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Reliable activation to novel stimuli predicts higher fluid intelligence

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ARTICLE INFO

Article history:

Received 17 November 2014

Accepted 28 March 2015

Available online 8 April 2015

Keywords:

EEG

Fluid intelligence

Time-frequency analysis

Inter-trial phase clustering

Neural variability

ABSTRACT

The ability to reliably respond to stimuli could be an important biological determinant of differences in fluid intelligence (Gf). However, most electrophysiological studies of Gf employ event-related potential (ERP) measures that average brain activity over trials, and hence have limited power to quantify neural variability. Time-frequency analyses can capture cross-trial variation in the phase of neural activity, and thus can help address the importance of neural reliability to differences in Gf. This study recruited a community sample of healthy adults and measured inter-trial phase clustering (ITPC), total spectral power, and ERP amplitudes elicited by Repeated and Novel non-target stimuli during two visual oddball tasks. Condition effects, relations among the EEG measures, and relations with Gf were assessed. Early visual responses to Repeated stimuli elicited higher ITPC, yet only ITPC elicited by Novel stimuli was associated with Gf. Analyses of spectral power further highlighted the contribution of phase consistency to the findings. The link between Gf and reliable responding to changing inputs suggests an important role for flexible resource allocation in fluid intellectual skills.

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Introduction

Electrophysiological research on intelligence has demonstrated a number of associations between features of event-related potentials (ERPs) and variation in intellectual skills. Perhaps the most consistent finding is the inverse relation between intellectual ability and the latency of the P300 component elicited by infrequent stimuli during oddball paradigms (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; De Pascalis et al., 2008; Liu et al., 2011; Troche et al., 2009; Walhovd et al., 2005). A number of these and other studies have also shown a positive relationship between P300 amplitude and intelligence (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; De Pascalis et al., 2008; Troche et al., 2009; Wronka et al., 2013), though some studies have not observed this relationship (e.g., Peltz et al., 2011). Similarly, studies examining ERP correlates of inspection time have demonstrated a number of associations between intelligence and early ERP components, with different studies variously identifying

component amplitudes, latencies, or wave shape characteristics as being the most predictive (see Deary, 2000, pp. 280–282; and Hill et al., 2011, for reviews).

Despite the overall success of the ERP approach, one limitation of these measures is that they inherently involve averaging neural responses over many trials. Although it is often implicitly assumed that averaged ERPs only reflect activity that is reliable across trials, in practice, effects such as trial-to-trial latency jitter can distort the resulting averages (Luck, 2014, p. 58). Thus, as several authors have pointed out (Barrett and Eysenck, 1992; Batt et al., 1999), ERP measures are necessarily limited in their ability to capture aspects of neural variability that might be of theoretical interest as potential biological mechanisms of intellectual variation. The significance of behavioral intra-individual variability to variation in intelligence is well-established through research on decision time variation (Jensen, 1992) and other measures (Fox et al., 2009; MacDonald et al., 2006; Stuss et al., 2003). At present however, there has been relatively little work investigating how neural variability (or its counterpart – reliability) might underlie variation in intelligence.

Going back over a decade, a number of previous studies investigated relations between neural variability and intelligence using the ERP-based “string length” and associated “variance” measures (Bates et al., 1995; Batt et al., 1999; Robinson, 1997). These indices aimed to assess the presence and significance of “errors” in neural transmission for differences in intelligence (Deary and Caryl, 1997). In essence, they quantified the length of the average evoked potential wave, with the

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rationale being that greater variability in neural transmission created greater variability in the waves elicited on individual trials, in turn leading to a smoother, *less* complex average wave in lower ability individuals, and thus a shorter string length (Hendrickson and Hendrickson, 1980). Although variability in neural responding is conceptually appealing as a variable that might differentiate high and lower ability individuals at the biological level, as recently recounted by Mackintosh (2011), there are a number of methodological concerns related to the string length measure (Robinson, 1997). After several groups found either zero or negative associations between string length and intelligence (Barrett and Eysenck, 1994; Batt et al., 1999), the measure largely fell out of favor. Thus, following the challenges to classic ERP measures of neural variability, the current ERP-intelligence literature is largely characterized by amplitude and latency effects that represent averaged responses over trials, with only a small number of reports investigating other measures (e.g., Jaušovec and Jaušovec, 2000; Saville et al., 2011).

In recent years significant progress has been made in the field of electrophysiology, particularly in terms of the increasing sophistication and ease of investigating time-frequency characteristics of neural responses (Makeig et al., 2004). These measures provide distinct information from ERPs, largely due to their ability to quantify variability in the phase of neural responses over trials, or the consistency of neural response timing in specific frequency bands and time points relative to experimental events. The importance of phase variation in neural dynamics is increasingly being recognized. Various phase-dependent measures are under investigation as possibly providing fundamental mechanisms for coordinating information processing in the brain (Buzsáki and Draguhn, 2004; Canolty and Knight, 2010; Varela et al., 2001), and abnormal phase dynamics differentiate healthy individuals from patient groups with various neurological and psychiatric conditions (Uhlhaas and Singer, 2006, 2010). In the case of cross-trial phase consistency, the inter-trial phase clustering measure (ITPC) quantifies the consistency of signal phase angle over trials, at each given time-frequency point relative to experimental events. Conceptually then, ITPC provides information about the overall consistency or uniformity of the neural response over trials, and thus may provide a more robust way to operationalize neural reliability.

Based on these considerations, the present study sought to revisit the construct of neural reliability in relation to intelligence, with a focus on the ITPC measure. The rationale for our specific approach is as follows. Given that efficient coordination of early perceptual circuits may be necessary for effective stimulus evaluation and responding, and the substantial literature supporting relations between basic sensory discriminations and intelligence (Jensen, 2006; Melnick et al., 2013), we reasoned that greater reliability in early perceptual processing might be especially associated with intelligence. We focused our analyses on fluid intelligence (Gf) in particular on the expectation that dynamic brain activity would relate most strongly to fluid rather than crystallized skills or broader constructs such as general intelligence (see for example, Neubauer and Fink, 2003). To assess ITPC's sensitivity to factors that might influence neural reliability, we manipulated stimulus familiarity in an effort to produce varying levels of demand on the early perceptual system. Last, to evaluate the specificity of ITPC to neural reliability apart from related measures and constructs, we conducted analogous tests of our hypotheses using ERPs and time-frequency measures of neural activity, and also assessed the extent of overlap among the measures.

To those ends, we studied early perceptual responses to visual stimuli as quantified by ITPC, total event-related spectral power ("total power"), and ERP amplitudes. Neural activity was elicited by *non-target* stimuli during a classic, two-stimulus, visual oddball task (involving many Repeated non-targets and infrequent unfamiliar target stimuli) and during an "inverted oddball" task (involving exposure to many Novel non-target stimuli interspersed with infrequent familiar targets). This design enabled examination of neural reliability in response to a single Repeated stimulus versus continuously changing

stimuli, and hence a test of the relations between consistent responding and intellectual ability at different levels of demand on the early perceptual system. The analogous comparisons with total power and ERP amplitudes sought to clarify the extent of unique information provided by ITPC.

Based on the expectation that reliable responding would be most facilitated by Repeated stimulus exposure and less facilitated under conditions of continuously changing stimuli (because different stimuli should recruit slightly different networks within the perceptual system; Cox and Savoy, 2003; Tanaka, 1996), we hypothesized that Repeated stimuli would elicit greater ITPC than Novel stimuli. Along the same lines, we hypothesized that while greater ITPC in general may predict higher Gf this should be especially true in the Novel stimulus condition. Because total power also captures non-phase-locked activation, and ERPs can be distorted by latency jitter (which reduces their sensitivity to phase-locking *per se*), we hypothesized no differences between Repeated and Novel stimuli for those measures, and weaker relationships between those measures and Gf. Finally, in light of the expected overlap between the three measures of stimulus-related activity all acquired from the same data, we conducted a series of planned, follow-up analyses to further assess the uniqueness of any observed effects.

Materials and methods

Participants

Study participants were recruited from the local community through an existing database of individuals who had participated in prior studies of intelligence and creativity (Jung et al., 2010a,b), and from an advertisement posted 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 neurological or psychiatric illnesses, and to ensure they had normal or corrected to normal vision. Participants were compensated \$15 per hour for their time. Thirty individuals between the ages of 18 to 30 participated in the study. Participants had between 11 and 18 years of formal education ($\mu = 14$, $SD = 2.2$), and were on average 23 years old at the time of cognitive testing and EEG recording. Following EEG data processing described below, a total of 29 participants (10 women) had sufficient numbers of artifact-free trials in both conditions, and were included in the final study dataset.

Stimuli

Stimuli consisted of 411 black and white line drawings depicting common objects (animals, tools, musical instruments, vehicles, etc.) which were taken from the larger set of 520 stimuli developed by the Center for Research in Language's International Picture Naming Project (Bates et al., 2003). Both the full set and subsets of these stimuli have been widely utilized in fMRI research (e.g., Saccuman et al., 2006; Stark and Squire, 2000) and EEG research on repetition priming (Gruber and Müller, 2005). The specific subset selected for the study was chosen on the basis of comparable visual complexity as assessed by digital file size, and comparable naming reaction times (Szekely et al., 2004). For each participant, a pseudo-random number generator was used to select a unique set of 289 stimuli from the larger subset.

Experimental session

Participants were seated in a sound and light-attenuated room for EEG acquisition. The stimuli consisted of black drawings on a white background and were in turn centrally presented on a larger gray background on a monitor located approximately 1.5 m in front of the participant. Drawings subtended 3.2° by 3.0° of visual angle. Participants completed a four-minute eyes-closed resting period prior to the

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