ERP correlates of the decision time-IQ relationship: The role of complexity in task- and brain-IQ effects

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1. Introduction

1.1. General background

A longstanding goal of intelligence research has been to identify simpler processes that might clarify the fundamental basis of the construct (Burt, 1909; Spearman, 1904). In the experimental tradition, such work has succeeded in establishing relations between intelligence and various chronometric and psychophysical tasks (Acton & Schroeder, 2001; Deary, Bell, Bell, Campbell, & Fazal, 2004; Deary, Der, & Ford, 2001; Sheppard & Vernon, 2008), suggesting that, indeed, variation in more basic processes is relevant to intelligence. Simultaneously, although physiological research on intelligence has gained considerable momentum (Haier, 2016), much of this progress has been in the anatomical realm (i.e., Parieto-Frontal Integration Theory (P-FIT); Jung & Haier, 2007; Basten, Hilger, & Fiebach, 2015; Deary, Penke, & Johnson, 2010; Gläscher et al., 2016; and similar models, Duncan, 2013), and sheds little light on the neural dynamics of chronometric effects. Thus, although each of these fields has had important success, neither approach alone informs their intersection.

An improved understanding of the neural basis of chronometric effects is crucial to broader reductive work on intelligence. While chronometric studies generally test hypotheses at the level of psychological processes (e.g., “mental speed”), the field should arguably seek to first identify neural mechanisms, which in turn can inform the relevant psychological dimensions. That is, by first understanding which neural networks underlie various task-IQ relations and why, the field may then be poised to understand how those ostensibly simpler processes contribute to broader intelligence. Given their excellent temporal resolution, experimental EEG and ERP studies are likely best positioned to clarify the neural basis of chronometric effects. However, due to a number of factors, the existing literature is somewhat limited in this respect.

1.2. Challenges in ERP-intelligence research

First, although many studies have documented various ERP-intelligence relations (for an early review, see: Deary, 2000, Chapter 9), the field as a whole remains relatively unintegrated, and permits only limited synthesis. For example, the bulk of this literature has focused on broadly psychophysical tasks such as the oddball paradigm, while a much smaller number of studies have examined more traditional elementary cognitive tasks (ECTs). Within the former group of studies, the best replicated effects have been the generally negative and positive relationships between...
intelligence and the respective latency and amplitude of the P300 component (Bazana & Stelmack, 2002; Beauchamp & Stelmack, 2006; Jaušovec & Jaušovec, 2000; Pascalis, Varriale, Fulco, & Fracasso, 2014; Pascalis, Varriale, & Matteoli, 2008; Troche, Houlihan, Stelmack, & Rammsayer, 2009; Walhovd et al., 2005; Wronka, Kaiser, & Coenen, 2013). A partially-overlapping group of studies has shown analogous effects on the mismatch negativity (Bazana & Stelmack, 2002; Beauchamp & Stelmack, 2006; Houlihan & Stelmack, 2012; Pascalis et al., 2014; Pascalis & Varriale, 2012; Troche et al., 2009).

The literature on ERP correlates of ECTs per se is not only more sparse, but also less consistent. A small number of studies have focused on Inspection Time, finding that shorter latencies (Burns, Nettelbeck, & Cooper, 2000), and larger amplitudes (Hill et al., 2011) of the N1 component, the rise time of the P2 (Y. Zhang, Caryl, & Deary, 1989) and the amplitude of the P3 component (Alcorn & Morris, 1996) are linked to higher intelligence. The remaining studies have examined a number of other tasks (e.g., flanker tasks, simple and choice RT, Sternberg) and ERP components (N100, P200, N200, P300, etc.), finding various mixed effects (Brumback, Low, Gratton, & Fabiani, 2004; Liu, Xiao, Shi, Zhao, & Liu, 2011; McGarry-Roberts, Stelmack, & Campbell, 1992; Schubert, Hagemann, Voss, Schankan, & Bergmann, 2015; Q. Zhang et al., 2007).

Thus, although each individual study provides support for the general approach, they have not yet coalesced around a small set of principles or the most relevant ERP correlates.

A second and perhaps related limitation of this literature relates to the fact that various ERP effects are often task- and regionally-specific. This is true even of studies examining the same ERP component. Taking the P300 as a well-studied example, although some studies have found evidence for smaller amplitudes as task difficulty increases (Pascalis et al., 2014; Sculthorpe, Stelmack, & Campbell, 2009), the evidence is mixed (Bazana & Stelmack, 2002; Beauchamp & Stelmack, 2006; Pascalis et al., 2008; Schubert et al., 2015). Similarly, it has been shown that variation in task parameters such as task saliency and difficulty (Kok, 1997, 2001), stimulus position (e.g., the position of an “x” within a series of “x’s” and “o’s”; Pelz, Gratton, & Fabiani, 2011) and memory encoding vs. retrieval (Houlihan, Stelmack, & Campbell, 1998) can affect P300 amplitudes in opposite ways.

Moreover, not only is the P300 differentially affected by various task parameters, but under particular conditions, distinct P3a and P3b components can be functionally and topographically dissociated (Kolossa, Kopp, & Fingscheidt, 2015). Unfortunately, despite important differences between the two in reflecting more bottom-up versus top-down attentional processes (Polich, 2007), the ERP-intelligence literature has not always maintained this distinction (for an exception see: Wronka et al., 2013). Thus, insofar as various manipulations not only affect the nature of a given ERP component, but also its contribution to between-subjects effects (e.g., Houlihan et al., 1998; Pelz et al., 2011; Troche et al., 2009), progress in this area will depend upon carefully delineating the ways in which experimental parameters affect correlations with intelligence. In short, while some ERPs may exhibit a straightforward and unconditional relationship to intelligence, the relations of others are apt to be task-, region-, and state-dependent.

A third and final challenge facing this literature concerns the spatial ambiguity inherent to EEG. Specifically, since the signal recorded at any given electrode represents a relative measurement (i.e., an electrical potential difference relative to an arbitrary reference) even studies that employ identical tasks and comprehensive electrode arrays may obtain different scalp topographies if they use different referencing schemes (Kayser & Tenke, 2010). This spatial ambiguity is then further compounded by volume conduction, in which the resistivity of the skull causes scalp surface potentials to be highly correlated or “smoothed” across nearby electrodes (Kayser & Tenke, 2015). Simultaneously, this entails that the signal recorded at each electrode reflects a weighted sum of all its underlying sources (Luck, 2014; Nunez & Srinivasan, 2006). Although alternative techniques can now greatly mitigate these difficulties (e.g., the Laplacian transformation, source localization methods), these have generally not been adopted in intelligence research. Thus, since much of this literature has generally used small electrode arrays and traditional referencing schemes, this limited spatial resolution has tended to preclude a more detailed discussion of the underlying neural mechanisms.

1.3. Present study

To help address these limitations, and advance mental chronometry, the present study re-examined ERP correlates of the DT-IQ relationship using contemporary techniques that enable more precise hypothesis testing. First, to permit more detailed inferences about the relevant neural processes, the study used the scalp surface Laplacian transform to better characterize brain potentials. As recently detailed by Kayser and Tenke (2015) the surface Laplacian relies on the mathematics of volume conduction and appropriate biophysical assumptions to transform the scalp-recorded surface potentials at each time point into a reference-free estimate of the current flowing between the skull and scalp at each electrode, providing estimates of cortical activity at the dural layer for localized sources (Kayser & Tenke, 2015; Nunez & Srinivasan, 2006). Thus, rather than reflecting the traditional potential difference in microvolts (μV), the transformed signal represents a current density estimate with a spatial extent (μV/cm²). Because the transformation involves taking a spatial derivative of the scalp topography (i.e., a rate of change), it highlights locations of large voltage changes between nearby electrodes (Kayser & Tenke, 2015). Thus, it acts as a spatial filter, and is most sensitive to local cortical generators at the expense of more distributed or deeper sources (Nunez & Srinivasan, 2006). As a result, use of the surface Laplacian greatly improves spatial resolution of local cortical effects.

Second, given the need to better characterize how experimental parameters influence ERP-intelligence relations, the present study employed multi-level modeling (MLM) in the analytic approach. Since MLM can accommodate nested data structures, it enables simultaneous modeling of within-subjects effects (condition effects) and between-subjects effects (individual differences), as well as their interactions (e.g., whether the magnitude of a condition effect depends on IQ: Raudenbush & Bryk, 2002). This approach is especially powerful in the context of mental chronometry, as it allows for testing longstanding questions such as whether an individual’s simple decision time (DT) versus their response decrement across more difficult conditions better predicts their intellectual ability (Deary et al., 2001; Jensen, 1998). Importantly, using an identical model structure, one can then test whether the neural correlates of DT are similarly influenced by task complexity, and whether complexity in turn moderates their relation to intelligence. An additional benefit of the MLM approach is that it allows for level 1 variables (condition effects) to vary across individuals (random effects), enabling better model fit for individual differences.

Finally, the present study adopted the conceptual approach originally advocated by Stankov and colleagues, which emphasizes appealing to task parameters over psychological processes in explaining chronometric effects (Stankov & Roberts, 1997). Specifically, there is a large body of evidence demonstrating that as a task becomes more complex, it relates more strongly to intelligence (Carroll, 1993; Dettmerman, 1987; Gottfredson, 1997; Jensen, 1987; Neubauer, 1991; Sheppard & Vernon, 2008; Stankov & Crawford, 1993). Statistically, this would imply that task parameters moderate the task performance-IQ relationship, with complexity presumably being this moderating factor. Stankov and Crawford (1993) define complexity as the number of component cognitive processes required to successfully perform a task. Inspired by that framework, a primary aim of the current study was to characterize whether and how DT and specific ERP components vary with increasing task complexity, and in turn, whether complexity alters their relations with IQ.

Arguably, the complexity account provides a crucial premise for electrophysiological studies. Namely, that as task parameters change
resulting in stronger correlations with intelligence, successful task performance should increasingly draw on the processes most implicated in the construct. On that basis, one would expect that as the task-IQ relationship increases, the task in question should more strongly draw upon the most important neural mechanisms. At the same time, there is of course also the possibility of more complex interactions. For example, the study by Neubauer and Fink (2003) explicitly examined the effect of complexity on EEG-IQ relations, and found a more nuanced pattern of effects. While task performance among their male participants did relate more strongly to ability under more demanding conditions, this same interaction was not found in the EEG measures. Thus, while complexity might affect brain-IQ correlations the same way it affects task-ability relations, these patterns might also dissociate across the two levels of analysis. In either case, just a small number studies have systematically addressed these questions (Caryl & Harper, 1996; Houlihan & Stelmack, 2012; Neubauer, Fink, & Schrausser, 2002; Zhang et al., 2007), highlighting the need for more work in this area. In short, by focusing more directly on the determinants of the task-ability relationship, and improving resolution of those effects in the brain, the present study aimed to better characterize the role of specific neural processes in the DT-IQ relationship.

1.4. Hypotheses

To that end, the present study examined the effect of task complexity on DT and its associated ERP correlates, and their relationships with IQ, as assessed via the widely-studied Hick paradigm (Hick, 1952). Task complexity was manipulated across three levels of potential target stimuli (“bits” of information in the Hick nomenclature), where 0, 1, and 2 bits corresponds to 1, 2, or 4 potential targets. The experimental conditions were statistically modeled in MLM at level 1, with DT in the 0-bit condition (i.e., simple DT) reflecting the model intercept, and dummy codes reflecting the change in DT from 0 to 1 bit and 0 to 2 bits (representing changes in task complexity). IQ was included as a level 2 predictor, acting as a cross-level interaction to test if the relationship between the outcome variable (i.e., DT or a given ERP feature) and IQ was moderated by the task condition (number of bits). For the model predicting DT, we hypothesized that DT would increase with increasing bits of information, and that IQ would predict the magnitude of those condition effects.

Given the lack of precedent for the present ERP approach, those analyses were motivated using a two-step process. First, a grand-average scalp map across all conditions and participants was examined to identify components revealed by the Laplacian transformation. As expected, this technique revealed a number of spatiotemporally-circumscribed neural processes in the time range prior to DT. Next, zero-order correlations were run between DT, IQ, and ERP components as a data-reduction strategy to motivate a set of formal models. Only those ERP features (amplitudes or latencies) that were significantly correlated with either DT or IQ were analyzed via MLM. Thus, this strategy reduced the number of models tested, thereby avoiding Type I errors.

For those ERP components for which correlations suggested latency effects, we expected to observe longer latencies with increasing task complexity, consistent with the prior ERP literature. Although similar considerations would intuitively suggest that ERP amplitudes would tend to decrease with increasing task demands (Polich, 2007), as noted above, these effects appear to be highly task-specific, and various parameters can have opposite effects. Thus, given the generally positive influence of attention and salience on ERP amplitudes (Kok, 1997) and the general structure of the Hick paradigm as an essentially simple task involving a highly salient visuospatial manipulation, we reasoned that the net effects of increasing target salience and task difficulty would result in higher amplitudes for all ERP components with increasing bit level. Finally, based on the above considerations related to the role of complexity in the task-ability relationship, we expected ERP measures to best predict IQ under higher bit conditions. In summary, we hypothesized that DT and ERP amplitude and latencies would all increase with increasing task complexity, and that IQ would moderate those effects.

2. Methods

2.1. Participants

One hundred and twenty-six undergraduate students were recruited through the University of Utah Psychology Department participant pool. All study procedures were reviewed and approved by the University’s Institutional Review Board, and all participants gave written informed consent prior to participating. All participants were right-handed, reported normal or corrected color vision and no history of neurological conditions, diagnosed psychiatric illnesses, or current psychoactive medications. Data from 15 participants were excluded from analyses for the following reasons: technical failures during EEG data recording (n = 7), disclosure of previous exposure to the WAIS-IV (n = 1), and excessive EEG artifacts (resulting in fewer than 30 useable trials per condition; n = 7). The final sample consisted of 111 participants (68 women), with a mean age of 22.63 (SD = 4.98, Range = 18–45).

2.2. Experimental task

The Hick paradigm was administered using a computer and response console interface with the screen located approximately one meter from the participants at eye level. Stimuli were displayed and behavioral data were recorded using Presentation software (version 16.3, Neurobehavioral Systems). Behavioral responses were gathered using the response console from the Behavioral Dyscontrol Scale-Electronic Version (Suchy, Derbidge, & Cope, 2007), which contains an array of five yellow buttons surrounding a red button, which acted as a home key. The lower right yellow button was not used, and the other four yellow buttons acted as possible response targets. Prior to beginning the task itself, each participant was administered 18 practice trials (in three separate blocks by condition) to ensure understanding of the task. Each trial replicated the button configuration of the console on the screen, with the color of the relevant buttons changing to indicate selection of the home key, inter-trial and inter-stimulus intervals (ISI), imperative stimuli, etc. (see Fig. 1). Following Neubauer (1991), to mitigate confounding effects of order and strategy, bit conditions (with 0, 1, and 2 bits corresponding to 1, 2, or 4 potential targets) were randomized across trials rather than in blocks, and the imperative stimulus immediately reverted to a neutral color following the release of the home key.

Each participant was administered 288 trials (divided into four

![Fig. 1. Trial structure for the Hick paradigm. An example trial from the 2-bit condition is shown.](image-url)
blocks separated by brief breaks) which were divided pseudo randomly into the three bit conditions. Participants performed the task using their first finger on their right hand. For each trial, participants were prompted to begin the trial when the on-screen depiction of the home key was illuminated in blue, at which time they were to press and hold the home key until their eventual response. Upon holding the home key, the possible target buttons for that trial (1, 2, or 4) were then illuminated in yellow. After fixed delay of three seconds, a warning tone (S1; 1000 Hz, 100 millisecond (ms) duration) sounded, which was followed by a variable ISI (range = 1000–2400 ms, sampled in 50 ms intervals from a rectangular distribution) and presentation of the imperative stimulus (S2). The S2 was presented by changing the color of the target stimulus from yellow to gray. Once the participant lifted their finger from the home button, the remaining target buttons were also grayed-out. Reaction time (RT) was measured as the time from the onset of the S2 until the participant's manual response, with decision time (DT) being the interval between the presentation of the S2 and the release of the home key. Following the response, there was a fixed 500 ms inter-trial interval. If participants removed their finger from the home button prematurely, or pressed it before the end of the ITI, an error noise was presented. Participants received no other feedback regarding their performance.

2.3. Procedure

2.3.1. Cognitive assessment

Upon arrival to the study and provision of informed consent, each participant was administered the eight subtest version of the Wechsler Adult Intelligence Scale-IV (Wechsler, 2008), which permits calculation of a pro-rated Full-Scale IQ (FSIQ). The subtests included (in order of administration) Block Design, Similarities, Digit Span, Matrix Reasoning, Arithmetic, Information, Symbol Search and Coding, and were administered by trained, supervised research assistants in a quiet room.

2.3.2. Electrophysiological recordings

Participants were then seated in a light- and sound-attenuated room for the Hick task and EEG recording. EEG signals were recorded using a 64 channel Ag/AgCl electrode WaveGuard Cap (Advance Neurotechnology, ANT Company, Enschede, The Netherlands) arranged according to the 10–10 system (Oostenveld & Praamstra, 2001). The continuous data were sampled online at 1024 Hz via the ASA-lab EEG data acquisition system (version 4.7.12, ANT Company, Enschede, The Netherlands), referenced to the average of all connected unipolar inputs (64 in all cases). Electrode AFz served as the ground. The average recording system (Oostenveld & Praamstra, 2001). The continuous data were sampled online at 1024 Hz via the ASA-lab EEG data acquisition system (version 4.7.12, ANT Company, Enschede, The Netherlands), referenced to the average of all connected unipolar inputs (64 in all cases). Electrode AFz served as the ground. The average reference was maintained offline for the traditional surface potential measurements. An additional set of two bipolar electrodes were placed above and below the left eye, and at the external canthi of both eyes to record the electrooculogram. Electrode impedances were maintained below 20 kΩ, with the majority of electrodes below 10 kΩ. Participants completed two 3.5 min eyes-closed and eyes-open resting conditions prior to completing the Hick task.

2.3.3. EEG pre-processing

EEG were processed using ASA-lab software package, as well as custom written MATLAB scripts (version R016b, Mathworks, Natick, MA) in conjunction with the Current Source Density (CSD) toolbox (Kayser, 2009; Kayser & Tenke, 2006), which is freely available online at: http://psychophysiology.cpmc.columbia.edu/Software/CSDtoolbox/. Scalp topographies were visualized using the EEGlab topoplot.m function (Delorme & Makeig, 2004). The continuous data were first down-sampled to 512 Hz, followed by removal of blink-related artifacts via the topographical principal components based method in ASA-lab. Individual channels were then visually inspected for drift, high frequency activity, or other artifacts, and suspect channels were interpolated using the spline interpolation method in ASA-lab. The continuous data was then segmented into epochs spanning from − 500 to 700 ms relative to the S2 for each condition. Epochs containing visually identifiable artifacts were excluded from analysis, and the remainder were loaded into MATLAB and individually linearly de-trended. An automated algorithm excluded any remaining trials with voltages exceeding 75 μV at any point, or an absolute voltage change of 60 μV within a 100 ms window. The results of the automated procedure were then visually inspected to ensure the quality of the remaining data, and the lowest common denominator of the remaining trials was taken to equalize trial counts across conditions. The Laplacian transformation was then applied to the single trials using the recommended default parameters from the CSD toolbox (head radius = 10 cm, spline flexibility = 4, and spline regularization constant = 10^−5). The trials were then divided into conditions, baseline-corrected from − 300 to − 100 ms prior to the S2, trimmed to a final length of − 300 to 700 ms, and averaged over trials. To facilitate accurate estimation of ERP component latencies, the resulting ERPs were then low-pass filtered at 10 Hz as per Luck's recommendation (Luck, 2014).

2.3.4. ERP analysis strategy

In order to obtain a maximally-unbiased assessment of potential condition effects on the surface Laplacian measurements (Cohen, 2014), ERPs were averaged across all participants and conditions by measurement type to produce grand-average scalp topographies. For the Laplacian-transformed data, inspection of this grand-average revealed two distinct posterior components following the S2 (see Fig. 2). The first of these was a bilateral parieto-occipital component, which peaked at approximately 300 ms post stimulus (likely a P2; Freunberger, Klimesch, Doppelmayr, & Höller, 2007), followed by a right-lateralized parietal positivity, peaking at approximately 500 ms (here termed SL-P3, possibly representing the latter portion of the late positive complex; Dien, Spencer, & Donchin, 2004). In addition, an intervening fronto-central negativity (potentially an anterior N2) was observed with a peak around 300–400 ms. This general scalp topography was also evident in each individual bit condition.

To maximize the reliability of the estimated ERPs, each component was calculated based on an average of two or more electrodes, in conjunction with a semi-automated procedure for determining peak ERP latencies. For each component, the peak amplitude following the S2 was identified and visually inspected individually to ensure that no artifactual local minima/maxima had erroneously influenced its calculation. The P2 was scored as the maximum peak between 200 and 500 ms and the N1 was scored as the negativity immediately preceding the P2 (approximately 100–250 ms). The N2 was scored as the peak negativity in each condition, while the SL-P3 was the highest peak in the time range following the P2 (approximately 300–700 ms). When there were multiple possible peaks, emphasis was placed on peaks that had a similar time course across conditions within an individual. Once each peak had been manually verified, its latency was recorded relative to the onset of the S2, and its mean amplitude was calculated as the average voltage within a surrounding 100 ms window. In this manner, the P2 component was calculated as the averaged activity across electrodes PO7 and PO8 reaching a maximum following the S2, and the N2 component was calculated as the peak negativity averaged across electrodes FCz and Cz. The SL-P3 was defined as the peak amplitude subsequent to the P2 component averaged across electrodes C4, C6, and CP4. To facilitate comparisons with the prior literature, the averaged referenced surface potential P300 (SP-P3) was calculated from electrode Pz, and then using the same semi-automated scoring procedure to find the maximum value following the S2. These data and related results are presented in the Supplementary material. Of note, the topography of the SP-P3 largely resembles that of the single SL-P3 component obtained from the Laplacian transformation (see Supplementary Fig. 1).

2.3.5. Analytic approach

The goal of the study is to examine how the relationship between DT/brain activity and IQ changes across conditions in the Hick
paradigm. To this end, we devised a set of multilevel models to better understand the neural correlates of the DT-IQ relationship. The variables tested using these multilevel models were selected on the basis of significant findings in zero order correlations in an attempt to reduce the number of models being tested. All MLM analyses were conducted in HLM7 (Raudenbush, Bryk, Cheong, & Congdon, 2011) and correlations were performed in MATLAB using the Robust Correlation toolbox (Pernet, Wilcox, & Rousselet, 2013), using the default values. Conventional Pearson r correlations are sensitive to outliers, which the percentage-bend correlation bypasses by down-weighting marginal outliers in its estimation of the linear relationship between the variables. Thus, the percentage-bend correlation is more robust in the presence of outliers and reduces Type I error (Pernet et al., 2013). In addition, the Robust Correlation toolbox provides 95% bootstrapped confidence intervals regarding the range of each effect, and a resulting decision about significance.

The multilevel models used a series of dummy codes at level 1 to code for the condition effects on the outcome variable (e.g., DT, P2 amplitude, etc.), which were then modeled at level 2 by IQ. The intercept of the level 1 model (β₀) corresponds to the level of the outcome variable in the 0-bit condition, while the two dummy code variables correspond to the change in outcome variable between the 0–1 (β₁) and the 0–2 bit (β₂) conditions. Multilevel modeling allows the condition effects modeled at level 1 to become individual difference variables to be modeled at level 2 and predicted by IQ as fixed effects (γ₀₀, γ₁₀, & γ₂₀). The IQ term at level 2 is a cross-level interaction and reflects whether the magnitude of the condition effects (γ₁₀ & γ₂₀) are related to IQ. An alternative and equally valid interpretation is whether the relationship between the outcome variable and IQ is moderated by the bit condition. This approach allows us to see whether the outcome variables and the 1 and 2 bit condition effects are correlated with IQ while controlling for the 0-bit condition.

MLM also allows the estimates of level 1 variables to vary as a function of individuals (random effects), as opposed to assuming that a condition effect has the same magnitude across all participants. As such, random effects were included for the estimates of the intercept (β₀, u₀), and the 1-bit (β₁, u₁) and 2-bit (β₂, u₂) dummy codes. Since only dummy codes were used in level 1, they were entered into the model un-centered. Level 2 variables (only IQ) were grand-mean centered. HLM7 offers robust estimation of fixed effects, which are reported. The equation for these models is depicted below, exemplifying DT as the outcome. The other models merely substitute ERP features as the outcome variables. Standardized coefficients are reported in the text, while Table 3 reports the unstandardized units of the coefficients (ms or μV/cm²).

\[ L1: \]
\[ DT_j = \beta_0 + \beta_1 \text{BIT}_1 + \beta_2 \text{BIT}_2 + e_j \]

\[ L2: \]
\[ \beta_0 = \gamma_{00} + \gamma_{01} \text{IQ} + u_j \]
\[ \beta_1 = \gamma_{10} + \gamma_{11} \text{IQ} + u_j \]
\[ \beta_2 = \gamma_{20} + \gamma_{21} \text{IQ} + u_j \]

3. Results

3.1. Descriptive statistics and zero-order correlations

The mean pro-rated FSIQ score was 110.8 (SD = 10.78, Range = 85–136), reflecting the undergraduate study sample. Median DT increased with increasing numbers of bits (0-bit: M = 310.41, SD = 66.99; 1-bit: M = 351.58, SD = 71.05; 2-bit: M = 372.12, SD = 71.52) as confirmed in the MLM analysis below. Descriptive statistics for the ERP components are presented in Table 1. As noted above, robust, zero-order correlations were examined to help motivate the inclusion of particular ERP features in the MLM analysis. With respect to IQ, both DT and the amplitude of the P2 had significant correlations in some of the bit conditions (DT: 0-bit: r = −0.36; 1-bit: r = −0.35; 2-bit: r = −0.36, all ps < 0.001; P2: 0-bit: r = 0.12, n.s.; 1-bit: r = 0.23, p = 0.019; 2-bit: r = 0.22, p = 0.026). No other ERP measures had significant correlations with IQ. With respect to DT, the amplitude of the P2, the latency of the N2, and both the amplitude and
Table 1
Descriptive statistics for ERP amplitudes and latencies.

<table>
<thead>
<tr>
<th>Bits</th>
<th>Amplitude</th>
<th>Latency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>SL-N1</td>
<td>Zero</td>
<td>−0.03</td>
</tr>
<tr>
<td></td>
<td>One</td>
<td>−0.07</td>
</tr>
<tr>
<td></td>
<td>Two</td>
<td>−0.06</td>
</tr>
<tr>
<td>SL-P2</td>
<td>Zero</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>One</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Two</td>
<td>0.25</td>
</tr>
<tr>
<td>SL-N2</td>
<td>Zero</td>
<td>−0.19</td>
</tr>
<tr>
<td></td>
<td>One</td>
<td>−0.23</td>
</tr>
<tr>
<td></td>
<td>Two</td>
<td>−0.25</td>
</tr>
<tr>
<td>SL-P3</td>
<td>Zero</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>One</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Two</td>
<td>0.22</td>
</tr>
</tbody>
</table>

Note: SL = Surface Laplacian Transformed; amplitudes reflect μV/cm²; Latencies are in milliseconds.

Table 2
Zero-order bend correlations of ERP amplitudes and latencies with decision time and IQ.

<table>
<thead>
<tr>
<th>ERP Component</th>
<th>ERPAmplitude</th>
<th>ERPLatency</th>
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<tr>
<td></td>
<td>DT</td>
<td>IQ</td>
</tr>
<tr>
<td>Bits</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>SL-N1</td>
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<td></td>
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<td></td>
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<td>SL-P2</td>
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<td>−0.345</td>
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<td></td>
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<td></td>
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Note: DT = Decision Time; SL = Surface Laplacian Transformed. All p-values are based on 95% bootstrapped confidence intervals. ERP-DT correlations reflect the relationship between each component and DT at the given number of bits, e.g., Zero-bit SL with Zero-bit DT, etc. Latencies reflect maximum and minimum latencies. ⁎⁎ p < 0.05, uncorrected. ⁎⁎⁎ Bonferroni corrected at p < 0.05/60.

3.2. Examination of condition effects in moderating the DT-IQ relationship

3.2.1. DT

The intercept of the level 1 model (γ00) was a significant predictor of DT (γ00 = −0.45, p ≤ 0.001), indicating that, as expected, a participant’s 0-bit DT predicts their DT across the various conditions. The condition effects (bit1 and bit2) were both also significant in the prediction of DT (γ10 = 0.54, p < 0.001; γ20 = 0.81, p < 0.001), such that DT was on average 41.17 ms slower in the 1-bit condition and 61.7 ms slower in the 2-bit condition. IQ significantly predicted DT in the 0-bit condition (γ10 = −0.30, p < 0.001), but did not significantly predict the 1-bit (γ11 = −0.03, p = 0.37) or 2-bit (γ21 = −0.04, p = 0.152) condition effects. This suggests that, contrary to expectations, the DT-IQ relationship did not increase with greater task complexity in the present iteration of the Hick paradigm. This is not to say that DT in the 1 and 2 bit conditions do not correlate with IQ (which is demonstrated by the zero-order correlations), but only that when all three conditions are modeled simultaneously, more intelligent people do not show a significantly different change in DT across conditions compared to less intelligent people. There were significant random effects for the intercept (u0: τ = 3904.20, χ² = 4909.02, p < 0.001) and 2 dummy code variables (u1: τ = 334.19, χ² = 314.61, p < 0.001 u2: τ = 495.07, χ² = 413.19, p < 0.001), indicating that the condition effects systematically varied as a function of person and were not fully explained by IQ.

3.2.2. P2 amplitudes

The P2 amplitude demonstrated significant zero-order correlations with DT and IQ, thus it was analyzed using MLM. The intercept of the level 1 model (γ00) was a significant predictor of P2 amplitude (γ00 = −0.37, p < 0.001), again indicating that the amplitude in the 0-bit condition predicts the amplitude across conditions. The condition effects (bit1 and bit2) both also significantly predicted P2 amplitude (γ10 = 0.46, p < 0.001; γ20 = 0.64, p < 0.001) such that the amplitude was on average 0.07 larger in the 1-bit condition (in μV/cm²) and 0.1 larger in the 2-bit condition. IQ was not a significant predictor of P2 amplitudes in the 0-bit condition (γ10 = −0.0001, p = 0.908) or 2-bit condition (γ11 = 0.13, p = 0.024) and 2-bit latency of the SL-P3 all were significantly correlated (see Table 2). Each of these was in turn included as an outcome variable in the subsequent set of MLMs.
amplitude was on average 0.02 and 0.02 larger (in latency was on average 27.67 ms and 30.03 ms longer and the SL-P3-3.2.3. N2 and SL-P3 χ² were both significant indicating that the condition effects systematically varied as a function of person and were not fully explained by IQ.

3.2.3. N2 and SL-P3

The N2 latency and both the latency and amplitude of the SL-P3 had significant correlations with DT, and hence were analyzed with MLM. The intercepts of the level 1 models (γ00) were all significant (N2-Lat: γ00 = 472.00, p < 0.001; SL-P3-Ampl: γ00 = 472.00, p < 0.001; SL-P3-Lat: γ00 = 472.00, p < 0.001). The condition effects (bit1 and bit2) were both significant in the prediction of N2 latency (γ10 = 0.24 p < 0.001; γ20 = 0.26, p < 0.001) and the SL-P3 amplitude (γ10 = 0.19 p < 0.001; γ20 = 0.16, p < 0.001), such that the N2 latency was on average 27.67 ms and 30.03 ms longer and the SL-P3-amplitude was on average 0.02 and 0.02 larger (in μV/cm²) in the 1- and 2-bit conditions (respectively). The SL-P3 latency did not have a significant 1-bit condition effect (γ10 = 0.02, p = 0.686), but did have a significant 2-bit condition effect (γ20 = 0.14, p = 0.013), such that it was 15.26 ms longer in the 2-bit condition. IQ did not predict either the 0-bit value (N2-Lat: γ01 = −0.14, p = 0.192; SL-P3-Ampl: γ01 = −0.01, p = 0.908; SL-P3-Lat: γ01 = −0.16, p = 0.098), nor the 1-bit (N2-Lat: γ11 = −0.02, p = 0.718; SL-P3-Ampl: γ11 = −0.02, p = 0.757; SL-P3-Lat: γ11 = 0.03, p = 0.637) or 2-bit condition effects (N2-Lat: γ21 = 0.1, p = 0.117; SL-P3-Ampl: γ21 = 0.01, p = 0.796; SL-P3-Lat: γ21 = 0.02, p = 0.642). For the N2 latency (u0: τ = 16,315.9 χ² = 1899.54, p < 0.001; u1: τ = 66.98 χ² = 355.23, p < 0.001; u2: τ = 6011.48, χ² = 438.83, p < 0.001), SL-P3 amplitude (u0: τ = 3.01, χ² = 176.92, p < 0.001; u1: τ = 0.00, χ² = 170.04, p < 0.001; u2: τ = 0.00, χ² = 148.11, p < 0.001), and SL-P3 latency (u0: τ = 12,227.28, χ² = 1354.59, p < 0.001; u1: τ = 1968.94, χ² = 209.09, p < 0.001; u2: τ = 1968.94, χ² = 204.81, p < 0.001), the random effects for the intercept and bit1 and bit2 variables were all significant, indicating that the condition effects for each ERP feature systematically varied as a function of person and were not fully explained by IQ.

4. Discussion

The current study examined neural correlates of the DT-IQ relationship, using methods that allowed for a more precise characterization of the implicated ERP components and their patterns of experimental and differential effects. The surface Laplacian transform revealed four ERP components in the time window of the surface potential P300 that, to our knowledge, have not been previously studied in the Hick paradigm or in relation to intelligence (though see: Schubert et al., 2015; which examined surface potentials). The observed components included two spatiotemporally distinct processes near the posterior cortices, including an earlier bilateral parieto-occipital component (likely a P2; Freunberger et al., 2007) and a later right parietal component ("SL-P3"); likely reflecting the latter portion of the late positive complex, as often associated with the surface P3; Garcia-Larrea & Cézanne-Bert, 1998; Matsuda & Nittomo, 2015; Sutton & Rutchkin, 1984). The Laplacian transform also highlighted potential roles for the N1, as well as an anterior N2 (Jemel, Achenbach, Müller, Röpcke, & Oades, 2002; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003; van Veen & Carter, 2002) or a Processing Negativity (Kok, 1997, 2001). Correlations indicated that the amplitude of the P2, the latency of the N2, and both the latency and amplitude of the SL-P3 were related to DT across bit levels (Table 2), while only the amplitude of the P2 and DT showed relationships with IQ. In contrast, while the surface potential P3 robustly predicted DT, it showed idiosyncratic effects with IQ, possibly reflecting its aggregation of multiple neural sources (see Supplementary material).

The Laplacian transform revealed several components which would have otherwise remained obscured, and through MLM, it allowed dissociations of their contributions to task performance vs. IQ. While DT and all three of the Laplacian ERP components analyzed displayed condition effects as a function of bit level, those effects do not necessarily reflect individual differences in intelligence. Rather, the neural processes they reflect appear to play different roles in DT versus IQ. For example, while the P2 amplitude did not show an association with IQ in the 0-bit condition, its increase in amplitude from 0 to 1-bit and 0 to 2-bits did. Conversely, while the N2 and SL-P3 components generally showed increasing amplitudes and/or latencies with increasing bits of uncertainty, and often zero-order correlations with DT, none of their condition effects related to IQ. This overall pattern is in stark contrast to the common assumption that the processes which promote faster response times in ECTs should also contribute to greater intelligence. Rather, it highlights the need to better understand which particular neural processes underlie the DT-IQ relationship and why.

4.1. The role of complexity in the task-ability relationship

As described in the Introduction, it is well-established that complexity plays an important role in the relationship between performance on a given task and intellectual ability. In a series of studies, Stankov and colleagues have further addressed the role of complexity in moderating the task-ability relationship, and the related question of what in turn makes any given task complex (Stankov, 2000; Stankov & Crawford, 1993; Stankov & Raykov, 1995). Although complexity can be operationally defined, at a conceptual level, it has been described as the number of cognitive elements contained in a task and the relations between them that must be apprehended in arriving at the solution (Stankov & Crawford, 1993; Stankov & Raykov, 1995). This same line of work has also emphasized a distinction between task difficulty and complexity, where difficulty is reflected in within-subjects effects (i.e., condition effects), and hypothetically, the relative dependence of task performance on similar types of cognitive processes. In contrast, complexity relates primarily to the task-ability relationship (i.e., patterns of covariance), and signifies a task’s relative dependence on distinct types of cognitive processes (Stankov, 2000; Stankov & Raykov, 1995).

This account of complexity and difficulty provides a natural framework for considering the implications of the present results, and suggests a nuanced picture regarding how those factors may operate in DT and ERP-IQ effects. First, based on the notion that difficulty primarily drives condition effects (Stankov, 2000), DT and all of the ERP features demonstrated clear effects of difficulty in the level 1 comparisons between simple DT and the two choice conditions (i.e., comparing 0 vs. 1-bit and 0 vs. 2-bits). Theoretically, this reflects increasing demands on similar processes. However, in contrast to predictions and prior literature (Deary et al., 2001; Sheppard & Vernon, 2008), IQ was not predicted by those condition effects. That is, because the increase in DT did not predict IQ, the present results do not support a stronger DT-IQ relationship between simple and choice DT, nor the claim for greater complexity in the 1 and 2-bit conditions. Stated another way, the present data are most consistent with the view that a given individual’s DT intercept in terms of Hick’s law is more related to their IQ than their slope across conditions (Deary, 2000; Jensen, 2006). This is in contrast to our hypothesis that the additional uncertainty about the target location at higher bits would require additional processes, thereby increasing complexity and causing the change in DT to covary with IQ.

Interestingly, although we did not find evidence for a complexity effect on DT, the change in P2 amplitude between simple and choice DT conditions was in fact moderated by IQ. Thus, this component showed evidence for difficulty as well as complexity effects. Not only did its amplitude increase with increasing task demands, but greater responsiveness to those demands predicted higher IQ. In contrast, while the
other Laplacian-based ERP features demonstrated difficulty effects, these effects showed no relation to IQ. These latter findings are consistent with the study by Neubauer and Fink (2003) who observed a similar pattern of EEG effects. Specifically, although they observed significant effects of task demands on EEG alpha power and event-related desynchronization, unlike their performance data, those effects did not interact with ability. Thus, like some of the current findings, those authors observed what would be likely considered a difficulty effect within the current framework.

4.2. A limitation and extension of the complexity account

Of note, while the complexity/difficulty account seems to otherwise accommodate the present results, the remaining DT-IQ effect in the 0-bit condition is more difficult to explain. Specifically, although complexity offers a compelling explanation for the level at which a given task will predict overall ability, it says little about why some tasks predict ability at all. This limitation is particularly acute for chromometric tasks, which by design minimize complexity in favor of conceptual and neural tractability. Thus, while increasing complexity would account for the typically larger task-ability relation for choice than simple RT, it is less clear how complexity explains why simple RT (or DT in the present case) predicts ability whatsoever (Deary et al., 2001). Similarly, for more psychophysical measures such as Inspection Time (Grudnik & Kranzler, 2001) and sensory discrimination (Acton & Schroeder, 2001; Deary et al., 2004), where the driver of individual differences appears to be the difficulty of the discrimination itself, it is unclear why increasingly fine discriminations would entail the coordination of greater numbers of distinct processes, as argued by the complexity account. In short, despite providing an otherwise powerful account of task-ability relations, complexity has difficulty explaining what appear to be the most experimentally tractable phenomena in intelligence research.

One potential remedy is to identify a more general moderating task dimension, in the form of response uncertainty. In this framing, uncertainty refers to the fact that any given task that elicits cognitive differences appears to do so, at least in part, by inducing uncertainty, or more precisely, indeterminacy, around the correct response (Fox & Mitchum, 2012). That is, when considered broadly, the various factors that moderate the task-ability relationship in any given task can all be construed as ways of rendering the correct response more or less uncertain on the basis of the information present in the task itself. For example, in DT and IT, the increasing numbers of targets or shorter stimulus presentations both serve to render the correct response increasingly indeterminate relative to the information presented. However, whereas the complexity account appears to lack an explanation for why simple DT might relate to intelligence at all, the more general notion of uncertainty highlights the variable ISI (Niemi & Näätänen, 1981) as a likely relevant dimension.

Similarly, in the psychometric domain, it can be seen how uncertainty accounts for the relatively high g-loadings of tasks, such as vocabulary and matrix reasoning, where the correct response is highly indeterminate relative to the stimulus prompts alone. In contrast, less g-loaded tasks (e.g., processing speed measures; Benson, Hulac, & Kranzler, 2010) involve items where correct responses are presented almost directly. Importantly though, because psychometric tasks clearly do involve numerous cognitive processes, complexity works well in the psychological domain. Yet, since it has difficulty explaining some ECT and ERP effects, the more general idea of uncertainty may be a useful extension at the lower level of discrete neural processes.

4.3. The role of uncertainty in ERP-ability relations

An uncertainty-based account seems particularly well-suited to integrate the present findings within the broader ERP and intelligence literature. For example, the P300 is thought to be involved in context updating (Polich, 2007), suggesting that it should be most sensitive to uncertainty around factors such as stimulus probability and inter-trial contingencies. Consistent with this, the P3-IQ amplitude relationship has been most often observed in studies employing the infrequent oddball task and similar paradigms (e.g., Bazana & Stelmack, 2002; Beuchamp & Stelmack, 2006; Jaušovec & Jaušovec, 2000; Troche et al., 2009; Walhovd et al., 2005), whereas paradigms that lack these contingencies, including the current study, have not always observed this relationship (Hansell et al., 2005; Pascalis et al., 2008). In a similar vein, the N2 potential is thought to belong to a family of components that are involved in detecting violations of expectations (Cavanagh, Zambrano-Vazquez, & Allen, 2012). Under this account, one would expect N2 amplitudes and related activity to best predict IQ when expectations are violated, and indeed this seems to be the case (Bazana & Stelmack, 2002; Beuchamp & Stelmack, 2006; Houlihan & Stelmack, 2012; Pascalis et al., 2014; Pascalis & Varriale, 2012; Troche et al., 2009; Van Den Bos, Crane, & Guroglu, 2012). However, as in the case of the P3, the present Hick paradigm did not invoke this type of uncertainty, potentially explaining why the N2 was unrelated to intelligence.

In contrast, in the current study, only the P2 was related to IQ. Following the logic above, this may be because the Hick paradigm most directly manipulates spatial uncertainty as to the location of the target. As suggested in the study by Freunberger et al. (2007), the P2 appears to be sensitive to early visual perceptual expectations, which may be the most relevant aspect of uncertainty within the Hick paradigm. Considering the present results more broadly, this overall framework suggests that IQ should be preferentially related to ERPs that process the aspects of uncertainty most present in the task. Indeed, the present study did not show relationships between the N1 and IQ, yet Inspection Time, which manipulates the duration of visual stimulus exposure, elicits IQ correlations primarily with N1 features, and less often with the P2 (Hill et al., 2011; Zhang et al., 1989; though see: Burns et al., 2000). Taken together, these studies highlight how uncertainty may be a general moderator of the relation between brain activity and IQ, but potentially only for brain activity corresponding to specific types of uncertainty. Additionally, uncertainty may also explain why neural resilience to various novelty effects is associated with higher fluid intelligence (Euler, Weisend, Jung, Thoma, & Yeo, 2015) and executive functioning (Euler, Niemeyer, & Suchy, 2016). Finally, an account of brain-IQ relations that emphasizes uncertainty also aligns well with the emerging view that environmental prediction may be a core principle of brain functioning in general (Bar, 2009; Clark, 2013, 2015; Friston, 2010; Friston & Kiebel, 2009; Hohwy, 2013).

4.4. Limitations

The present study faces three main limitations. The first of these is the undergraduate study sample and the slightly restricted range of IQs, which may have decreased the strength of those effects and also limited generalizability. At that the same time of course, the restricted range suggests that the observed effects will likely be stronger when tested in a more representative sample. Second, the present study failed to find evidence that complexity moderates the DT-IQ relationship in this version of the Hick paradigm. Although this may reflect manipulation of only three bit-levels, and hence just a limited range of complexity, a complexity effect has been found in several prior studies that employed a similar number of bits (Deary et al., 2001; Neubauer, 1991). Although procedural differences distinguish the present study from the former (Deary et al., 2001), insofar as the current paradigm was explicitly modeled after Neubauer (1991), the latter discrepancy is more difficult to explain. One possibility may be the difference between the two IQ measures used (i.e., the Ravens vs. the WAIS-IV), such that the spatial nature of the Hick paradigm better lends itself to correlations with the more perceptually-loaded Ravens than with Full-Scale IQ. There is some precedent for larger activity-ability effects for fluid intelligence tasks.
than broader indices (Neuhammer & Fink, 2003), which may also apply here.

Although future studies are needed to test the explanation above, some current support for it comes from the fact that complexity did moderate the P2-IQ relationship. Tentatively, this highlights a potential dissociation between the neural computations required for a task and eventual task performance itself, such that a given ERP may reflect just a single computational process within a given task. Thus, it may be the interaction between spatial and temporal uncertainty (i.e., the variable ISI) that drives the primary increase in the task-ability relationship in other DT studies (Deary et al., 2001), in that, whatever drives the base relationship must also be present in the 0-bit condition. If so, this of course provides a basis for investigating all of the various neural processes that may be involved in the DT-IQ relationship. To the extent that the neural processes underlying the ISI-intelligence relation are distinct from those related to the P2, such findings would actually further validate the complexity account of task-ability relations, as well as its extension via the notion of response uncertainty.

Last, despite being a relatively large study by standards of ERP research, the principle ERP-IQ effect on the P2 amplitude is nevertheless small and may reflect a limitation of finding ERP correlates of IQ in general. In particular, ERPs aggregate neural responses over many trials and may distort important aspects of the underlying neural activity (Luck, 2014). Alternative measures that provide more representative indices individual neural events (e.g., trial-to-trial phase-locking) may be more sensitive to intelligence-related activity under some conditions (Euler et al., 2015). Similarly, although the surface Laplacian provides superior spatial resolution of more local cortical activity, it of course lacks sensitivity to more global and subcortical sources that may be relevant to IQ. Overall, given the challenges inherent to physiological mapping of psychological processes to neural activity, and further relevant to IQ. Overall, given the challenges inherent to physiological mapping of psychological processes to neural activity, and further relevance to IQ. Overall, given the challenges inherent to physiological mapping of psychological processes to neural activity, and further relevance to IQ. Overall, given the challenges inherent to physiological mapping of psychological processes to neural activity.

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