantaneous power of the signal in a given frequency bin at a given time. In this way, single –trial total activity (TA) was calculated by serially convolving each sample within each respective frequency bin, trial, and channel with a frequency-specific wavelet, where the value of each sample is expressed in microvolts squared. The average of single-trial TA was in turn obtained giving average TA. Average EA over trials was obtained by subjecting the ERP to the same procedure and removing the average power in the baseline interval from the entire epoch. Average IA was calculated by subtracting the non-baseline corrected EA from TA, and subtracting the average IA in the baseline interval from the entire epoch.

Overall EA/IA.

EA/IA power was calculated time-locked to stimulus presentation in Conditions A and B for all experimental blocks from all 128 EEG channels. To reduce the number of analyses an average of 10-posterior channels was utilized for examining effects of stimulus exposure and repetition on EEG variables. Specifically, this measure was derived from the average of channels corresponding to Oz, Pz, and 8 channels variously identical with or in close proximity to P3, P4, O1, and O2 in the international 10-20 system. This analysis strategy is well-represented in studies of visual priming (Gruber and Muller, 2002). Overall spectral power was obtained for EA/IA in both conditions divided into the first and second blocks of 40 artifact-free trials, and into the first four blocks of 20 artifact-free trials. The highest EA and IA response, their latency, and frequency in Hz were separately extracted from the overall data from 2-50 Hz in 100 frequency bins of 0.5 Hz width, and from 0-500 ms post-stimulus.

Alpha EA/IA.

Visual inspection of the overall grand means indicated post-stimulus peaks at approximately 10Hz across both Blocks and Conditions. In order to investigate potential repetition and stimulus effects within this frequency range alpha band power was extracted from the average 8-12Hz power in the period from 50-450ms post-stimulus for EA and IA in both conditions.

Gamma EA/IA.

Based on prior literature showing an induced gamma band response reaching a maximum between 260-380 ms post stimulus in response to visual stimuli (Gruber and Muller, 2002) grand means of induced activity across conditions were examined for the 22 participants for whom 80 artifact-free trials were available. Visual inspection revealed a maximum induced gamma peak at approximately 285ms post-stimulus in the induced activity for both conditions (Figures 7 and 8). Based on this observation in the grand means, evoked and induced gamma band activity was extracted by taking the peak gamma amplitude

200-400ms post stimulus from 30-50 Hz. The peak gamma amplitude was taken within this window.

Statistical Analyses

Following pre-processing and spectral analysis, physiological and other study data were analyzed in SPSS 15.0. Primary study hypotheses pertaining to EA/IA ratios were tested by means of repeated measures ANOVAs (2x2) where block had two levels each containing 40 trials (Block), across the Repeated and Once stimulus conditions (Condition). Exploratory follow-up tests were conducted using 20-trial blocks in some instances to further delineate effects of Block. Huynh-Feldt adjustments for violations of the sphericity assumption were utilized in follow-up analyses containing more than two within-subjects levels (Luck, 2005). Secondary analyses were conducted to investigate effects of EA and IA alone in the alpha and gamma bands. Finally, correlation analyses were utilized to identify dependent measures which significantly related to general intelligence for use in correlated vectors analysis. Directed significance tests were used to obtain p-values for correlations which were hypothesized *a priori.* For those tests, an asymmetrical ratio of the hypothesized critical region to alpha value of 0.8 was used to obtain directed p-values (Rice and Gaines, 1994.).

Results

Demographic Information

Thirty individuals (19 men, 11 women) aged 18 to 30 participated in the study. Participants had between 11 and 18 years of formal education (Mean13.9, SD 2.162), and were on average between 22 and 23 years old at the time of cognitive and electrophysiological testing. Due to excessive artifacts in their EEG data, eight participants were excluded from most analyses (4 men and 4 women). Three of the eight participants were found to have fewer than 80% artifact-free trials in one or both conditions and were not examined further. One of the eight participants (a female) was doubly excluded due to a missing Object Assembly Subtest. One other participant had a bad channel among those included in the ten-channel average. Thus, 22 participants were utilized for primary analyses, and 25 had sufficient valid data for secondary analysis pertaining only to Block 1 (see EEG data validity section below). Excluded participants were on average 21 years old at the time of cognitive and EEG testing, and had 14.6 years of education. Excluded participants did not significantly differ from the larger sample with respect to intellectual ability ($t(27) = -1.657$, $p = .109$), nor with regard to education ($t(27) = 1.014$, $p = .320$). Educational information was not available for one participant. Table 1 presents demographic information for the study participants.

Table 1

Participant Demographics (n = 22)

	Mean	SD	Minimum	Maximum
Age at EEG testing	23.00	3.91	18.00	30.00
Age at Cognitive Testing	22.72	4.04	18.00	31.00
Education[a]	13.71	2.03	11.00	18.00
Sex	1.31	.48	1.00	2.00

[a] (n = 21)

The average WAIS-III Full-Scale IQ (FSIQ) score for the entire sample was 113 (15.18 S.D.; range 88-138). Tables 2 and 3 list the descriptive statistics for the WAIS-III index scores, and subtest scaled scores. Male and female participants did not differ with respect to FSIQ ($t(20) = -1.305$, $p = .207$) or g ($t(20) = -1.636$, $p = .117$). Figure 1 depicts the frequency distribution of the sample FSIQ scores.

Table 2

WAIS-III Full-Scale Intelligence Quotient (FSIQ) and Index Standard Scores

(n = 22)

	Mean	SD	Minimum	Maximum
FSIQ	113.23	15.19	88.00	138.00
Working Memory (WMI)	109.18	14.29	86.00	136.00
Verbal Comprehension (VCI)	116.64	17.33	88.00	140.00
Processing Speed (PSI)	105.41	9.16	91.00	120.00
Perceptual Organization (POI)	111.36	13.99	88.00	133.00

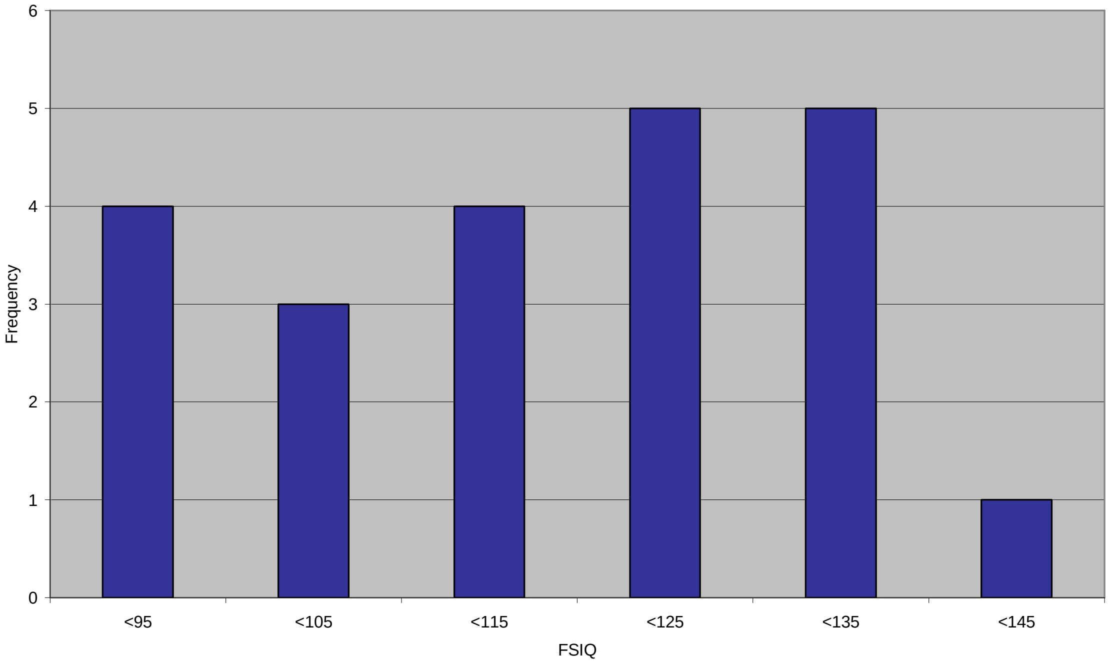
Table 3

WAIS-III Subtest Scaled Scores (n = 22)

	Mean	SD	Minimum	Maximum
Picture Completion (PC)	11.64	3.02	7.00	18.00
Vocabulary (VO)	14.18	3.30	9.00	19.00
Digit Symbol Coding (CD)	10.50	2.30	7.00	15.00
Similarities (SC)	12.05	3.43	5.00	17.00
Block Design (BD)	11.86	2.62	7.00	17.00
Arithmetic (AR)	11.45	2.72	6.00	17.00
Matrix Reasoning (MR)	12.14	2.68	8.00	16.00
Digit Span (DS)	11.36	2.95	7.00	19.00
Information (IN)	12.42	3.30	6.00	17.00
Picture Arrangement (PA)	10.55	2.92	6.00	15.00
Comprehension[a] (CO)	12.29	2.49	8.20	15.80
Symbol Search (SS)	11.55	2.18	8.00	15.00
Letter-Number Sequencing (LN)	11.91	3.12	6.00	19.00
Object Assembly (OA)	10.36	2.85	6.00	18.00

[a] Estimated Comprehension Scaled Score

Figure 1. Frequency Distribution of FSIQ scores (n = 22)



Extraction of the g Factor

Principal components analysis of the 13 WAIS-III subtest scaled scores and the estimated Comprehension subtest score yielded a first three components which cumulatively accounted for 65% of the variance between subtests, and a first component which accounted for 44% of the subtest variance (first component eigenvalue = 6.162, second component eigenvalue = 1.823). Thus, this first factor was utilized as the index of *g* in the current study. Factor loadings of the 14 subtests are depicted in Table 4.

Table 4

WAIS-III Factor Loadings on the First Principal Component (n = 22)

Subtest	Factor Loading	Subtest	Factor Loading
CO [a]	.960	LN	.669
VO	.848	PA	.572
IN	.830	DS	.532
SI	.815	CD	.463
MR	.754	OA	.374
BD	.724	PC	.364
AR	.713	SS	.152

[a] Estimated Comprehension Scaled Score

Experimental Task Performance

Participants achieved a high level of accuracy when responding to oddball target stimuli, indicating good attention to the task. On average, participants missed or incorrectly responded to less than one out of the 48 targets in the two stimulus conditions. Average reaction times for the Once stimuli in the Repeated visual condition was 495.17 ms (79.56 SD), and 474.29 ms (66.66 SD) for the Repeated stimuli in the Once visual condition. Paired samples t-tests indicated that participants were marginally faster to respond to Repeated stimuli relative to previously unseen Once stimuli in their respective target conditions ($t(21) = 1.966$, $p = .063$).

In the third behavioral condition participants displayed the fastest reaction times for Repeated stimuli (mean RT = 622.64 ms, 75.06 SD), followed by novel stimuli (mean RT = 915.03, 89.65 SD), and Once-viewed stimuli (mean RT = 949.69, 85.53 SD). The difference between Once and Novel reaction times was not significant ($t(21) = -1.608$, $p = .123$), though participants were significantly faster to respond to Repeated stimuli in the third condition relative to Once stimuli ($t(21) = -34.723$, $p < .000$) and Novel stimuli ($t(21) = -17.089$, $p < .000$). There was also a significant effect of Condition on participants' response accuracy (repeated measures ANOVA 3-levels of Condition, Greenhouse-Geisser corrected $F(1.456,30.573) = 55.274$, $p < .000$). Follow-up Paired-sample t-tests indicated that participants were significantly more accurate for Repeated stimuli than either Once or Novels, and were also significantly more accurate for Novel stimuli than Once. As the behavioral results disconfirm any linear effect of repetition on reaction time (i.e. participants required more time to respond to and were least accurate for the Once relative to the Novel condition) electrophysiological data from the Novel condition were not analyzed further in the current study.

Sample EEG Data Characteristics

Following artifact rejection and removal of the three datasets with fewer than 80% artifact free trials in either or both conditions, the overall dataset was examined to determine the minimum number of valid trials for analysis. As shown in Table 5, the remaining 27 participants had a minimum of 47 and 53 analyzable trials in the Repeated and Once Conditions, respectively. Thus, 40-trial blocks were selected as the lower-bound for analysis for a single block in either condition; and within this larger group, 22 participants had a total of forty valid trials in each block and condition. Hence, 40-trial blocks were chosen as the largest number of common trials for achieving optimal reliability for EA and IA analyses. In turn, twenty-trial blocks were adopted for purposes of further delineating any significant effects of observed in the larger blocks.

Table 5

EEG Data Validity (n = 27)

	Mean	SD	Range	Minimum	Maximum
Valid Rep Trials	143.48	58.80	193.00	47.00	240
Valid Once Trials	148.37	50.73	187.00	53.00	240

Electrophysiological Spectral Analyses

Grand mean TFRs were obtained for the 22 participants who had sufficient numbers of artifact free-trials to compute two forty-trial blocks in each condition. As indicated in Table 6 the mean frequency of greatest EA across Block and Condition was 6.37 Hz (3.03 SD), while the mean frequency of greatest IA was 5.93 (3.19 SD). The mean latency of peak EA was 261.63 ms and mean latency for peak IA was 383.25 ms (see Table 7). Figures 2 and 3 depict the grand-mean TFRs for the Repeated and Once Conditions across Blocks. Although ERP analyses were not conducted in the present study, grand-mean ERPs are presented for completeness. Figure 4 depicts the study grand-mean ERPs for each Condition across blocks 1 and 2, in each of the ten channels that were later averaged. Figure 5 depicts ERPs from 10-channel grand-means for each block across conditions.

Table 6

Frequency of Peak Power by Block and Condition (n = 22)

EA				
	Mean	SD	Minimum	Maximum
Rep Frequency Peak EA1	6.84	3.08	2.00	12.00
Rep Frequency Peak EA2	6.66	3.02	2.50	10.50
Once Frequency Peak EA1	6.73	3.02	2.00	12.00
Once Frequency Peak EA2	5.25	2.99	2.00	11.00

IA				
	Mean	SD	Minimum	Maximum
Rep Frequency Peak IA1	5.36	3.44	2.00	13.00
Rep Frequency Peak IA2	6.93	2.98	3.00	11.50
Once Frequency Peak IA1	6.14	3.11	2.00	12.50
Once Frequency Peak IA2	5.30	3.22	2.00	10.50

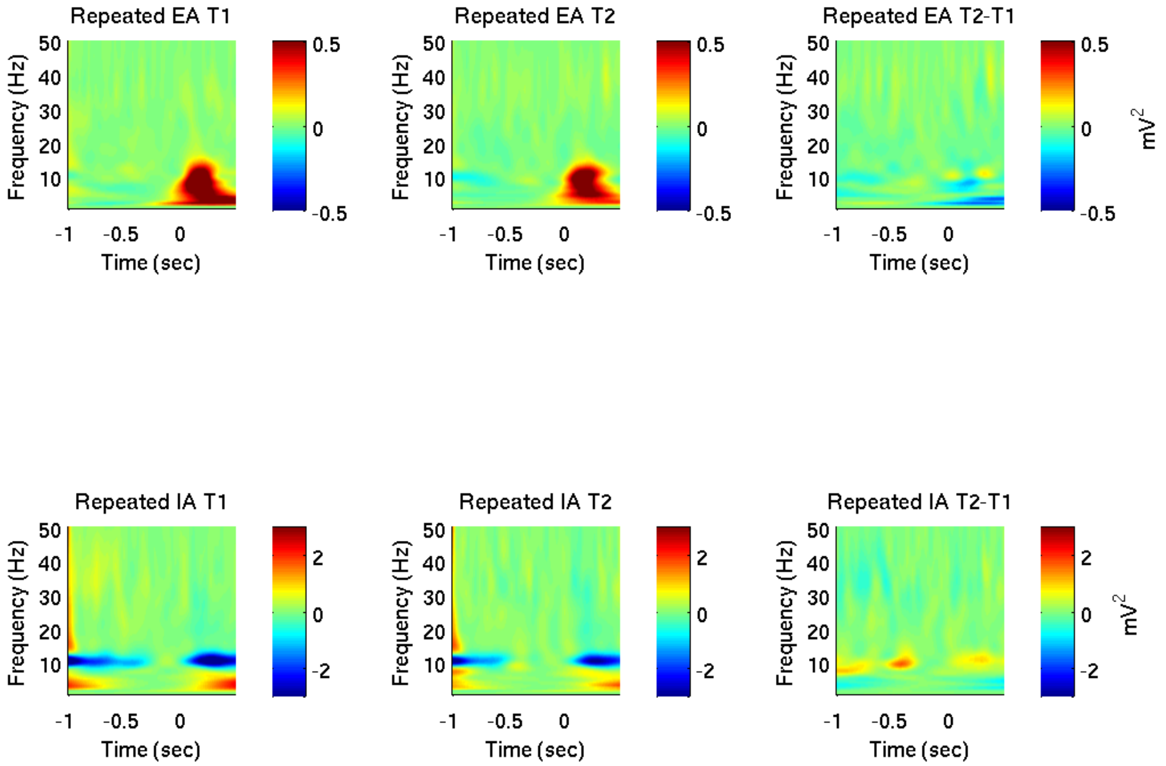
Table 7

Latency of Peak Power by Block and Condition (n = 22)

EA				
	Mean	SD	Minimum	Maximum
Rep Latency Peak EA1	238.98	100.33	140.63	500
Rep Latency Peak EA2	232.15	117.17	0	500
Once Latency Peak EA1	264.92	118.77	113.28	500
Once Latency Peak EA2	310.45	141.56	113.86	500

IA				
	Mean	SD	Minimum	Maximum
Rep Latency Peak IA1	424.71	129.06	0	500
Rep Latency Peak IA2	370.82	178.05	0	500
Once Latency Peak IA1	321.89	167.40	0	500
Once Latency Peak IA2	415.57	139.88	0	500

Figure 2. Grand Mean TFRs Repeated Condition



Repeated EA T1

Repeated EA T2

Repeated EA T2-T1

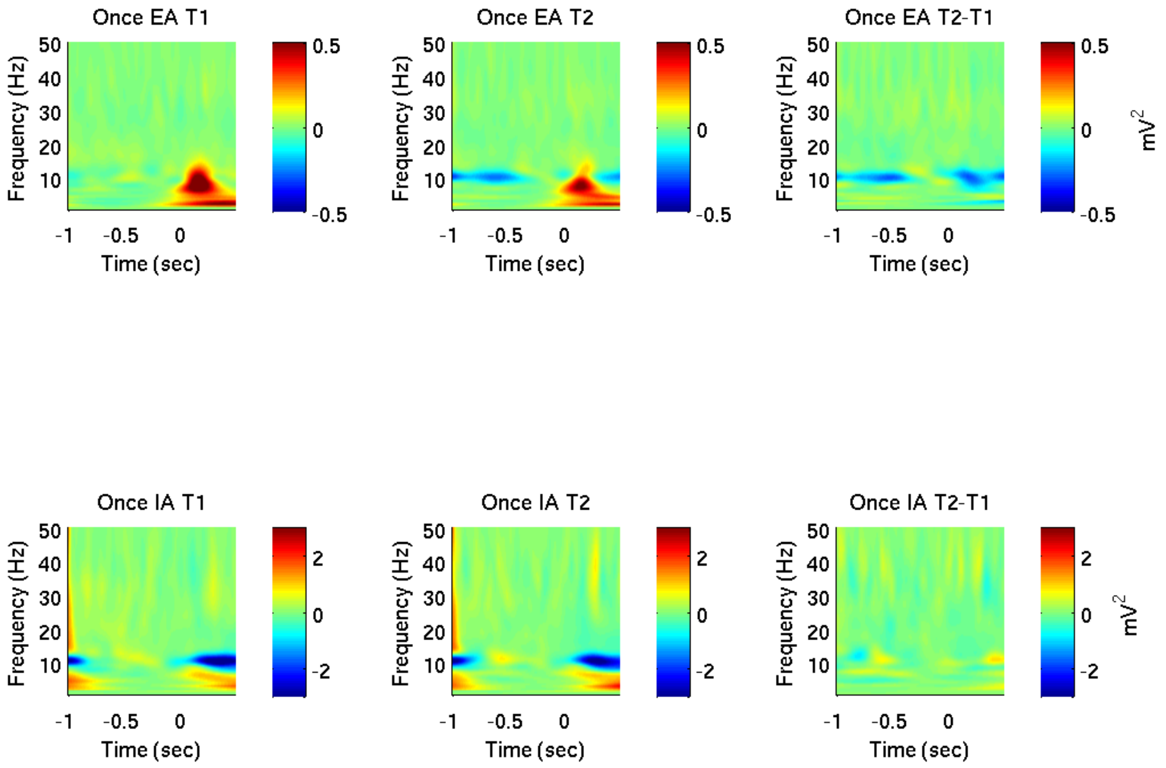
Repeated IA T1

Repeated IA T2

Repeated IA T2-T1

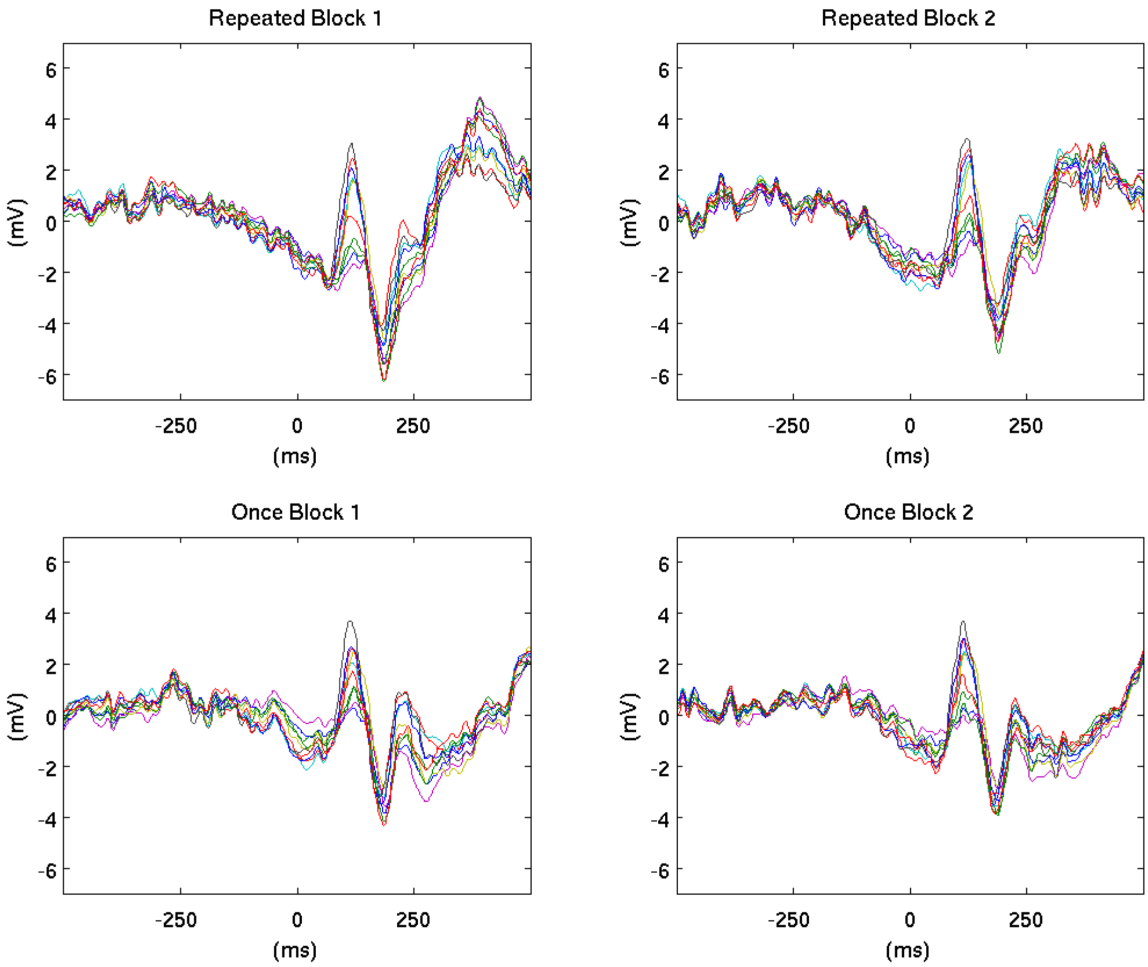
Grand Mean Ten-Channel Average (n = 22). Top row depicts EA at Blocks 1, 2, and their difference (2-1) from left to right. Corresponding IA blocks are depicted below. Baseline EA and IA was calculated using FSUW from 240 -0 ms pre-stimulus.

Figure 3. Grand Mean TFRs Once Condition



Grand Mean Ten-Channel Average (n = 22). Top row depicts EA at Blocks 1, 2, and their difference (2-1) from left to right. Corresponding IA blocks are depicted below. Baseline EA and IA was calculated using FSUW from 240 -0 ms pre-stimulus

Figure 4. 10-Channel Grand-Mean ERPs across Blocks and Conditions (n = 22)


Repeated Block 1

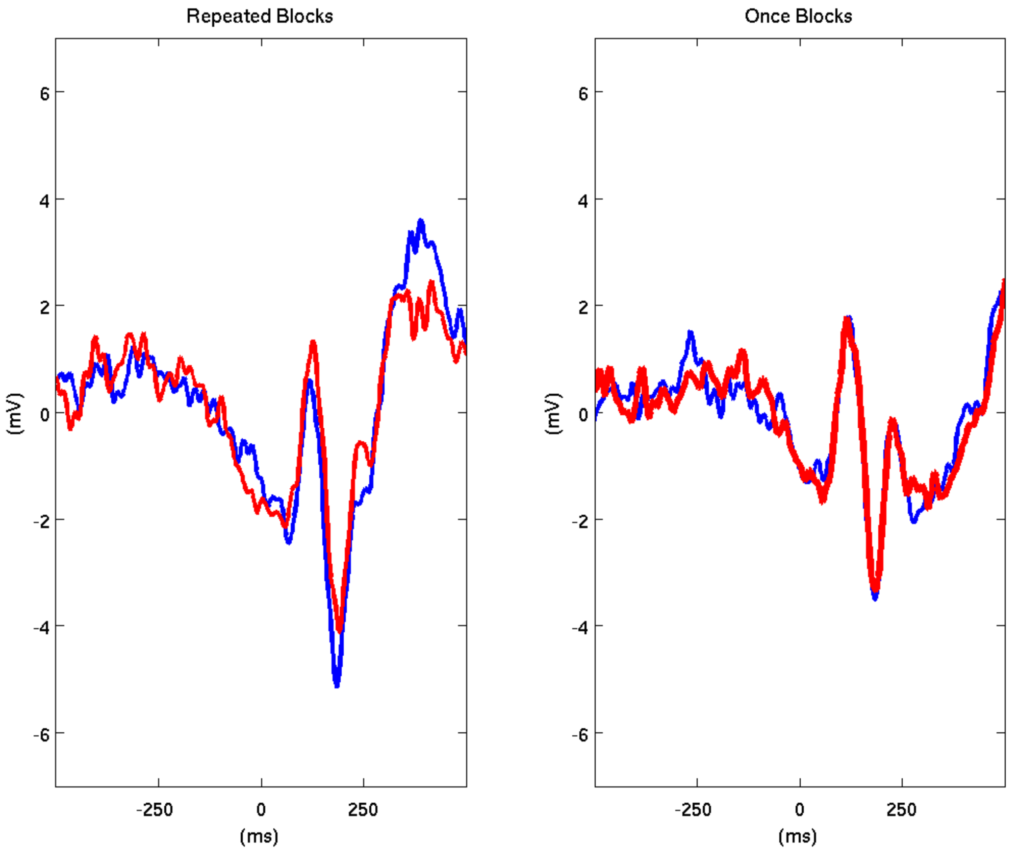
Repeated Block 2

Once Block 1

Once Block 2

Each ERP depicts the grand-means for each the 10-channels overlaid on one another. Epochs were -1000 to 1000 ms pre to post-stimulus. As excessive blink artifacts prevented analyses later than 500 ms post-stimulus, -500 to 500 ms pre to post-stimulus are shown.

Figure 5. Overall Ten-Channel Average Grand-Mean ERPs (n = 22)



Block 1 is depicted in blue, block 2 in red for each condition. Epochs were -1000 to 1000 ms pre to post-stimulus, -500 to 500ms pre to post-stimulus are shown.

Overall EA/IA 40-trial Blocks

Examination of the baseline-corrected grand mean TFRs suggested a decrease in overall EA and IA across 40-trial blocks in both the Repeated and Once Stimulus Conditions, as depicted in Figures 2, and 3, and Table 8.

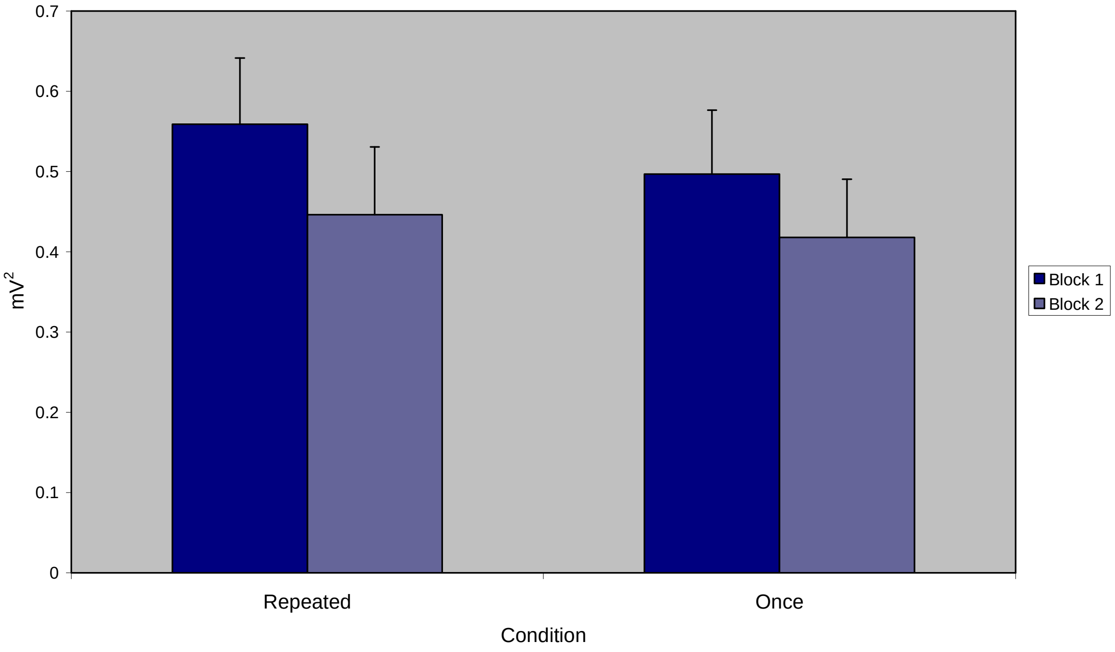
Table 8

Maximum Overall EA/IA Ratios 40-trial blocks (n = 22)

	Mean	SD
Overall Rep EAIA 1	.559	.387
Overall Rep EAIA 2	.446	.373
Overall Once EAIA 1	.497	.397
Overall Once EAIA 2	.418	.340

Consistent with this observation, a 2x2 repeated measures ANOVA of the overall ratio of maximum EA/IA across blocks (Block by Condition) revealed a small but significant main effect of Block ($F(1,21) = 4.559$, $p = .045$; partial eta squared = .178), with EA/IA ratio decreasing over trials in both conditions, as shown in Figure 6.

Figure 6. EA/IA Ratio



The main effect of Condition and the Block by Condition interaction were not significant, nor were the interaction effects when the general intelligence variable was entered into the model. Thus, the current study found support for an effect of stimulus exposure on the EA/IA ratio. Results did not find support for the hypothesized *increase* in EA/IA over time in the Repeated stimulus condition. Rather, EA/IA ratio significantly decreased over stimulus exposures in both conditions, suggesting a general habituation effect. Current results are hence in contrast to the increase in EA/IA ratio which was observed in single-session pilot data.

Pearson correlations between *g* and the four EA/IA ratios were positive, though only the correlation between Once EA/IA at block 2 was significant (*r*(22) = .431, *p* = .045 (two-tailed); all correlations average two-tailed p-value = .066). When tested via directed tests the correlation with *g* in the Repeated condition approached significance (Time 1 = *r*(22) = .39, *p* = .056), Time 2, *r*(22) = .36, *p* = .078), while the EA/IA ratio of both blocks of the Once condition were significant (Time 1, *r*(22) = .41, *p* = .048; Time 2, *r*(22) = .43, *p* = .035). Table 9 depicts the correlations between *g* and EA/IA ratio collapsed across conditions. Collapsing the forty-trial data across both blocks and conditions revealed a significant positive correlation with g (*r*(22) = .503, *p* = .017, two-tailed;R^2 = .25). Correlations with EA/IA ratio difference scores (i.e. Ratio of Block 2 minus the Ratio of Block 1) were not significant in either condition (all *p*s <.157; average *p* = .449). Thus, the primary hypothesis that change in EA/IA ratio in the Repeated condition would correlate with *g* was not supported.

Table 9

Correlations between General Intelligence and Overall EA/IA 40-trial Blocks Collapsed across Condition (directed tests, n = 22)

	General Intelligence	EA/IA1	EA/IA2
General Intelligence	1	**.411*** **p = .046**	**.473*** **p = .021**
EA/IA 1		1	.688** p = .000
EA/IA2			1

Overall EA/IA 20-trial Blocks

A 4x2 repeated measures ANOVA of the overall ratio of maximum EA/IA across 20-trial blocks (Block by Condition) revealed no significant main effects or interactions, either with or without entering general intelligence into the model. However, examination of the cell means suggested a divergent effect between conditions across the first and second 20-trial blocks (see Table 10). Specifically, EA/IA ratio non-significantly increased over the first two blocks of the Repeated condition and decreased over the same interval in the Once condition. Although not significant, the direction of means is consistent with prior predictions.

Table 10

Maximum Overall EA/IA Ratios 20-trial blocks (n = 22)

	Mean	SD
Rep EAIA 1	.606	.510
Rep EAIA 2	.660	.402
Rep EAIA 3	.568	.505
Rep EAIA 4	.459	.386
Once EAIA 1	.587	.355
Once EAIA 2	.455	.326
Once EAIA 3	.547	.544
Overall Once EAIA 4	.463	.404

Again, several correlations between ratio scores and the general intelligence factor were tested and found to be positive and either significant or marginally significant (Blocks 2 and 3-Repeated Condition, Blocks 2-4 Once Condition). Two-tailed tests revealed several significant positive associations which are depicted collapsed across conditions in Table 11. Correlations between general intelligence and difference scores of ratios (Block 4 minus Block 1 and Block 2 minus Block 1) were not significant. Collapsing the twenty-trial EA/IA data across both blocks and conditions (given the absence of block or condition effects) revealed a significant positive correlation with g ($r(22) = .594$, $p = .004$, two-tailed).

Table 11

Correlations between General Intelligence and Overall EA/IA 20-trial blocks, collapsed across condition (two-tailed, n= 22)

	General Intelligence	EA/IA1	EA/IA2	EA/IA3	EA/IA4
General Intelligence	1	.279 p = .209	**.449*** **p = .036**	**.531** **p = .011**	**.468** **p =.028**
EA/IA 1		1	.283 p = .202	.394 p = .069	.454 p = .034
EA/IA2			1	.448 p = .037	.386 p = .076
EA/IA3				1	.289 p = .192
EA/IA4					1

Finally, given that IA was often found to be nearly an order of magnitude larger than EA (see Figures 2 and 3), correlations were tested between general intelligence and total power (comprised largely of power due to IA) to determine the importance of the contribution of EA to the present ratios. Correlation analyses examining total power across 40 and 20-trial blocks and conditions revealed no significant relationships with general intelligence (all *p*s < .138; average 40-trial *p* = .346, average 20-trial *p* = .391), suggesting that the ratio of EA/IA better captures the relationship between EEG power and intelligence than total power alone.

Alpha EA/IA

As noted above, pilot data indicated an increase in alpha band EA/IA ratio to repeated stimuli in experimental sessions separated by one day in eight subjects. To investigate this effect, a 2x2 repeated measures ANOVA was conducted for Block by Condition on alpha band EA/IA ratio in the 40-trial blocks. Preliminary results revealed an outlier whose ratio exceeded more than five times the sample standard deviation. After this individual was removed from the analysis, the test revealed a significant main effect of greater alpha power in the Repeated Condition (*F* (1, 20) = 5.731, *p* = .027; partial eta squared = .223). Although examination of the cell means suggested that alpha EA/IA increases over blocks in both conditions (see Table 12) neither this effect nor the Block by Condition interaction were significant. An exploratory test of the Block effect in the Repeated stimulus condition alone was not significant (*F* (1, 20) = .2114, *p* = .161, n.s.). Correlation analyses revealed no significant relationships between Alpha EA/IA and cognitive ability.

Table 12

Maximum Alpha EA/IA Ratios (n = 21)

	Mean	SD
Rep Alpha EAIA 1	.491	1.962
Rep Alpha EAIA 2	.698	2.122
Once Alpha EAIA 1	-.160	1.529
Once Alpha EAIA 2	.079	1.018

A repeated measures ANOVA of EA alone which examined Block and Condition again demonstrated a small main effect of greater alpha power in the Repeated Condition

(*F*(1,21) = 4.522, *p* = .045; partial eta squared = .177) but no significant effect of Block or interactions. The complementary test of alpha IA revealed no significant effects, nor were there any significant correlations between alpha EA or IA and cognitive ability.

Gamma EA/IA

After removing two outliers with ratios more then five times the sample standard deviation, a 2x2 repeated measures ANOVA was conducted testing the effects of Block and Condition on gamma power ratio. Cell means are shown in Table 13.

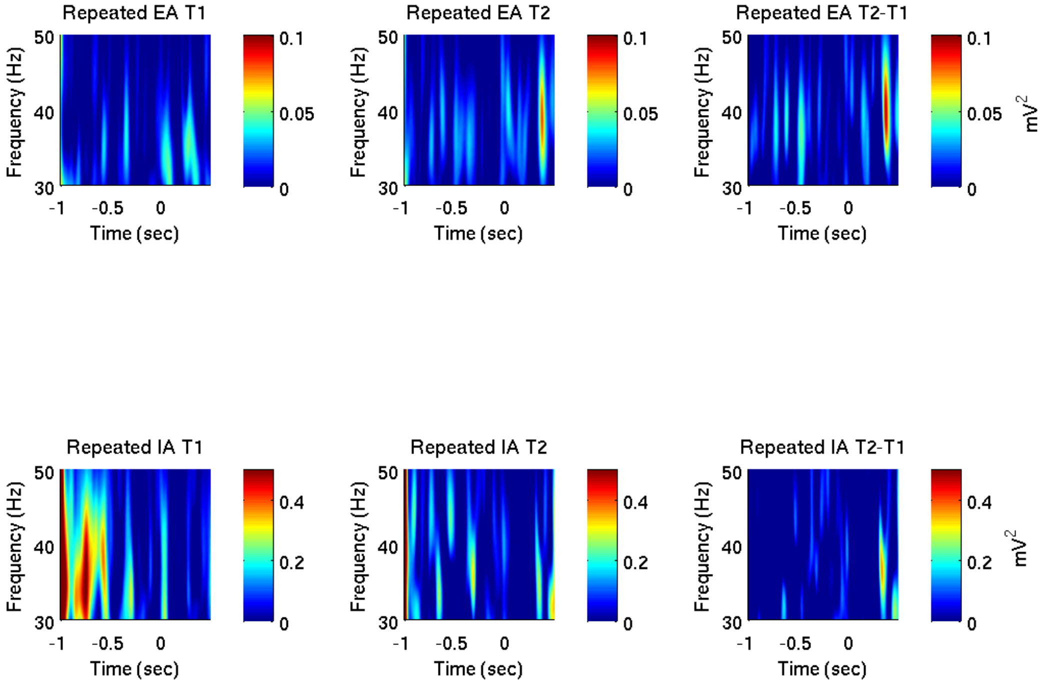
Table 13

Maximum Gamma EA/IA Ratios (n = 20)

	Mean	SD
Rep Gamma EAIA 1	.220	.264
Rep Gamma EAIA 2	.040	.343
Once Gamma EAIA 1	.145	.204
Once Gamma EAIA 2	.118	.177

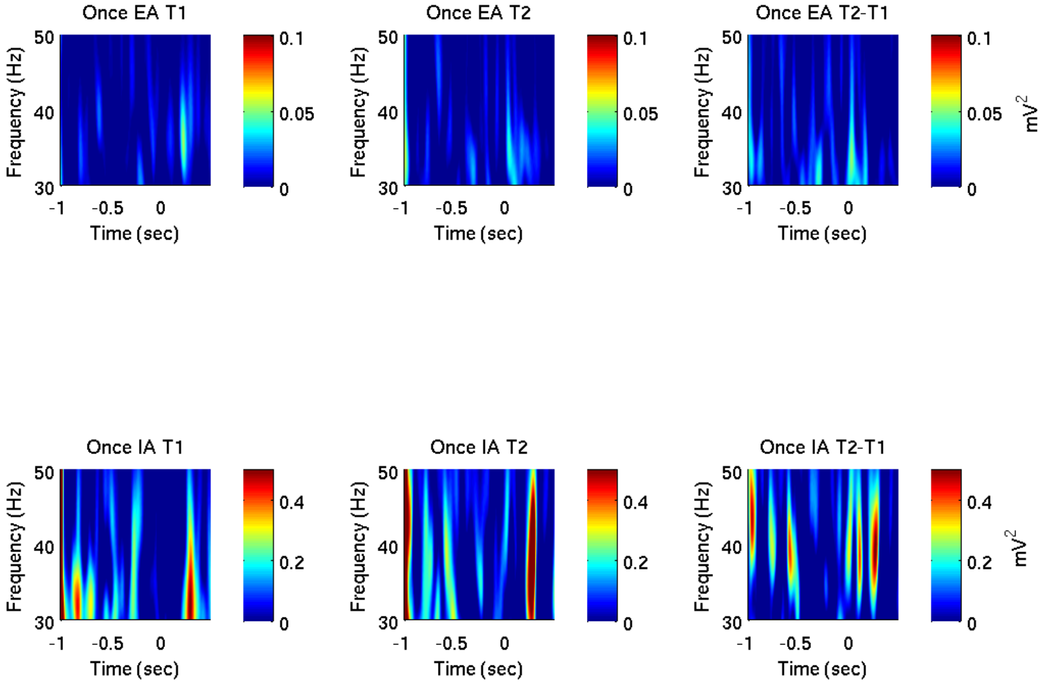
The analysis revealed a strong trend effect of decreasing ratio over time (*F* (1, 19) = 4.339, *p* = .051; partial eta squared = .186), while the effects of Condition and Block by Condition interaction were not significant. There were no significant interactions when *g* was entered into the model, nor when the Block by *g* effect was tested in each condition alone. Figures 7 and 8 depict gamma EA and IA TFRs for the Repeated and Once stimulus conditions.

Figure 7. Gamma Grand Mean TFRs Repeated Condition



Grand Mean Gamma Ten-Channel Average (n = 22). Top row depicts EA at Blocks 1, 2, and their difference (2-1) from left to right. Corresponding IA blocks are depicted below. Baseline EA and IA was calculated using FSUW from -240 -0 ms pre-stimulus

Figure 8. Gamma Grand Mean TFRs Once Condition



Grand Mean Gamma Ten-Channel Average (n = 22). Top row depicts EA at Blocks 1, 2, and their difference (2-1) from left to right. Corresponding IA blocks are depicted below. Baseline EA and IA was calculated using FSUW from -240 -0 ms pre-stimulus

Gamma IA 40-trial Blocks

Given prior findings of a reduction in induced gamma power following repeated stimulus exposure (Gruber & Muller, 2002, 2005), effects of Block and Condition on gamma IA alone were tested. Although cell means suggested that gamma IA actually increased over time in the current study (see Table 14), neither the effect of Block nor Block by Condition effect was significant.

Table 14

Gamma IA by Block and Condition (n = 22)

	Mean	SD
Rep Gamma IA 1	.460	.450
Rep Gamma IA 2	.526	.661
Once Gamma IA 1	.615	.507
Once Gamma IA 2	.779	.655

The main effect of Condition approached significance (*F*(1, 21) = 3.466, *p* = .077), where the Once condition elicited greater induced gamma power. When *g* was added to the model the main effect of Condition remained marginally significant (*F*(1, 20) = .3508, *p* = .067), and a significant Block by *g* interaction was observed (*F*(1, 20) = 4.931, *p* = .035; partial eta squared = .204). Post-hoc correlation analyses revealed significant inverse relationships between g and gamma IA the first block of both the Repeated condition (*r*(22) = -.517, *p* = .014) and Once (*r*(22) = -.581, *p* = .005) condition, indicating an inverse relationship between gamma IA at block 1 and intellectual ability. This relationship remained significant when collapsing across conditions (*r*(22) = -.628, *p* = .022). There were no significant relationships with gamma IA and the second 40-trial block in either condition, or when averaged across condition.

Gamma IA 20-trial Blocks

Finally, the effects of Block and Condition were tested in the 20-trial blocks by means of a 4x2 repeated measures ANOVA which included *g* in light of the previously observed relationship. This test revealed no significant main effects of Block, Condition, or Block by Condition interaction, however the Block by *g* interaction approached significance ($F(3, 60) = 2.641$, $p = .057$; partial eta squared .117). Post-hoc paired samples t-tests revealed no significant differences between the various levels of Block when no variance due to *g* was accounted for.

Correlated Vectors Analyses

The variables which were of theoretical interest or showed significant relationships with *g* in the above analyses were utilized in correlated vectors analyses. In particular, we examined the correlation between the column vector of the WAIS-III factor loadings on *g*, and the column vector of subtest correlations with the following variables: EA/IA ratio in the first 40-trial block, collapsing across conditions; EA/IA ratio in the second 40-trial block, collapsing across conditions; gamma IA in the first 40-trial block collapsing across conditions; and the difference between gamma IA in the repeated stimulus condition between the first and second 40-trial blocks. Table 15 below lists the conventional Pearson correlations between *g* and the study variables. Of note, when collapsed across condition the value of gamma IA in the first block accounts for 39% of the variance in *g*.

Table 15

Pearson Correlations between General Intelligence and EEG Power (two tailed, n =22)

	General Intelligence	Gamma IA Block 1 Overall	Gamma IA Rep Diff	Time 1 EA/IA Overall	Time 2 EA/IA Overall
General Intelligence	1	**-.628****	-.393	.411	**.473***
		P = .002	p = .071	p = .058	**p = .026**

Table 16 lists the Pearson correlations between the respective column vectors of subtest *g*-loadings and study variables; and Table 17 lists the rank-order correlations between the column vectors of study variables and *g*-loadings. The Pearson correlation between the columns vector of gamma IA at block 1 and column vector of g-loadings corresponds to an R^2 = .63.

Table 16

Correlations between General Intelligence and EEG Power Column Vectors (two tailed, n = 22)

	General Intelligence	Gamma IA Time 1 Overall	Gamma IA Rep Diff	Time 1 EA/IA Overall	Time 2 EA/IA Overall
General Intelligence	1	**-.794****	.462	.211	.114
		p = .007	p = .096	p = .470	p = .698

The *p*-values listed in Table 17 provide the conventional significance test in the correlation vectors approach (Jensen, 1998). Altogether, these tests revealed a highly significant correlation between the vector of subtest *g* loadings, and the vector of subtest correlations with overall time 1 gamma IA ($R^2 = .70$), and a marginally significant relationship between the *g*-vector and the vector of WAIS subtests and gamma difference scores.

Table 17

Rank-Order Correlations between General Intelligence and EEG Power Column Vectors (two tailed, n = 22)

	General Intelligence	Gamma IA Time 1 Overall	Gamma IA Rep Diff	Time 1 EA/IA Overall	Time 2 EA/IA Overall
General Intelligence	1	**.837**** **p = .002**	.464 p = .095	.257 p = .375	.235 p = .418

These relationships were subsequently tested between overall gamma IA at Block 1 and overall EA/IA Block 1 in the larger group of 25 participants. Results revealed a significant effect of overall gamma IA (Pearson: *r*(25) = -.609, *p* = .021; correlated vectors: *r*(25) = .776, *p* = .001; rank-order $R^2 = .60$), and no relationship between g and EA/IA (Pearson: *r*(25) = -.0318, *p* = .914; correlated vectors: *r*(25) = -.165, *p* = .573).

The significant inverse relationship between gamma IA and *g* indicates that relative to lower ability individuals, individuals with greater intellectual ability exhibit less of an increase in gamma IA (relative to baseline), when presented with a visual stimulus. From this, it is additionally necessary to determine whether individuals who differ in intellectual ability also differ with respect to the amount of pre-stimulus gamma IA they exhibit. To test this, both the smaller (N = 22) and larger (N = 25) data samples were divided according to *g* scores via a median split. One-way ANOVAs were conducted to test the null hypothesis of no difference between high and low *g* groups with respect to baseline gamma IA. Neither test was significant (smaller sample: $F(1,22) = .121$, $p = .731$; larger sample: $F(1,25) = 1.770$, $p = .196$), thereby supporting the notion that higher ability individuals do not simply exhibit less baseline gamma IA than lower ability individuals, but rather exhibit less activation in response to stimuli.

Discussion

Effects of EEG Power and Phase-locking on Neuroplasticity and Intelligence

This study sought to investigate the relationship between individual differences in intelligence and electrophysiological spectral neuroplasticity following exposure to visual stimuli. Prior findings in the intelligence literature and pilot data utilizing MEG spectral analysis motivated several hypotheses. First, it was hypothesized that repeated exposures to the same visual stimulus would result in an increase in phase-locked EEG spectral power (EA), and a simultaneous reduction in non-phase-locked spectral power (IA). Second, it was hypothesized that this pattern of increasing EA/IA over stimulus exposures would be stimulus-specific and hence would not be observed in an analogous condition involving the same number of exposures to novel stimuli. Third, it was hypothesized that the predicted change in EA/IA ratio would significantly relate to individual differences in intellectual ability. Given the substantial prior literature linking gamma-band IA in particular to visual stimulus processing (Tallon-Baudry, Bertrand, Delpeuch, & Pernier, 1996) as well as to visual repetition priming (Conrad et al., 2007) hypotheses were also evaluated with respect to gamma IA.

Overall Maximum EA/IA

The current study found an effect of stimulus exposure on the ratio of EA/IA, although not in the hypothesized direction. Contrary to hypotheses, it was observed that the ratio of maximum EA/IA actually *decreased* as a function of stimulus exposure, and did not exhibit stimulus specificity (i.e. repeated vs. novel). There were several differences between the current and pilot study which may account for the unexpected effect. First, the pilot study analyzed data from four subjects, as opposed to 22 for most analyses performed in the current study. Also, the pilot data were analyzed within an 8-40 Hz range while the current study expanded this to include frequencies from 2-50 Hz. The decision to expand the frequency range was motivated by examination of the current study grand-means which indicated substantial EA and IA in the range below 8Hz, raising the possibility that pertinent exposure-related change might also occur in a lower frequency range. Nonetheless, the broader frequency range may have resulted in increased variability in the frequencies of maximum EA/IA relative to those obtained in the prior analysis. Similarly, although separate analyses were conducted within the alpha band (due to previous finding linking alpha power to intellectual ability, e.g., Neubauer, Freudenthaler, & Pfurtscheller, 1995; Klimesch, 1999), this frequency range may have been inordinately restrictive to replicate the prior effect. Last, the current study calculated maximum EA and IA separately in each epoch and then derived their ratio, as opposed to linking one value to the peak of the other, irrespective of its own peak. While the current measure yields the proportion of each activity at its maximum across epochs (and hence quantifies overall average max-EA/max-IA), it may instead be desirable to calculate ongoing IA at the time of peak EA latency (or vice versa) to control for differences in the relative slope of the respective activities.

For example, examination of Figure 5 suggests important differences in the relative amplitudes of the P1-N1 ERP complex from block one to block two in the Repeated stimulus condition, while the P1-N1 complex appears nearly identical across blocks one and two in the Once condition. However, examination of Figure 6 which depicts the results of the repeated measures analyses of the maximum EA/IA ratios indicates a general effect of block irrespective of condition, rather an effect of block within the Repeated condition. Thus, it may be the case that failing to link the maximum EA value to its contemporaneous IA value (irrespective of its own maximum) in the derivation of the EA/IA ratio accounts for the failure to observe the hypothesized stimulus-specific effect. Given the apparent interaction of block by condition on the P1-N1 complex suggested by the ERPs in Figure 5, a critical future direction is to recreate the overall EA/IA ratios by linking the peak of one value to the ongoing value of the other.

Despite the failure to find support for the hypothesis in the predicted direction, the finding that overall peak EA/IA decreases over stimulus exposures irrespective of stimulus type nonetheless appears to represent a form of neuroplasticity. However, the fact that the effect was not specific to the repeated stimulus condition is inconsistent with the notion that the decrease in power ratio over blocks represents a "sharpening" of a stimulus-specific neural network. On the contrary, the general decrease in EA/IA ratio over exposures irrespective of stimulus novelty may simply signify habituation and/or fatigue of the neural regions which process visual stimuli. After the recommendation by Cohen (1998), the observed value of partial eta squared = .178 indicates that the decrease in EA/IA across conditions represents a "small" effect of stimulus exposure.

Subsequent tests for associations between *g* and EA/IA power ratios revealed positive though typically marginally significant relationships between intellectual ability and EA/IA across both stimulus exposures and types. When the ratios were averaged across block and condition, the relative proportion of phase-locked to non-phase-locked neural activity (EA/IA) accounted for approximately 25% of the variance in *g* scores. Similar relationships were not observed when correlations were tested between *g* and total power, despite the fact that IA constitutes the majority of the activity within the total spectral power measure. Thus, current results suggest that the relative proportion of phase-locked to non-phase-locked power and not simply the amount of overall power (or induced power alone) uniquely relates to cognitive ability.

A potential hypothesis to account for the significant conventional correlation relies on the contribution of phase-locked power to the evoked portion of the EA/IA ratio. The present study employed variable inter-stimulus intervals (ISI) to minimize expectancy effects, and utilized a visual oddball paradigm in which standard and target stimuli were randomly interspersed. Behavioral data confirmed that participants were highly accurate in responding to the target stimuli, increasing likelihood that they were attentive to the task. Thus, the positive relationship between *g* and the proportion of phase-locked to non-phase-locked neural activity was observed in the context of good attention, but uncertainty as to the type and onset of each visual stimulus. As stimuli were presented at a variable ISI, participants would not be expected to automatically exhibit phase-locked responses to stimulus onset. Rather, the evoked portion of the EA/IA ratio may have resulted from *phase-resetting*, or the change from the phase of the network's ongoing oscillation to the phase of the stimulus onset.

Theoretically, phase-resetting refers to a model of ERP generation where the increase of power observed in the ERP/EA results from a "reset" of the phase of ongoing oscillations in the neural populations to the phase of stimulus onset (Sauseng et al., 2007). This concept is often contrasted with the classical notion of ERP generation positing that the observed increase in power results from a stimulus-evoked increase in activity, irrespective of ongoing oscillations (Shah et al., 2004). It has been previously shown in a visual experiment that non-target ERPs are substantially generated by stimulus-locked phase-resetting of EEG components (Makeig et al., 2002).

As greater intellectual ability was associated with more positive EA/IA ratios, and hence a greater proportion of phase-locked activity, the current results suggest that the observed correlation may have resulted from increased phase-resetting in higher *g* participants. By extension then, the properties of a neural network that enable it to become phase-locked to a stimulus may in part drive differences in cognitive ability. As noted above, it has previously been demonstrated in large samples that flexibility and rigidity in resting EEG phase dynamics are respectively linked to higher and lower IQ scores (Thatcher et al., 2008). While phase-resetting was not explicitly characterized in these data, the current aggregate EA/IA ratio may well capture the extent of successful phase-resetting simply by the nature of the activity types comprising the proportion. Also consistent with this hypothesis, prior work investigating individual differences in visual discrimination ability indicated that participants who performed better on a visual discrimination task exhibited significantly greater phase-locking than poor performers in the 8-14 Hz range (Hanslmayr et al., 2005b).

Despite the positive relationship between EA/IA ratio and *g*, tests of difference scores derived from the EA/IA ratios were not significant. When EA/IA ratios were broken down into smaller blocks, cell means suggested that (consistent with the primary hypothesis) EA/IA ratio might increase between the first and second twenty trials in the Repeated condition and decrease in the Once condition. However, this interaction was not significant, nor did it interact with *g*. Thus while the EA/IA ratio both exhibited a modest neuroplasticity effect, and was linked with cognitive ability, the effect of neuroplasticity did not significantly impact the relationship between power ratio and cognition.

Alpha EA/IA and EA

Alpha band analyses were undertaken for several reasons. First, prior data which motivated the study demonstrated an increase in the EA/IA ratio to repeated stimuli across exposures, which occurred within the 8-12 Hz range. Also, alpha power and phase characteristics have been linked to performance in numerous EEG visual perception experiments (e.g. Basar, Schurmann, Basar-Eroglu, & Karakas, 1997; Hanslmayr et al., 2005b), as well as the EEG literature on intelligence (Grabner et al., 2003; Neubauer et al., 2004).

When the above relationships were tested only in the alpha range, neither the effect of stimulus exposure nor the link between alpha EA/IA ratio and intelligence was significant. Analyses did reveal a small but significant effect of stimulus type, with greater alpha EA/IA in the repeated stimulus condition. This indicates that repeated exposure to a specific stimulus elicits a higher ratio of phase-locked to non-phase-locked activity, relative to mere repetitive exposure of any kind. This implies either that, contrary to hypotheses alpha power is actually reliably elicited by a repeated stimulus (and does not change over exposures), or simply that the present methodology was unable to capture change which did occur. The effect of greater alpha power in the repeated condition persisted when tested in EA alone, suggesting that the stimulus effect is related to the relative proportion of phase-locked power in that condition.

Unlike the analyses which were undertaken in a broader frequency range, there was no relationship between either greater proportional or absolute phase-locked alpha power in the repeated condition and *g*. The failure to demonstrate this effect may be accounted for by the fact that the average frequencies exhibiting maximum power were actually in the 4-8 Hz (theta) range as opposed to the higher alpha range. Examination of the study grand means (Figures 2 and 3) suggests independence in higher versus lower frequency bands below 20 Hz (especially in induced activity), which is further supported by general findings in the EEG literature demonstrating that divergent processes in alpha and theta power support cognitive performance (Klimesch, 1999). In particular, it has been argued that superior performance on cognitive and memory tasks is related to event-related alpha suppression and theta enhancement, respectively. Hence, it may be that while phase-locked alpha power reflects stimulus-specific visual processing, the ratio of phase-locked to non-phase-locked theta power indexes the more general linkage between synchronous theta activity and cognitive performance.

A second consideration which bears on the alpha-band analyses is the notion that each study participant's individual alpha frequency band should be determined independently, which was not implemented in the present study. In the review of alpha and theta oscillations cited above, Klimesch (1999) discussed prior research demonstrating age-related increases in the dominant alpha frequency early in life, following by decreases in the decades following age twenty. Similarly, that review notes that increased alpha frequency is associated with faster reaction times and superior memory performance. Taken with the aforementioned findings demonstrating divergent task-related oscillatory processes in the alpha and theta band, these studies suggest that the individual determination of each participant's alpha band may improve precision in testing the relationships between alpha EA/IA and *g*.

Gamma IA

As a preliminary step before analyzing effects on gamma IA alone, the effect of exposure and stimulus type was tested in the gamma EA/IA ratio. Those analyses demonstrated a marginally significant effect of decreasing EA/IA ratio over blocks, which was not linked to variation in intellectual ability. While the gamma EA/IA ratios decreased over blocks, this effect was not significant when tested in gamma IA by itself. This is in contrast to consistent observations of decreasing gamma IA in a series of visual repetition priming studies (Gruber & Muller, 2002; Gruber, Malinowski, & Muller, 2004; Gruber & Muller; 2005; Conrad et al., 2007). While the present study was modeled after these experiments in several ways, one potentially critical difference was in the number of exposures to repeated stimuli that participants received.

Specifically, the present study employed a total of 240 trials in both the Repeated and Once stimulus conditions in an effort to replicate the pilot MEG study, as well as to achieve optimally reliable EA/IA ratios. As opposed to examining differences between conditions with the same repeated versus all novel stimuli, the prior repetition priming studies examined differences between initial, and only the first several repeated presentations collapsed across many stimuli (i.e. less than 5 presentations of each single stimulus). Stated another way, they compared groups of stimuli as a function of their *ordinal presentations*, and hence decreasing novelty, not simply comparing many novel against many repeated presentations. Thus, decreasing gamma IA has been consistently observed when comparing initial to early repeated presentations of a given set of stimuli, as opposed to comparing greater than 20 or 40 trials of a single-stimulus to all novel stimuli. It may be that participants did exhibit an effect of decreasing gamma IA in the first several repeated trials, but that this reached asymptote and hence was undetectable in the present study. Despite this important methodological difference, the current study nonetheless found evidence for a significant relation between gamma IA and IQ.

Gamma IA and Intelligence

Tests of the effects of stimulus type and exposure indicated a marginally significant effect of greater power in the Once condition, and a significant interaction between block and *g* where there was a negative relationship between *g* and gamma IA in the first block. Subsequent correlations tested in each condition at block 1 uniformly revealed a significant inverse relationship between gamma IA and IQ. When collapsed across conditions, this relationship accounted for just over 39% of the variance in *g* among participants, a large effect size. In order to better determine whether this relationship holds between gamma IA and *g per se* their association was tested using the correlated vectors approach.

The method of correlated vectors refers to a test of the relationship between two column vectors, which are themselves comprised of correlation coefficients and/or factor loadings. This involves obtaining the conventional Pearson correlation between the vectors, as well as the rank-order correlation between them. The coefficient ranks are given by the relative g-factor loadings (vector 1) and the size of the correlations between the tests used to derive *g* and the third variable (vector 2) (Jensen, 1998). Here, the relation was tested between the vector of each WAIS-III subtest's *g* factor-loading and the vector of subtest correlations with overall gamma IA at block 1. Consistent with the prior result, these tests revealed highly significant and substantial conventional and rank-order correlations between the vectors (R^2 ~ .63-70). Thus, it is appropriate to conclude that the inverse relationship between individual gamma IA and *g*-factor score is in fact due to a substantial association with *g* itself, rather than to idiosyncratic effects which might bias regression-estimated *g*-factor scores. Since the factor loadings show a strong rank-order relationship with gamma IA, it is more likely that gamma IA truly indexes the general component underlying variation in test performance, rather than a specific cognitive ability. While the nature of the relationship dictates that more *g*-loaded tests will be more correlated with gamma IA, this is due to their shared variance via *g*, and likely not due to a specific relation between gamma IA and those particular cognitive abilities. The large and significant relationship persisted when tested in the larger sample, though was somewhat less robust (rank-order $R^2 = .60$). Overall, this signifies that higher ability individuals exhibit relatively less induced gamma power to a visual stimulus (200-400 ms post-stimulus) in the early portion of the experiment.

Critically, when both the smaller and larger sub samples of participants were divided into high and low *g* groups, no differences were observed between groups in gamma IA in the baseline pre-stimulus period. While the failure to reject the null hypothesis cannot be unequivocally taken as proof of no difference, it nonetheless undermines the possibility that high *g* individuals simply exhibit less gamma IA at all times. Rather, it appears that higher ability individuals exhibit less gamma *activation* in response to stimuli compared to lower ability individuals.

The finding that high *g* individuals activate less to the onset of a visual stimulus suggests that, consistent with the neural efficiency hypothesis (Haier et al., 1988), the brains of higher ability individuals exert fewer resources to process stimuli compared to their lower ability counterparts. This relationship also appears consistent with the prior repetition priming literature showing decreased induced gamma power following repeated stimulus exposure. That is, the inverse relationship between stimulus repetition and gamma IA suggests that less induced gamma IA signifies some kind of adaptive mechanism in the brain. Taken together, the inverse relation between *g* and gamma IA in the first experimental block and the independently established inverse relation between repetition and gamma IA might be reconciled in one of two ways.

First, it might be the case that while on-average all individuals exhibit decreasing gamma IA to repeated stimuli, higher ability individuals exhibit a more rapid decrease. This would imply an adaptive property in the brains of more intelligent individuals, and would represent a true a link between neuroplasticity and *g,* similar to the originally hypothesized relation. Conversely, it might instead be the case that by virtue of their neural network properties (for example better visual stimulus resolution), higher *g* individuals simply exhibit an optimal level of gamma IA following stimulus onset, while the responses of lower ability individuals exhibit a "tuning" effect to repeated stimuli. This tuning effect might later converge with the optimal behavior exhibited by networks of high *g* individuals. Findings supporting the latter hypothesis would be most consistent with greater *neural efficiency* in higher ability individuals, and a plasticity effect in lower ability individuals. It may be the case that a hybrid of these two, or an alternative model, best reconciles inverse relations between induced gamma power, repetition, and intelligence. Thus, one critical future direction suggested by the present findings is to better replicate prior observations of decreasing gamma IA with repetition in both high and low intellectual ability groups.

Another alternative or complementary approach would be to investigate any individual differences in gamma IA between high and low-*g* individuals in the baseline period as a whole. Specifically, while the current analyses indicate a strong effect of differential activation in the post-stimulus period as a function of intelligence, it is conceivable that high and low-*g* groups might also differ in their patterns of pre-stimulus activity changes, especially over the course of an experiment involving many similar stimulus exposures. For example, although there were no group differences in baseline gamma IA (extracted 240 to 0 ms pre-stimulus and averaged over trials), it may be that in the present experimental context (where participants acclimate to a lengthy series of visual stimuli), higher or lower ability individuals exhibit preparatory neural changes during the larger baseline window over the course of many trials. Such effects would only be observed in analyses where the pre-stimulus baseline window itself was the period of interest. Thus, while current results implicate less gamma activation from the pre- to post-stimulus period as importantly related to intelligence, they do not speak to any preparatory changes which might occur in either group across trials in the expectant, pre-stimulus period.

Potential Mechanisms linking Gamma IA and Intelligence

Interest in induced gamma activity first arose from basic research showing that synchronous > 40 Hz oscillations between adjacent cortical neurons were linked to the specific properties of a visual stimulus (Gray & Singer, 1989), though were not linked to stimulus onset across trials. From this, it was hypothesized that high frequency cortical oscillations importantly relate to stimulus representation and feature binding, and that oscillatory phase in particular might provide a code by which neurons could resolve diverse properties of stimuli within the visual field. Later EEG studies demonstrated induced gamma oscillations in humans occurring at approximately 280 ms post-stimulus, which were greater in tasks where subjects experience perceptually coherent feature-binding (Tallon-Baudry, et al., 1996). As noted, subsequent work has consistently observed relationships between induced gamma power between 200-400 ms which is modulated by perceptual and cognitive task characteristics (Fries, 2009).

Gamma activity has been found in many neural populations across species, including in human cortex and some subcortical areas; and likely plays a role in several different aspects of brain functioning (Fries, 2009). For present purposes, a heuristic framework of local cortical gamma oscillations can provide a fruitful way of thinking about how high frequency activity might relate to cognition. Several models have been proposed based on reciprocal coordination between excitatory pyramidal cells and inhibitory interneurons (Fries, Nikolic, & Singer, 2007). One holds that the gamma cycle begins when stimulus input drives excitatory pyramidal cells that in turn drive an associated and recurrently active interneuron network. The excitatory cells that drive the cycle are hypothesized to preferentially respond to the characteristics of the eliciting stimulus. Those excitatory cells which do not preferentially respond to those stimulus features are less excited and hence do not drive the network initially. In turn, the interaction of the strongly activated pyramidal cells with their associated inhibitory interneurons sets the phase the overall network, while initially poorly activated cells remain out of phase. Since continued firing by all cells is delayed until inhibitory currents dissipate, those that were insufficiently activated early-on remain only weakly excited and out of phase, resulting in a “winner-take-all” process.

Consistent with the notion that gamma activity signifies stimulus representations (Singer, 1999), mechanisms have been proposed whereby decreasing induced gamma activity could facilitate superior object representations in the neural networks which process a given stimulus, as well as better object recognition. One computational study devised a model to explain how reductions in gamma IA to repeated stimuli could create “sharper” stimulus representations and better reaction times via a winner-take-all mechanism (Moldakarimov, Bazhenov, & Senjowski, 2010). In that simulation, spiking neurons responded to inputs (stimuli) as parts of larger inhibitory networks. The neuron units received inputs of different strengths, which represented different levels of activation. Units began the simulation with randomly varying connection strengths between them, while the connections responded to input according to Hebbian learning rules. Despite an initially synchronous response in all the simulated neural populations, repeated stimulation increased synchrony in only two of five simulated populations, and decreased synchrony in the others.

The overall result was a decrease in the number of connections and activated units within the local network and in the resulting simulated local-field potentials (LFPs) over the course of repeated inputs. When the power of the LFPs was examined, they demonstrated reductions in the gamma power range over repeated stimulation. At the unit level, the process resulted in fewer units with stronger connections responding to the same input over repetition. The authors also tested a second, higher-level network connected to the first, which operated according to winner-take-all principles. When repeated stimulation sharpened the lower-level network, it increased competition among populations in the downstream network (via winner-take-all competition) and in turn reduced overall network reaction time following repetition. Therefore results were interpreted as consistent with the “representation sharpening hypothesis” where fewer cortical neurons are able to better represent a stimulus following repeated exposure.

Within the repetition priming literature, the observed reductions in gamma IA in the scalp EEG are hypothesized to reflect an analogous sharpening mechanism resulting in distinct cortical object representations. Moving up a level of analysis, studies performing source-analysis have suggested that induced gamma responses to meaningful visual stimuli result from activity in and directional phase-locking between bilateral occipito-parietal, left inferior and lateral and occipito-temporal, and right middle frontal and precentral regions (Gruber, Trujillo-Barreto, Giabbiconi, Veldes-Sosa, & Muller, 2006; Supp, Schlogl, Trujillo-Barreto, Muller, & Gruber., 2007).

The current study utilized an average of posterior channels analyzed in sensor space, which is consistent with other reports using similar methodology (Gruber & Muller, 2002). This fact, as well as the effects of volume conduction and specific choice of reference (Luck, 2005), somewhat hinder strong statements as to the specific sources underlying the effects. Still, several inferences may be drawn. Given the similarity of the stimuli employed to those of studies that performed source analysis, it is plausible that many of the same regions underlie the current effect. Thus, it is likely that the induced gamma response resulted at least in part from the synchronous oscillation and interaction of cortical networks in posterior occipito-parietal regions, with contributions from frontal and lateral temporal sources. Notably, a very similar network has been identified as reliably showing relationships between intelligence and brain structure (Jung & Haier, 2007). As discussed above, that review identified regions including the inferior and superior parietal lobules; inferior, middle, and superior temporal regions; and lateral occipital sites as importantly contributing to a larger network related to intelligence. Perhaps also consistent with current intelligence findings, lesion data has linked variation in *g* to predominantly left hemisphere gray matter and fiber tracts that appear to overlap with areas identified in the prior source-analysis studies (Glascher et al., 2010). These sites included gray matter in the left superior parietal region and right occipito-parietal junction, and left hemisphere white matter linking temporal, parietal and frontal structures.

The present EEG methodology do not provide sufficient spatial resolution to determine whether the relation between induced gamma and *g* results from brain-wide individual differences, or from differences within the regions identified in prior source-analysis studies. However, many of the regions implicated in intelligence appear to overlap with those thought to be active in the task. In light of this, a plausible hypothesis is that the effects are at minimum attributable to differences in the overlapping regions (or their interactions); though the relationship between gamma IA and *g* may still hold in other experimental modalities involving other regions. Going forward, a promising future direction would be to conduct source analyses investigating activity within those regions which overlap between the repetition priming literature and the P-FIT. Not only would these analyses shed light on those sources most responsible for the effects observed in the averaged scalp EEG, but they could further illuminate the temporal and phase-relationships between the activity within each region. In turn, such analyses could inform the relative importance of inter- and intra-regional activity for intelligence, by allowing a direct assessment of the correlation between the power or phase of the various sources and individual differences in *g*. At present, most conceptualizations of induced gamma activity[1] emphasize models of local

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[1] Recent research has highlighted "high gamma" (> 80 Hz) oscillations (conducted via electrocorticography measurements in epilepsy patients undergoing surgery) as indexing robust relationships between neural activity and perception and cognition (Canolty et al., 2007; Towle et al., 2008). At present, available evidence points to distinct physiological (Oke et al., 2010; Ray, Crone, Niebur, Franaszczuk, & Hsaio, 2008), and functional correlates of low (30-80 Hz) vs. high gamma oscillations (Edwards et al., 2009), suggesting distinct mechanisms from those underlying the current effects.

cortical interactions (Fries, 2009; Gonzales-Burgos & Lewis, 2008), and hence imply differences in local activity rather than an interaction effect. Thus, the relation between gamma IA and *g* may be most likely related to individual differences in either the efficiency or plasticity of local cortical networks among more intelligent individuals. Eventually however, it will be necessary to implement source analyses in the present data (or utilize MEG or electrocorticography in other samples) to ascertain the specific regional cortical phenomena underlying the link between induced gamma activity and *g*.

Following from the representational sharpening hypothesis and the other considerations noted above, one of two explanations for the inverse relation between induced gamma and *g* appears likely. People with greater intellectual ability either arrive at each situation with more plastic and quickly adapting networks, or with optimally “sharp” neural representations resulting from more efficient networks. A test of these competing ideas would require methodology that could reliably elicit and identify (or rule-out) plasticity, were it to occur. Going forward, this might be accomplished through experiments involving nonsense stimuli repeated over many trials, across different experimental intervals (e.g. minutes, days), and requiring participants to make a binary judgment of novelty on each trial. Single-trial analyses of overall phase-resetting/phase-locked power versus the *slope* of phase-resetting/power over intervals could then be used to test links between intelligence, experimental performance, and neural plasticity versus efficiency.

Limitations

The current study had several limitations, which are addressed in order of their potential impact on the results. First, although a highly significant relationship between intellectual ability and induced gamma IA was observed, recent research has raised concerns that the visual posterior gamma IA observed in this and other visual studies may actually be an artifact of ocular movements. Despite the compelling framework for gamma oscillations, research using simultaneous eye-tracking and scalp EEG has demonstrated a convincingly close correlation between the presence and absence of small (less than 1 degree from fixation), non-phase-locked ocular artifacts in the form of miniature saccades to broadband (20-100 Hz) induced gamma band responses (Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). Based on several experiments these authors conclude that the frequently reported gamma IA recorded from the scalp EEG from 200-400 ms post-stimulus is not actually the result of neuronal activity, but rather results from eye-movements. They suggest that the observed inter-trial variability results from a post-stimulus phase of saccadic inhibition (after 100 ms) which subsequently rebounds at approximately 200-300 ms, resulting in an “induced” artifact measured by the scalp EEG.

The same authors further argue that the predominantly posterior EEG scalp topography of both the saccades and the induced gamma response results from the choice of a nose tip EEG reference, which was unknown prior to its utilization as the reference in the current study. On the contrary, several prior reports on which the current study stimuli were modeled utilized either Cz as the reference electrode or an average reference, and still observed a significant induced gamma band response with a posterior topography (Gruber, & Muller, 2002; Gruber & Muller, 2005; Martinovic, Gruber, & Muller, 2007).

At the same time, Yuval-Greenberg et al. (2008) note that the observed link between EEG gamma IA and microsaccades cannot discount other findings of significant relations between induced gamma activity and cognition in many intracerebral recording studies or in MEG studies under certain conditions (see also Jerbi et al., 2009). Moreover, other authors note that the early EEG work on induced gamma power explicitly evaluated contributions due to muscle artifacts and concluded they were not significant (Fries, Scheeringa, & Oostenveld, 2008). Going forward, the observed highly significant relationship between gamma IA and *g* will need to be further explored in conjunction with eye-channel data and alternative referencing (Melloni, Schwiedrzik, Wibral, Rodriguez, & Singer, 2009), to better address the potentially significant contribution of this third variable. Nonetheless, it is quiet remarkable that an artifact of eye movements (deviating less than 1 degree from fixation) would relate to so many cognitive variables as has been indicated by a substantial literature.

In the event that microsaccades did account for the large inverse relationship between induced gamma power and *g*, it would nonetheless raise intriguing questions as to the relation between visual inspection and intelligence. Apropos of the current issue, research investigating the relation between cognitive ability and visual orientation has shown that working memory capacity is related to anti-saccade task-performance (looking in the opposite direction of a visual cue), though not pro-saccades (Conway, Kane, & Engle, 2003).

Similarly, there is a classic and considerable literature on inspection time (IT) and intelligence (Deary & Stough, 1996). Two meta-analyses of the correlation between inspection time and IQ scores revealed an average inverse relationship of approximately -.30 prior to correcting for attenuated reliability, and -.51 after correction (Kranzler & Jensen, 1989; Grudnik & Kranzler, 2001), with the earlier meta-analysis concluding that IT was likely more related to perceptual organization than to *g*. The current study did not correct for attenuation of reliability in the subtest scores. However this correction would very likely increase the strength of the relationship between gamma IA and *g* beyond the observed $r = -.628$, implying a stronger relationship than that due to IT alone.

Another pertinent consideration in light of the micro-saccade concern is the observation that correlations between gamma IA and *g* were both significant, in the same direction, and approximately the same size in both repeated and once stimulus conditions. Prior work has shown decreasing gamma IA over repeated exposures of meaningful stimuli, and increasing gamma IA over repeated exposures of meaningless stimuli in the period under discussion (Conrad et al., 2007). If these differences result purely from differences in the number or amplitude of eye muscle movements over exposures, one might expect a larger effect in the Once stimulus condition relative to the Repeated condition, due to increased visual inspection of the novel stimuli (Berlyne, 1966). Similarly, the argument that saccadic suppression between 100-200 ms post-stimulus accounts the rebound of gamma IA between 200-400 ms appears ill-equipped to account for numerous studies demonstrating reduced gamma IA in the repetition priming paradigm. As a single example, it appears implausible that such a reliable (and apparently general) effect of saccadic suppression and enhancement would be influenced in opposite directions by exposure to meaningful versus meaningless stimuli.

Although these consideration do not exclude the possibility that the current gamma IA is linked to micro saccades indexing a general orienting response, other EEG studies of gamma IA have identified an earlier (~ 90 ms), evoked gamma response which is thought to reflect orienting to the onset of a stimulus (Tallon-Baudry et al., 1996). Finally, given findings in similar visual studies implicating reciprocal interactions involving inferior temporal, superior parietal, and middle frontal areas in object recognition (Supp et al., 2007), it may be that scalp-recorded EEG gamma IA is necessarily confounded by saccadic activity due to the activity of frontal-eye-fields and micro saccades on visual object processing.

A second limitation of the current study was the failure to replicate the previous findings of decreasing gamma IA over repeated stimulus exposures, or to identify robust and stimulus-specific neuroplasticity effects in general. This might have been better accomplished by linking each trial in which the visual response was of interest to a behavioral response, rather than to use a target detection paradigm. In particular, many different stimuli might have been presented numerous times each, with participants making a binary response as to whether they had seen each stimulus. In turn the stimulus-locked visual responses could have been analyzed according their ordinal number of stimulus exposures and linked to accuracy and reaction time. While a third condition was implemented to afford such as test, behavioral data suggested that participants' determination of relative stimulus familiarity (Repeated vs. Once vs. Novel) was not linearly related to response time or accuracy. In light of the apparently complex relationship and/or potentially bimodal distribution of responses to 'Once' stimuli in the third condition, those electrophysiological effects were not further explored in the present report.

Several other limitations of the current study pertain to statistical and sample-size considerations. First, several analyses were likely hampered due insufficient statistical power. For example, cell means of the 20-trials blocks in the Repeated condition were consistent with the predicted effect of increasing EA/IA. This effect was potentially not significant due to insufficient statistical power. Also, the primary prediction that intelligence would relate to increased EA/IA in the Repeated vs. Once stimulus condition, could not be tested in a single model due to the large sample size which would have been required for an adequately powered test of a 4-way interaction. Lack of power also compelled the application of directed rather than two-tailed significance tests of several hypothesized relationships. In addition, given the novel hypotheses generated from pilot data and the generally exploratory nature of study, many tests were performed without correcting for experiment-wise error rates. This raises the possibility that some significant findings arose simply due to chance, increasing the need to for replication. Last, the study current study had to exclude over a quarter of the total sample from some analyses due to excessive blink artifacts (both a statistical and methodological concern). While comparable rejection rates have been observed in other reports using similar methodologies (Gruber, Malinowski, & Muller, 2004; Gruber & Muller, 2002), the loss of several participants may limit the generalizability of the findings.

Summary and Conclusions

This experiment sought to characterize the relationship between electrophysiological neuroplasticity and individual differences in intelligence. Using many exposures of repeated and novel visual stimuli, relations between stimulus exposure, type, and *g* were tested in several time-frequency measures of phase-locked and non-phase-locked activity. The primary hypothesis that the ratio of phase-locked to non-phase-locked activity would increase following exposure to a repeated stimulus was not supported, nor was the hypothesized relationship between the posited increase in this ratio and intelligence. The study did find evidence for a modest decrease in this ratio in low and high frequency ranges over stimulus exposures, irrespective of stimulus type, suggesting a neural fatigue or habituation effect. Higher ratios in the alpha band were observed in the repeated stimulus condition in the absence of an exposure effect.

Several significant relationships were demonstrated between electrophysiological measures of phase and non-phase-locked activity and *g*. A positive relationship was observed between *g* and the proportion of maximum evoked to induced theta-band activity across epochs and conditions. This effect was not accounted for by total power, highlighting the significance of phase-locked activity in particular to the relationship. This was consistent with prior studies demonstrating a positive relation between superior phase-resetting and increased intellectual ability.

Conversely, there was a highly significant inverse relationship between non-phase-locked gamma activity and intellectual ability. There was a substantial and significant rank-order correlation between induced gamma and *g*-factor loading indicating a robust relationship with general cognitive ability. While methodological limitations likely impeded identification of true *g*-neuroplasticity effects, overall results highlight the sensitivity of electrophysiological measures of oscillatory phase to individual differences in cognitive ability. Current controversies in the EEG literature complicate the interpretation of the relationship between high frequency oscillations and *g*. However, tentative conclusions suggest that more intelligent individuals either exhibit better optimized evoked responses or more rapid plasticity than other individuals. The observation of multiple significant, though independent relationships between intelligence and indices of neural-phase locking speaks most strongly to the importance of *efficient* stimulus processing for adaptive functioning, than to rapid neuroplasticity. Future research in this area should endeavor to better characterize the relative importance of transient versus persisting changes in neural networks for intelligence and adaptive behavior.

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