Rethinking Neural Efficiency: Effects of Controlling for Strategy Use

Paolo Toffanin University Medical Center Groningen and University of Groningen Addie Johnson and Ritske de Jong University of Groningen

Sander Martens

University Medical Center Groningen and University of Groningen

A sentence verification task (SVT) was used to test whether differences in neural activation patterns that have been attributed to IQ may actually depend on differential strategy use between IQ groups. Electroencephalograms were recorded from 14 low (89 < IQ < 110) and 14 high (121 < IQ < 142) IQ individuals as they performed the SVT with either a spatial or verbal strategy. Event-related desynchronization in upper alpha (9.5-12.5 Hz) and theta (4-6 Hz) bands showed that different strategies evoked different activation patterns, but these patterns did not differ between groups. However, an IQ-related correlate was found in the preparation interval. Thus, although processing patterns during task performance seem to depend on the strategy used for task execution, preparation for task processing may depend on IQ.

Keywords: neural efficiency, intelligence, strategy control, event-related desynchronization

Theories of intelligence and intelligence testing have been a part of modern society for more than 100 years (Hunt, 1995; Sternberg, 2003). In the last 20 years, thanks to the development of neuroimaging techniques, investigation of the biological bases of intelligence (i.e., differences in brain and neural functioning) has gained increasing interest and has enjoyed considerable success. One theory that has evolved from research on the neural underpinnings of intelligence is the neural efficiency theory (see Vernon, 1993, for a review). Neural efficiency describes the negative correlation between brain activity under cognitive load and intelligence. It is indexed by both a lack of processing activity in brain areas irrelevant for good task performance and a more focused use of specific, task-relevant areas (Jausovec & Jausovec, 2001, 2004b; Neubauer, Freudenthaler, & Pfurtscheller, 1995).

The introduction of neural efficiency theory has given rise to a new approach to the study of intelligence in which imaging techniques are used to study differences in task performance, including the use of the electroencephalogram (EEG; Gevins & Smith, 2000) or functional magnetic resonance imaging (fMRI; Gray et al., 2005) for studying performance in working memory tasks, measuring nerve conduction velocity to examine individual differences in the performance of speed of information processing tasks (e.g.,

This research was supported by a VENI grant from the Netherlands Organization for Scientific Research awarded to Sander Martens.

Correspondence concerning this article should be addressed to Paolo Toffanin, School of Behavioural and Cognitive Neuroscience, NeuroImaging Center, P.O. Box 196, 9700 AD Groningen, the Netherlands. E-mail: p.toffanin@med.umcg.nl Vernon & Mori, 1992), measuring EEG during administration of fluid intelligence tests (e.g., Jausovec & Jausovec, 2003), measuring neural activity in simple speeded-processing tasks with fMRI scanning (Rypma et al., 2006), or using positron emission tomography (PET) during mathematical reasoning tasks (Haier & Benbow, 1995).

A consistent pattern emerging from these studies is that relatively high IQ (HIQ) individuals differ from relatively low IQ (LIQ) individuals in terms of a differential suppression of frontal area activity, with HIQ individuals generally relying on parietal regions and LIQ individuals using both parietal and frontal regions during task performance. Such topographical patterns have led to the suggestion that LIQ and HIQ individuals differ in the use of neural circuits, especially nonfrontal ones (see, e.g., Jausovec & Jausovec, 2005). However, Duncan et al. (2000) have suggested an alternative interpretation of differences in intelligence. They have proposed that the frontal lobe, the seat of executive control, is the neural base of general intelligence. Duncan et al. based this assumption on PET evidence showing that frontal area recruitment was an increasing function of the amount of g (where g represents general intelligence or Spearman's g) required by the task.

The assumptions that the frontal lobe is critical in intelligence (Duncan et al., 2000) and that the performance of higher intelligence individuals is associated with lower levels of frontal-lobe activation (as suggested by the neural efficiency theory; e.g., Jausovec & Jausovec, 2005) may seem contradictory. However, it may be that the two patterns of findings simply reflect two time points in the development of skilled performance.

Performing any but the simplest task requires discovery or learning of a strategy to solve it, and executive control plays an important role in strategy choice and deployment (Koechlin, Ody, & Kouneiher, 2003). The finding of Duncan et al. (2000) that increasing the difficulty of a task resulted in increased recruitment of frontal areas may reflect an increase in time spent devising a

Paolo Toffanin and Sander Martens, University Medical Center Groningen, Groningen, the Netherlands, and School of Behavioural and Cognitive Neuroscience, NeuroImaging Center, University of Groningen, Groningen, the Netherlands; Addie Johnson and Ritske de Jong, Department of Psychology, University of Groningen.

strategy for performing the task. If tasks are well learned or do not impose heavy cognitive demands on the performer, frontal area activation would be expected to be relatively low. This would be in line with the relative frontal suppression shown by HIQ individuals in the studies that are taken to support the neural efficiency theory: Absence of frontal activation in HIQ individuals could reflect that the task load was within the capabilities of the participant and that the strategy used to perform the task had been established. LIQ individuals, on the other hand, could be assumed to be actively involved in the solution of the task, as reflected by a broader and longer activation of brain areas.

Two specific predictions follow from the view that frontal lobe recruitment depends on both intelligence and the familiarity with the task. One prediction is that HIQ individuals will show a high activation level in the frontal lobe at the beginning of the testing session as they engage in an active search for the best strategy to solve the task. Once they have settled on a strategy, a shift to nonfrontal areas should occur. LIQ individuals, on the other hand, will often fail to fully automate task instructions or to develop a strategy for performing the task, with the result that activation patterns will remain relatively constant throughout the testing session. In line with this prediction, Gevins and Smith (2000), found that, in comparison with low-ability individuals, high-ability individuals displayed more frontal activity in the early stages of task performance during a spatial version of an n-back working memory task (in which the spatial position of a letter stimulus was to be compared with the position of the first item displayed or the item presented one or two items back) activity that gradually shifted to parietal sites. The authors argued that the shift to parietal sites reflected the automation of processing (see also Koch et al., 2006). Low-ability individuals, in contrast, relied on the frontal lobe for the duration of the test (for similar findings, see Jausovec & Jausovec, 2004b).

A second prediction is that differences between HIQ and LIQ individuals should disappear when both groups have practiced until reaching an equal performance level. One way in which these hypotheses can be tested is by looking at event-related desynchronization (ERD). ERD shows robust correlations with mental effort (Nunez, Wingeier, & Silberstein, 2001), such that the alpha rhythm (8-12 Hz) decreases (note that an amplitude decrement reflects desynchronization) with increases in mental effort, whereas the frontal theta band (4-8 Hz) tends to increase (note that amplitude increment reflects negative desynchronization)¹ with increases in mental effort. In other words, in a state of relaxation or "idling" state, alpha waves are of a relatively high amplitude or synchronized. A change to a more active state desynchronizes the alpha rhythm. With regard to ERD, neural efficiency theory predicts that HIQ individuals, who require less effort to perform a task, will show less desynchronization in the alpha band as well as less negative desynchronization of the theta band in comparison with LIQ individuals. A study by Grabner, Stern, and Neubauer (2003) supported the hypothesis that differences in ERD between HIQ and LIQ individuals will disappear when the task performed is familiar to both groups. The authors showed that patterns of ERD of two groups of relatively HIQ or LIQ experienced taxi drivers differed while performing the novel task of memorizing routes on an artificial map but not on the familiar task of thinking about routes to take in their own city. These findings support the hypothesis that development of an efficient strategy, and the correlated activation or deactivation of the frontal lobe, plays a role in intelligence differences.

Despite the promises of neural efficiency theory in explaining differences in intelligence at a neural processing level, a number of studies have failed to support the theory. For example, Klimesch (see, e.g., Klimesch, 1997, 1999) studied performance in long-term memory tasks, such as semantic and episodic memory tasks, while measuring EEG. Computation of ERD revealed a larger desynchronization in the upper alpha band (10–12 Hz) and a larger negative desynchronization of the theta band for good as compared with poor memory performers, which is just the opposite of what neural efficiency theory would predict.

Differences in activation patterns between IQ groups have often been interpreted as differences in neural efficiency. However, as suggested by studies, such as Klimesch (1997, 1999), such a conclusion may not be warranted. Jausovec and Jausovec (2005) presented an analysis of studies investigating neural efficiency theory, and they divided them into studies that supported the neural efficiency theory and studies that did not. Jausovec and Jausovec attributed the discrepancies found between these studies to the restricted number or narrowness of the frequency bands used (e.g., exclusive analysis of theta and alpha bands, or restricting the analysis field to solely the upper components, i.e., between 10 and 12 Hz in the alpha band) or to the poor temporal resolution of the measurements performed (e.g., PET and ongoing EEG do not provide good temporal resolution). A closer inspection of the studies surveyed by Jausovec and Jausovec brings two other critical points to the fore. First, the IQ ranges used were relatively narrow (many investigations were restricted to individuals with average or high intelligence, e.g., university students). Second, and perhaps more important, the strategies with which the task could be performed were not controlled for. Gevins and Smith (2000) and Jausovec and Jausovec (2004a, 2004b, 2005) have suggested that higher ability participants tend to better identify strategies needed for the solution of the task at hand. The use of different strategies in the two groups could account for the observed differences in brain activation.

Differences in strategy use have, to our knowledge, not been explicitly investigated in studies of brain use as a function of intelligence. However, it has been shown that ability differences as measured by standard psychometric tests can be related to strategy differences—see, for example, Sternberg and Weil (1980) for strategy differences in solving transitive inference problems; Mathews, Hunt, and MacLeod (1980) for sentence verification; and L. A. Cooper and Regan (1982) for mental rotation problems. Because people differing in ability also tend to adopt different strategies for performing tasks—or do so at different times in performance—it is possible that strategy use has been a confounding factor in the study of neural processing correlates of intelligence. Our goal was to determine whether intelligence-related differences in neural processing would be found when strategy was controlled for.

¹ Note that in the literature, negative value of ERD is frequently referred to as event-related synchronization (ERS); however, to be consistent, we use only the term ERD and its polarity (i.e., positive or negative).

Experiment

To test whether intelligence-related differences in neural processing would still be found when task performance strategy is controlled for, we had LIQ and HIQ individuals perform the sentence verification task (SVT; Clark & Chase, 1972) under two instructional conditions (Mathews et al., 1980). The task requires participants to judge whether a sentence describing the spatial relation of two symbols correctly matches a following picture (e.g., whether the sentence "star is below plus" matches the picture of a star below a plus). In the linguistic strategy condition, the sentence was to be read as quickly as possible without sacrificing understanding and then compared with the picture to determine whether the sentence matched the picture, whereas in the imagery strategy condition, stimuli and relations described in the sentence were to be represented as a visual image and then compared with the picture. We chose to present the linguistic strategy condition first for all participants to reduce the chance that participants would use an imagery strategy even when the instructions were to use the linguistic strategy (for evidence that individuals with high spatial abilities preferentially use an imagery strategy, see, e.g., MacLeod, Hunt, & Mathews, 1978; Mathews et al., 1980).

Additionally, we modified the traditional SVT in two ways to support the use of the linguistic strategy. First, because Tversky (1975) showed that an imagery strategy was more likely to be used when there was a temporal separation between the display of the sentence and the display of the picture, we used a 0-ms interval between the presentations of the sentence and the picture. Second, unexpected stimuli (stimuli not mentioned in the sentence) were introduced into the set of stimuli. Unexpected pictures discourage the use of imagery recoding when the linguistic strategy is supposed to be used (Kroll & Corrigan, 1981). For example, on a trial in which a heart above a star is displayed after the sentence "plus is above star," imagining a plus above a star is an inefficient strategy. To prevent differences observed at the EEG level from being attributed to a difference in the materials used, we also used unexpected pictures in the imagery strategy condition.² Throughout the experiment, EEG was recorded with a 64-channel system.

Time–frequency analysis, using Morlet wavelets, was used to compute instantaneous amplitude (IA) and power for EEG frequencies ranging from 4 to 75 Hz (for details, see Gladwin, Lindsen, & de Jong, 2006; Tallon-Baudry & Bertrand, 1999). These instantaneous values, reflecting dynamics of cerebral processing, were analyzed for main effects of IQ and strategy and for possible interactions of these factors.

Method

Participants

A total of 37 right-handed native Dutch speakers, with normal or corrected-to-normal visual acuity, and no history of neurological problems, were tested in an initial session consisting of intelligence testing and practice with the SVT. Participants were recruited through advertisements and reported no cognitive disabilities (including reading or writing deficits), did not use medications or drugs that could impair task performance, were right handed, and were younger than 45 years old. Of the 37 participants who participated in the initial session, 2 were excluded for failing to meet the accuracy criterion of 80% correct in the

SVT, and 7 chose not to continue in the experiment. Of the remaining 28 participants, two groups were formed and matched on age and sex (see Neubauer, Grabner, Fink, & Neuper, 2005, for implications of sex differences and the neural efficiency hypothesis), leaving 14 participants per group. The HIQ group contained individuals (19–38 years of age; M = 25.4; 7 women) with a university level of education and a relatively high intelligence (IQ = 121–142; M = 127.7). The LIQ group included individuals (18–37 years of age; M = 21.9; 7 women) mostly having an intermediate vocational level of education and a relatively low intelligence (IQ = 89–110; M = 101.7).

Intelligence Test

Intelligence was measured by a shortened version of the Groningen Intelligence Test (Luteijn & van der Ploeg, 1983). The Groningen Intelligence Test is a test of general intelligence used in the Netherlands, much as is the Wechsler Adult Intelligence Scale (Wechsler, 1981). Five of the nine subtests, administered in a fixed order, were used, including the vocabulary test, the spatial ability test, the mental arithmetic test, the verbal analogies test, and the verbal fluency test. In the vocabulary subtest, participants are asked to indicate which of five alternative words is synonymous with a given word.

The spatial ability subtest requires participants to indicate which two-dimensional shapes from a larger set are needed to exactly fill up a given space on the test page. To do this, participants need to mentally rotate the shapes. In the mental arithmetic subtest, participants are asked to complete as many sums of three two-digit numbers as possible within 1 min. The verbal analogies subtest is a multiple choice test in which the participant must indicate which of five alternatives is related in the same way to a given word as words in an example are related. Each of these subtests included three practice items and at least 20 test items. The verbal fluency subtest requires participants to produce as many words as possible in a given category within 1 min. This subtest was done twice, once with animals and subsequently with professions as the given category. Test administration took approximately 45 min. We computed IQ using the Groningen Intelligence Test norms corrected for sex.3

² Introduction of unexpected pictures discouraged the use of the imagery strategy but did not exclude it. Imaging a picture that represents a negative sentence is difficult. Imaging an affirmative sentence has a unique outcome, which can be compared with only one figure, whereas there are five possible positive matches with a negative sentence. One strategy is to imagine the one picture that does not represent the sentence (i.e., gives a false response). Negative sentences can be imaged by imaging the elements and relation contained in the sentence and responding "False" if that image matches the picture. This strategy was verbally explained during the presentation of the first negative sentence trial in the practice session for the imagery strategy.

³ Because of the relevance of sex differences for neural efficiency (e.g., Neubauer et al., 2005) we normalized IQ for sex differences. Using uncorrected norms would have led to the same group composition and slightly different ranges. Using uncorrected norms, the IQ of the HIQ group ranged from 120 to 143 (M = 128.60) and that of the LIQ group from 90 to 115 (M = 103.79).

Stimuli and Apparatus

We controlled stimuli generation and response collection using a program created with E-prime 1.1 (Psychology Software Tools Inc., Pittsburgh, PA) and running on a Pentium IV computer equipped with a 17-in. (43.18-cm) monitor with a refresh rate of 100 Hz. Stimuli were presented in black on a white background. Sentences were presented in 20-point Courier New font, and pictures were constructed by combining two symbols in a vertical arrangement subtending 1.2 of visual angle at a viewing distance of approximately 60 cm. Symbols were a heart, star, and a plus (each 8.5 mm high and 7.5 mm wide); only one symbol of each type could appear in a given display. Sentences were constructed to describe the relationship of the two symbols, varying the symbols (heart, star, or plus), the order of the two symbols (which symbol was mentioned first), the polarity of the sentence (affirmative or negative, e.g., "heart is below plus" vs. "heart is not below plus"), and the markedness of the term describing the spatial relation of the two symbols (e.g., "plus is above star" vs. "plus is below star"). A picture was considered "unexpected" if it contained an element not mentioned in the sentence. All sentences were presented in Dutch, for which the words heart (hart), star (ster), and plus (plus) all have four letters. Combinations of sentences and pictures resulted either in a true or false response (truth value). Sentences varied accordingly to polarity and truth value. Because the use of unexpected pictures introduced a higher number of true-negative (TN) and false-affirmative (FA) items compared with the number of false-negative (FN) and true-affirmative (TA) items (a ratio of 5:1), FN and TA items were presented five times each, and TN and FA items were presented one time each for a total of 240 trials.

Procedure

The experiment consisted of three sessions carried out on 3 separate days. In the first session, which took approximately 90 min, the intelligence test was administered, and participants completed a familiarization phase in which they performed 36 trials of the SVT and were allowed to ask questions. They were then instructed to use the linguistic strategy in an additional practice session. Practice blocks consisted of 24 trials each. If participants made errors repeatedly, the appropriate response to the specific trial was explained, or the participant was advised to slow down to enhance accuracy. In each practice block, a minimum accuracy level of 80% had to be achieved; participants who failed to reach that criterion received as many practice blocks as necessary to reach the accuracy criterion. On average, one to five practice blocks were necessary to achieve the criterion. A practice session, also with accuracy criterion, was also included before each experimental session. In the second session, which took approximately 90 min, participants performed the SVT using the linguistic strategy while EEG was measured.

After a break of approximately 15 min, they were then instructed on how to use the imagery strategy and were given an additional practice session. In the third session, which took approximately 90 min, participants performed the SVT using the imagery strategy while EEG was recorded.

At the start of each trial, a fixation cross was displayed in the middle of the screen for 1,500 ms and was then presented in bold

for another 500 ms to alert the participant to the imminent presentation of the sentence. The sentence remained in view until the participant pressed the space bar, after which it was immediately replaced by a picture that either matched or did not match the description given by the sentence. The time between onset of the sentence and the press of the space bar, referred to as comprehension response time (CRT), was recorded for later analysis. Participants were instructed to press the S key on the computer keyboard when the sentence was true (i.e., when it provided a correct description of the picture) and to press the L key when the sentence was false (i.e., when it did not provide a correct description of the picture). The time between onset of the picture and the true/false response, referred to as verification response time (VRT), was also recorded, as were errors in sentence verification. Performance feedback was presented on each trial (the word "correct" or "incorrect" presented in Dutch at fixation for 500 ms), after which a 1,500 ms fixation cross was displayed in the middle of the screen before the next trial.

EEG Recording

The EEG was recorded with a tin 64-channel electro-cap (Electro-cap International Inc., Eaton, OH). All scalp positions in the International 10-20 System were used, with additional sites located midway between the 10 and 20 locations (Sharbrough et al., 1991) and four electrode positions 10% inferior to the standard parieto-occipital (PO) electrodes (PO9, O9, PO10, O10; see Figure 1). The amplifier was a REFA 8-72 (Twente Medical Systems, Enschede, the Netherlands). Brain electrical activity was amplified 20,000 times with a digital finite impulse response low-pass filter with a cutoff frequency of 135 Hz. Data were digitized to 22-bit accuracy at a rate of 500 Hz and stored on a hard disk for subsequent off-line analysis. Electrophysiological inputs were configured as a reference amplifier: All channels were amplified against the average of all connected inputs. Two electrodes were connected to the mastoids, the average of which served as an off-line reference for the EEG signal. An electrode on the sternum was used for the patient ground. Horizontal electrooculogram left (HEOGL), horizontal electrooculogram right (HEOGR), vertical electrooculogram left above eye (VEOGL+), and vertical electrooculogram left below eye (VEOGL-) recorded the bipolar input for the electrooculogram. Electrode impedances were kept below 5 kOhm for all the electrodes during the experiment. Data acquisition was controlled through Brain Vision Recorder (Version 1.03, BrainProducts GmbH, Munich, Germany).

Data Analysis

Behavioral data analysis. Sentence comprehension and picture VRTs less than 200 ms or greater than three standard deviations above the mean (computed per participant) were considered outliers and were removed from the data set. Less than 1% of trials were eliminated.

EEG data analysis. Preprocessing of the data was executed with Brain Vision Analyzer (BrainProducts GmbH, Munich, Germany). Data were downsampled to 250 Hz, referenced to the average of the two mastoids, and then filtered with a time constant of 1 s and a high cutoff of 100 Hz (Butterworth Zero Phase Filters, which are a type of filtering implemented in Brain Vision Ana-



Figure 1. The electrode clusters used for time–frequency and event-related desynchronization analyses. Data from outlined electrodes were averaged to form regions of interest (ROIs). Those ROIs are labeled (nasion to inion) as follows: anterio–frontal (AF), frontal (F), frontal–central (FC), central (C), centro–parietal (CP), parietal (P), parieto–occipital (PO), and occipital (O). FP = frontal pole; FT = fronto–temporal; T = temporal; IZ = inion; Z identifies the midline.

lyzer, at 24 dB/oct). We globally corrected the EEG trace for direct current drifts (Hennighausen, Heil, & Rosler, 1993) using an interval of 400 ms (200 ms before and after either sentence or picture onset). We corrected eye blink artifacts using the ocular correction algorithm of Gratton, Coles, and Donchin (1983). Epochs of 9.5 s each were segmented, including the 3.5 s preceding and the 6 s following the stimulus onset (either the sentence or the picture). Epochs on which responses were incorrect or response times (RTs) longer or shorter than 3 standard deviations from the mean were excluded from the analysis. Using this procedure, we removed a total of 5.74% of the trials, ranging from 0.41% to 9.43%, SD = 5.48 trials per participant. Data were visually inspected for artifacts, and bad segments were removed. We applied baseline correction using the 100-ms interval before stimulus onset.

IAs. IAs of the preprocessed epochs were computed for each trial by means of a convolution with a complex Morlet wavelet (for details, see Gladwin et al., 2006; Tallon-Baudry & Bertrand, 1999). Formally,

$$IA(t, f) = |w(t, f) \times s(t)|,$$

where s(t) is the original EEG data of one channel, and w(t, f) is a suitably normalized, complex form of the Morlet wavelet:

$$w(t,f) = \left\{ \frac{1}{\sqrt{\sigma_f} \times \sqrt{\pi}} \times \exp\left[\frac{-0.5}{2\pi\sigma_f t} \times \exp(i2\pi f t)\right] \right\},\$$

where *f* is the center frequency of the wavelet, and σ_f is the standard deviation of its Gaussian envelope in the frequency domain. Averaged IAs were computed by averaging across trials.

Twenty-two Morlet wavelets with center frequencies in the range from 4 to 75 Hz and different uncertainty parameters, $\sigma_{,p}$ were used. The 22 frequencies (with uncertainty parameter within parentheses) were 4 (1), 6 (1), 7 (1), 8 (1), 9 (1), 10 (1), 12 (2), 14 (2), 16 (2), 18 (2), 20 (2), 23 (3), 26 (3), 30 (4), 35 (4), 40 (4), 45 (4), 55 (4), 60 (4), 65 (4), 70 (4), and 75 (4). A notch filter at 50 Hz with a standard deviation of 1 Hz was used to remove the possible influence of residual line current (50 Hz). The IAs over groups of electrodes were averaged to create the following regions of interest (ROIs; see Figure 1): antero–frontal (AF3, AFZ, AF4); frontal (F3, FZ, F4); frontal–central (FC3, FC1, FCZ, FC2, FC4); central (C3, C1, CZ, C2, C4); centro–parietal (CP3, CP1, CPZ, CP2, CP4); parietal (P3, P1, PZ, P2, P4); parieto–occipital (PO3, POZ, PO4); and occipital (O1, OZ, O2).⁴

Matlab (The MathWorks, Natick, MA) and SPSS (SPSS Inc., Chicago, IL) were used for statistical testing and visualization. The data were smoothed in the frequency domain by averaging across three consecutive wavelets and in the temporal domain by using a low-pass filter (passband = 0-1.5 Hz, 40 dB cutoff at 2.5 Hz). This degree of smoothing was chosen in an attempt to deal with possible intersubject variability in the precise time–frequency location of effects (see, e.g., Klimesch, 1999).

Prior to statistical analysis, IA data were log-transformed to normalize them across participants. As a first step in the statistical analysis, we performed a global test—that is, a test across all possible combinations of time, frequency, and ROI—for any statistically significant main or interaction effects of IQ and strategy. The false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995) was used to control for the effects of the large number of comparisons involved in these tests. The alpha level for the FDR procedure was set at .05 (for an average of 5% false alarms).

Frequency bands that showed significant and potentially interesting effects in the global, FDR-based analysis, were examined further with an analysis of ERD within each of these frequency bands. Following convention, we computed ERD using instantaneous power (i.e., the square of the IA), according to the following formula:

$$%$$
ERD $(t) = \{ [R - A(t)]/R \} \times 100,$

where R represents mean power during the reference interval (from 2 to 0.5 s preceding sentence onset, averaged across trials), and A(t) represents the instantaneous power, also averaged across trials. Changes in power are thus represented as a percentage of the reference/baseline values, where positive ERD values indicate power decreases (indicating cortical activation), and negative ERD values indicate power increases⁵ (reflecting cortical deactivation). The time course of ERD was computed and represented for the same ROIs used in the analysis of IA (AF, F, FC, C, CP, P, PO, O).

Results

Reaction Times

The behavioral analysis suggested that the participants were able to follow the instructions to use each strategy at the appropriate time in that the patterns of CRTs and VRTs were similar to those that have been used to distinguish between the two strategies in previous experiments (e.g., MacLeod et al., 1978; Mathews et al., 1980).

In particular, CRT was shorter using the linguistic strategy (1,100 ms) than when using the imagery strategy (3,691 ms). The critical Polarity \times Truth Value \times Strategy interaction was significant for VRT. According to MacLeod et al. (1978) and others (e.g., Mathews et al., 1980), the use of the linguistic strategy should result in a Polarity × Truth Value interaction because of the fact that negative sentences, being linguistically more complex, need more processing than affirmative sentences. Furthermore, sentence and picture representations can be more easily compared when the two are congruent (Gough, 1965). Thus, the nature of the Polarity \times Truth Value interaction is such that TA trials are responded to more quickly than FA trials, but FN trials are easier than TN trials (Carpenter & Just, 1975). With the imagery strategy, the latencies for affirmative trials are comparable with negative trials (with no main effect of polarity), because the complexity of the negative sentences is resolved at the time that the representation of the sentence is created. However, FN and TA responses are faster than the TN and FA ones. Because the speed of response is irrespective of whether the sentence is affirmative or negative, the Polarity \times Truth Value interaction is absent. The left and right histograms in the upper part of Figure 2 show CRTs for the two groups of participants for the imagery and linguistic strategy conditions, respectively. The CRTs were subjected to a mixed analysis of variance (ANOVA) with strategy (linguistic vs. imagery) and polarity (affirmative vs. negative) as within-subject factors and group (HIQ vs. LIQ) as a between-subjects factor.

A general advantage for the HIQ group was observed, but the difference between the two groups was not significant (p > .20). The main effect of strategy was significant, with CRT being faster in the linguistic than in the imagery strategy condition, F(1, 26) = 47.25, p < .001, MSE = 3.973.451. The Group \times Strategy interaction was not significant (p > .80), suggesting that both groups executed the task according to the given instruction.

Participants were faster reading affirmative sentences than negative sentences, F(1, 26) = 90.8, p < .001, MSE = 39,357. The Polarity × Strategy interaction, F(1, 26) = 48.56, p < .001, MSE = 73,265, reflected that this difference was more evident in the imagery strategy condition, where negative predicates had to be fully comprehended before visual images could be generated. Neither the Polarity × Group nor the Strategy × Polarity × Group interaction (p > .60) was significant. The left and right histograms in the middle part of Figure 2 show VRTs for the two groups of participants for the imagery and linguistic strategy conditions, respectively.

These data were analyzed with a mixed ANOVA, with strategy (imagery vs. linguistic), polarity (affirmative vs. negative), and truth value (true vs. false) as within-subject factors and group (HIQ vs. LIQ) as a between-subject factor. Overall, the HIQ group was

⁴ Note that Z stands for central line. It comes from the internationally standardized 10-20 system which is usually employed to record the spontaneous EEG. In this system, the head is represented using the coronal plane (anterior to posterior) and sagittal plane (left to right). Because the letter C was already used to identify the central line (in the coronal plane), the letter Z was used to identify the medial line (central line in the sagittal plane).

⁵ In line with this convention (i.e., negative ERD reflects power increase), negative ERD was plotted upward.



Figure 2. From top to bottom: comprehension response times (CRTs), verification response times (VRTs), and percentage of errors for the imagery and the linguistic strategy conditions (left and right panels, respectively). In the upper panels, CRTs (in seconds) are displayed as a function of sentence type (affirmative and negative). In the middle panels, VRTs (in seconds) are displayed as a function of trial type: true affirmative (TA), false affirmative (FA), false negative (FN), and true negative (TN). White bars represent high IQ (HIQ) individuals, gray bars represent low IQ (LIQ) individuals. Error bars represent the standard error of the mean.

significantly faster than the LIQ group in verifying the picture, F(1, 26) = 5.1, p < .04, MSE = 965,996. VRT was shorter in the imagery than in the linguistic strategy condition, F(1, 26) = 57.8, p < .001, MSE = 243,974. Responses to true trials were faster than responses to false trials, F(1, 26) = 10.67, p < .003, MSE =23,865, and responses to affirmative sentences were faster than those to negative sentences, F(1, 26) = 141.5, p < .001, MSE =39,357; the Polarity \times Truth Value interaction, F(1, 26) = 41.7, p < .001, MSE = 29,198, was also significant. The Strategy \times Polarity \times Truth Value interaction, F(1, 26) = 5.85, p < .02, MSE = 18,491, suggests that the two groups were executing imagery and linguistic strategy as instructed. The Strategy \times Polarity interaction, F(1, 26) = 17.77, p < .001, MSE = 25,626, is consistent with differences in strategy use (see Reichle, Carpenter, & Just, 2000). Reichle et al. (2000) stated that the variables polarity and truth value affected performance more in the linguistic than the imagery strategy condition, giving reliable Strategy imesPolarity and Strategy \times Truth Value interactions. However, we failed to find the Strategy \times Truth Value interaction (p < .20). Only one interaction with group—the Polarity \times Group interaction, F(1, 26) = 6.21, p < .02, MSE = 39,357—was found (all other ps > .20).

Accuracy

The overall mean percentage of error, shown in the left and right histograms in the bottom part of Figure 2 (imagery strategy condition on the left and linguistic strategy condition on the right), was low. Moreover, no evidence of speed–accuracy trade-off was found. Percentage of error was analyzed with a mixed ANOVA with strategy (imagery vs. linguistic), polarity (affirmative vs. negative), and truth value (true vs. false) as within-subject factors and group (HIQ vs. LIQ) as a between-subjects factor. The HIQ group made fewer errors than the LIQ group, F(1, 26) = 6.5, p < .02, MSE = 33, and more errors were made with the linguistic strategy than the imagery strategy, F(1, 26) = 20.03, p < .001, MSE = 10. Moreover the two factors interacted, F(1, 26) = 7.78, p < .01, MSE = 10, such that the percentage of errors in the linguistic strategy condition was nearly twice that of the imagery strategy condition for the LIQ group (10.7% vs. 5.7%, respec-



Figure 3. Threshold false discovery rate (FDR) map showing significant amplitude differences between imagery and linguistic strategy conditions at sentence onset (sentence). Each subplot is a time–frequency plot showing data points at which the difference was significant according to the FDR procedure. Time and frequency are plotted in the horizontal and vertical axes, respectively. Each subplot refers to one of the regions of interest shown in Figure 1. The cutoff *t* value for these results, given by the FDR procedure, was 3.04.

tively) but not for the HIQ group (5.5% vs. 4.4%, respectively). Fewer errors were made with affirmative than negative sentences, F(1, 26) = 49.61, p < .001, MSE = 12, and with false than true trials, F(1, 26) = 10.25, p < .003, MSE = 12. The Polarity \times Truth Value interaction, F(1, 26) = 29.3, p < .001, MSE = 11, was also significant, reflecting strategy related differences as reported in the analysis of the VRTs, as was the Strategy \times Polarity interaction, F(1, 26) = 28.45, p < .001, MSE = 7. Sentence polarity had a smaller effect in the imagery as compared with the linguistic strategy condition. Apart from the Group \times Strategy \times Polarity \times Truth Value interaction, F(1, 26) = 4.98, p < .03, MSE = 5, no interaction with strategy was significant (p > .10). Together with the above reported Group \times Strategy \times Polarity \times Truth Value interaction, the Group \times Polarity interaction, F(1,26) = 5.05, p < .03, MSE = 13, was significant; no other interaction with group was significant (ps > .25).⁶

IA

The IA data for all eight ROIs (AF, F, FC, C, CP, P, PO, O) were subjected to the FDR procedure. Three tests were performed,

one for a main effect of IQ, one for a main effect of strategy, and one for an interaction of IQ and strategy. All tests were performed separately on the segments time locked to the onset of the sentence and to the onset of the picture. Only the tests for strategy differences yielded significant results. Even when alpha was raised to levels as high as .20 (indicating a willingness to accept an average of 20% of false positives), no significant main effects of IQ or IQ \times Strategy interactions were found.

Figures 3 and 4 show FDR threshold *t* maps for the comprehension and verification intervals, respectively. Figure 3 shows strategy differences in the sentence-onset epochs, t(26) = 3.04, p < .001, where *t* represents the minimum threshold *t* value, and *p* represents the associated significance level. Figure 4 shows the

⁶ Separate analysis of performance data based on only verbal or spatial ability, respectively, yielded generally the same pattern of results. However, for the error rates, verbal ability was found to have a bigger effect on percentage of error (2.5% vs. 5.4% for high vs. low verbal ability participants) than was spatial ability (3.5% vs. 4.4% for individuals with high vs. low spatial ability).



Figure 4. Threshold false discovery rate (FDR) map showing significant amplitude differences between imagery and linguistic strategy conditions at picture onset (picture). Each subplot is a time–frequency plot showing data points at which the difference was significant according to the FDR procedure. Time and frequency are plotted in the horizontal and vertical axes, respectively. Each subplot refers to one of the regions of interest shown in Figure 1. The cutoff *t* value for these results, given by the FDR procedure, was 3.22.

strategy differences in the picture-onset epochs, t(26) = 3.22, p < .001. As can be seen in Figure 3, there were three main areas of significant strategy-related differences. First, in the alpha frequency range (8–12 Hz), IAs were higher in the imagery than in the linguistic strategy condition.

The effect appeared to consist of two components with different topography. The first, occurring within 300-900 ms after sentence onset, was visible from frontal to parietal sites; the second, within 1-2 s after sentence onset, was visible from fronto-central to parieto-occipital sites. Second, in the theta frequency range (4-8 Hz), IAs were higher in the linguistic than in the imagery strategy condition. The effect appeared to consist of two components with different topography. The first component, occurring within 700-1,500 ms after sentence onset, was visible from frontal to occipital sites; the second, occurring within 1-3 s after sentence onset, was visible from antero-frontal to parieto-occipital sites. Third, in the mu-beta frequency range (8-20 Hz), IAs were higher in the linguistic than the imagery strategy condition. This effect was broadly distributed across the scalp with a region-dependent time course: Posterior areas had an earlier onset (approximately 2.5 s) than anterior areas (approximately 3 s); offset was approximately 4 s after sentence onset, independent of the region.

Figure 4 shows six areas of significant strategy-related differences. Approximately 1 s before picture onset, in the theta frequency range (4-6 Hz), IAs were higher in the linguistic than in

the imagery strategy condition, and were distributed from central to parietal areas. Within 500 ms after picture onset, in the higher alpha and lower beta frequency range (10–18 Hz), IAs were higher in the linguistic than in the imagery strategy condition, and were distributed from antero-frontal to posterior areas. Within 1 s after picture onset, in the theta frequency range (4-8 Hz), IAs were higher in the imagery than in the linguistic strategy condition, and were distributed from fronto-central to centro-parietal areas. Between 1 and 1.5 s after the onset of the picture, in the beta frequency range (18-24 Hz), IAs were higher in the imagery than in the linguistic strategy condition, and were distributed from frontal to parietal regions. Between 1 and 2 s after picture onset, in the mu frequency range (9-13 Hz), IAs were higher in the imagery than in the linguistic strategy, and were broadly distributed across the scalp. From 2 to 3.5 s after picture onset, in the theta frequency range (4-6 Hz), IAs were higher in the linguistic than the imagery strategy condition, and were broadly distributed across the scalp.

The strategy-related effects revealed in the initial global analysis were selectively subjected to further tests with more circumscribed ERD analyses targeted at specific, relevant frequency bands. In particular, ERD analysis was targeted at the theta and upper alpha bands. Although the initial results of the ERD analyses also showed substantial strategy-related differences in the beta band (16–26 Hz) as well as in the associated mu band (9–13 Hz with a scalp distribution centered at parieto–central locations), subse-



Figure 5. Alpha event-related desynchronization (ERD) time courses for high IQ (HIQ) and low IQ (LIQ) groups in the imagery and linguistic strategy conditions at sentence onset (sentence) for each region of interest. Time and percentage of ERD are plotted in the horizontal and vertical axes, respectively.

quent analyses showed such differences to be straightforward consequences of the well-known fact that mu-beta rhythms strongly desynchronize prior to and during response execution (e.g., Gladwin et al., 2006) and the fact that RTs were very different for the two strategies. For these reasons, these latter effects were not further explored.

In light of our research objective regarding IQ-related effects, we decided to maintain the distinction between IQ groups in these follow-up analyses despite the fact that no IQ-related effects were present in the global analysis. This is justified because IQ-related effects on cerebral dynamics in the present study are likely to be subtle, given that subtle effects could be missed when correcting for a large number of multiple comparisons as implemented in the FDR procedure, and might have a much better chance to show up in more targeted analyses. We focus on those frequency bands that showed large strategy-related effects, reasoning that these would also be the ones most likely to show IQ-related differences.

Alpha ERD

Because ERD differences between groups or tasks may in some cases reflect differences in power in the reference interval rather than differences in power in the test interval (Doppelmayr, Klimesch, Pachinger, & Ripper, 1998), we first tested for possible baseline relative differences in alpha (9.5–12.5 Hz) power between the two groups. No IQ-related differences in baseline alpha power were found (p > .80).

Figure 5 shows the percentage of ERD in the alpha frequency band for both groups in the two strategy conditions, relative to the sentence onset. Consistent with the patterns shown in Figure 3, alpha ERD between 0.5 to 2 s after sentence onset was higher in the linguistic than in the imagery strategy condition. The time course of the alpha ERD observed in Figure 5 in the interval between 2 to 4 s after sentence onset is also consistent with the results shown in Figure 3, such that in the linguistic strategy condition, the desynchronization of the alpha rhythm gradually decreased, whereas in the imagery strategy condition, desynchronization was high for a longer period. Note that no IQ-related differences in alpha ERD were apparent in these two intervals. However, in the 300 ms preceding the sentence onset, an IQrelated difference was observed: LIQ individuals showed a positive desynchronization, whereas HIQ individuals showed a negative desynchronization, F(1, 26) = 4.89, p < .03, MSE = 77. This



Figure 6. Alpha event-related desynchronization (ERD) time courses for high IQ (HIQ) and low IQ (LIQ) groups in the imagery and linguistic strategy conditions at picture onset (picture) for each region of interest. Each subplot refers to one of the regions in the electrode clusters in Figure 1. Time and percentage of ERD are plotted in the horizontal and vertical axes, respectively.

latter effect did not interact with strategy (p > .70), suggesting that it is a relatively "pure" IQ-related difference.

Figure 6 shows the alpha ERD for the epoch time locked to the picture onset. Consistent with the results shown in Figure 4, ERD time course at picture onset was generally comparable between strategies. Alpha desynchronization was higher at picture onset for the imagery than for the linguistic strategy condition, and was substantially reduced at the end of the verification processing; this reestablishment of the postprocessing alpha rhythm happened earlier for the imagery than the linguistic strategy. No IQ-related differences were apparent.

An additional analysis of alpha ERD was performed with time intervals similar to the ones used by Neubauer et al. (1995). Neubauer et al.'s event-related periods were as follows: (a) from 1.0 to 0.5 s before sentence onset (prestimulus interval), (b) from 250 to 125 ms before the CRT, (c) from 125 to 375 ms after the CRT, and (d) from 250 to 125 ms before the VRT. Similar ERD temporal intervals were estimated considering sentence onset and response executions. The averaged power in the upper alpha band was subjected to a mixed ANOVA, with ROI (AF, F, FC, C, CP,

P, PO, O), strategy (imagery vs. linguistic), and time interval (preceding CRT, after CRT, preceding VRT) as within-subject factors and group (HIQ vs. LIQ) as a between-subjects factor. The prestimulus interval was excluded from the analysis because its values were close to baseline, and the increased variance due to its extreme values would have biased the outcome of the ANOVA (see Figure 7).

The time course of the percentage of ERD differed between the two groups, as reflected by the Time Interval × Group interaction, F(2, 52) = 4.08, p < .02, MSE = 576. No other tests yielded evidence for IQ-related differences in ERD (all ps > .20). Percentage of ERD increased with the time spent on the trial, F(2, 52) = 28.6, p < .001, MSE = 576; was higher in the posterior regions than in the anterior regions, F(7, 182) = 11.01, p < .001, MSE = 492; and its spatial distribution differed as a function of time (Time Interval × ROI interaction), F(14, 364) = 10.01, p < .001, MSE = 47, increasing slowly but consistently at the frontal regions and showing an abrupt increment followed by a steep decrement in the posterior regions (see Figure 7). With regard to strategy differences, ERD amplitude was lower in the linguistic



Figure 7. Time course and topography of the alpha event-related desynchronization (ERD) with time intervals similar to the ones of Neubauer et al. (1995). Percentage of ERD is plotted as a function of time interval (specified in the Results section) for the imagery strategy condition (solid lines) and for the linguistic strategy condition (broken lines). Note that, for clarity, pairs of regions of interest (ROIs) were averaged together to create the following ROIs: frontal (the average of antero–frontal and frontal), central (the average of fronto–central and central), parietal (the average of centro–parietal and parietal), and occipital (the average of parieto–occipital and occipital). CRT = comprehension response time; VRT = verification response time.

than in the imagery strategy condition, F(1, 26) = 15.98, p < .001, MSE = 1,719, independently of ROI or time interval (both ps >.20). However, the ROI × Time Interval × Strategy interaction, F(14, 364) = 3.27, p < .01, MSE = 17, shown in Figure 7, reflects that topography and time course of the percentage of ERD were affected by the strategy used. Between strategies differences in ERD time course were more pronounced at the VRT interval in which changes in ERD were more marked in the linguistic than in the imagery strategy condition. Moreover, in the VRT interval, ERD time course at central and occipital locations crosses over between the two strategies.

In summary, the topography and time course of alpha ERD were affected by the strategy used, and ERD was generally higher with the imagery strategy than the linguistic strategy. In general, the two groups showed a similar pattern in that the ERD time course did not differ for the IQ groups except at the interval before the onset of the sentence. Analysis of the ERD in the analogous time intervals as those used by Neubauer et al. (1995) yielded a substantial difference at a strategy level but no IQ-related differences.

Theta ERD

Figures 8 and 9 show the theta ERD for epochs time-locked to the onset of the sentence and the picture, respectively. No IQrelated differences in baseline theta power were found (p > .3). To distinguish between so-called evoked and induced changes in theta power, we performed analysis of theta ERD both with and without a correction for average event-related potentials (see Tallon-Baudry & Bertrand, 1999, for an extensive discussion regarding this issue). Though this produced somewhat different overall time courses for theta ERD, it did not affect any differences related to strategy or IQ. For this reason, we only report the results for ERD computed from instantaneous power uncorrected for event-related potentials.

In Figure 8, consistent with the results shown in Figure 3, between 0.5 and 3 s after sentence onset, theta ERD was lower in the linguistic than in the imagery strategy condition. IQ-related differences, independent from strategy effects (Group \times Strategy interaction; p > .16), were found during the 0.5 s warning interval



Figure 8. Theta event-related desynchronization (ERD) time courses for high IQ (HIQ) and low IQ (LIQ) groups in the imagery and linguistic strategy conditions at sentence onset (sentence) for each region of interest. Time and percentage of ERD are plotted in the horizontal and vertical axes, respectively.

preceding sentence onset, in which theta desynchronization was lower for HIQ than for LIQ individuals, F(1, 26) = 5.0, p < .03, MSE = 3,510. Given the timing of this ERD decrement relative to the onset of the warning stimulus and the following sentence, this would seem to reflect preparatory activity. A test for IQ-related differences in theta ERD in the interval between 1 and 2 s after sentence onset did not yield significant results (p > .20).

Figure 9 shows, consistent with the results shown in Figure 4, that in the interval from 2 to 4 s after picture onset, theta ERD was lower in the linguistic than in the imagery strategy condition. We find it interesting that in the interval between 0.5 and 2 s after picture onset, there seems to be a remarkable similarity between the peak latencies of negative theta desynchronization and mean RT across groups and strategies, with differences in the peak latencies being closely proportional to differences in RT; this is clearest at parietal sites. This suggests that the differences in theta ERD following picture onset are most readily explained in terms of differences in processing speed.

Discussion

The primary aim of this study was to investigate whether previously documented IQ-related differences in degree and pattern of neural activation during SVT performance (Neubauer et al., 1995) persist when the strategies used in task performance are controlled by means of explicit instructions. To this end, we measured EEG while groups of LIQ and HIQ individuals performed the SVT using either a linguistic or a spatial-visual (imagery) strategy. Analysis of the behavioral data suggests that both IQ groups used the two distinct strategies according to instruction. Most important, CRT (sentence comprehension time) was much shorter in the linguistic as compared with the imagery condition and polarity of the sentence had a major effect on CRT only in the imagery condition. Both results indicate more extensive processing of the sentence prior to onset of the picture in the imagery condition. An interesting finding is that no significant IQ-related effects on CRT were obtained.

More evidence of appropriate strategy use was obtained in the analysis of VRT. VRT was substantially shorter in the imagery condition than in the linguistic condition. Even more important, a significant Polarity \times Truth Value \times Strategy interaction was found for VRT, which—according to several authors (i.e., MacLeod et al., 1978; Mathews et al., 1980)—satisfies the litmus test for the distinction between the linguistic and imagery strategies. VRT was slower and more error prone for the LIQ group,



Figure 9. Theta event-related desynchronization (ERD) time courses for high IQ (HIQ) and low IQ (LIQ) groups in the imagery and linguistic strategy conditions at picture onset (picture) for each region of interest. Time and percentage of ERD are plotted in the horizontal and vertical axes, respectively.

especially for the more difficult trials in the linguistic condition (e.g., TN trials). However, there was no Polarity \times Truth Value \times Strategy \times IQ interaction. Overall, the behavioral data strongly indicate that both groups performed the task according to the instructed strategy and suggest a modest overall advantage of HIQ over LIQ individuals with respect to both speed and accuracy of task execution.

A global analysis of IA across a wide range of EEG frequency bands and aggregated electrode positions revealed no significant IQ-related differences, whereas several strategy-related effects were obtained in the theta band and the upper alpha frequency band. A more focused analysis of the time course of these latter effects, in terms of ERD, showed a substantial and widely distributed decrease of upper alpha power and increase of theta power during task execution, consistent with the suggestion of Nunez et al. (2001) that alpha power is reduced but theta power enhanced during effortful processing. In general, the difference in the temporal profiles of power changes in these two frequency bands as a function of strategy, and, hence, the strategy-related differences in the overall analysis, are probably best interpreted as a straightforward consequence of the substantial differences in dynamics and overall duration of processing between these strategies as reflected in the RT results. Qualitative differences in processing between the two strategies may also have contributed to the different ERD profiles. However, even if present, such contributions are difficult to separate from, and are likely to have been overshadowed by, the differences between strategies in overall duration of processing in the present study.

The lack of IQ-related differences in upper alpha ERD during SVT performance in the present study contrasts with the findings of Neubauer et al. (1995). Neubauer et al. found significantly stronger upper alpha ERD at frontal sites for LIQ as compared with HIQ individuals during SVT performance. Although Neubauer et al. did not control for possible strategy differences between IQ groups, the present results show that strategy-related differences in upper alpha ERD are not limited to frontal regions but widely distributed across the scalp, which makes it unlikely that a confounding of IQ and strategy in Neubauer et al.'s study can fully account for the differences between our study and theirs. A more plausible account for these differences is suggested by the fact that participants in our study received relatively little SVT training as compared with the much more extensive practice given to the participants in Neubauer et al.'s study (note that these participants had also taken part in a previous study using the SVT conducted by Neubauer & Freudenthaler, 1994). Whereas the limited practice in the present study may have prevented task automation in either IQ group, the more extensive practice given in Neubauer et al.'s (1995) study may have enabled their HIQ participants, but not LIQ participants, to achieve a high level of automation in SVT performance. As task automation has been linked to reduced involvement of frontal regions in task performance (Koch et al., 2006; Owen, Evans, & Petrides, 1996), we suggest that different amounts of SVT practice between the two studies provide a plausible, but admittedly speculative, explanation of the difference in results regarding IQ-related differences in frontal upper alpha ERD. This possibility deserves further systematic study.

Whereas no IQ-related differences in EEG power were found during actual task execution, two differences were obtained during the 0.5 s warning or preparation interval preceding sentence onset. First, a phasic enhancement of theta power during the warning interval, found most prominently at fronto-central sites, was present in both groups but was found to be significantly stronger in the HIQ group. Second, HIQ, but not LIQ, individuals showed a broadly distributed phasic enhancement of upper alpha power during the warning interval. A similar change was reported in Neubauer et al. (1995) for the interval between sentence offset and picture onset, where a 500-ms blank interval was placed. This interval could be interpreted as a preparatory period for the execution of the sentence-picture comparison. An interesting finding is that higher amplitudes of fronto-central theta rhythm during the preparation interval in task-switch paradigms have been linked to enhanced quality or effectiveness of advance preparation (Gladwin et al., 2006). As advance preparation in task-switch paradigms has been argued to require successful retrieval and maintenance of task goals and task sets (Mayr & Kliegl, 2000), Gladwin et al.'s (2006) findings seem consistent with results linking theta rhythm to processes involved in memory retrieval and working memory (Gevins & Smith, 2000; Klimesch, 1999). Thus, the stronger phasic enhancement of theta power found in HIQ individuals might indicate more adequate, or more adequately timed, preparatory activity in these individuals.

The finding of a concurrent phasic enhancement of upper alpha power in HIQ individuals may seem paradoxical, given the traditional view of alpha synchronization as a cortical "idling" process (Pfurtscheller, Stancak, & Neuper, 1996). However, more recent evidence has suggested an alternative interpretation, in which alpha synchronization is thought to reflect active inhibitory control of task-irrelevant brain regions (N. R. Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Klimesch, 1999). From this perspective, phasic alpha synchronization during the warning interval in HIQ individuals might reflect enhanced inhibition of taskirrelevant brain regions, which has been suggested to be a critical component in the configuration and maintenance of selective task sets (Monsell, 1996, 2003). In other words, it may be a reflection of the active process of focusing on the task and thus inhibiting task-irrelevant brain regions (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999), or of the suppression of the flow of irrelevant information (Jensen, Gelfand, Kounios, & Lisman, 2002; see also Fink, Grabner, Benedek, & Neubauer, 2006, for considerations along this line). This evidence that HIQ individuals may have been able to achieve better preparatory control prior to stimulus onset is consistent with the behavioral results indicating overall superior SVT performance by HIQ as compared with LIQ individuals.

That preparatory set may be a crucial determinant of quality of task execution is also suggested by a series of studies linking accuracy of subsequent memory retrieval to brain activity (induced by trial-by-trial cuing of relevant stimulus information) prior to stimulus presentation (for evidence using fMRI, see, e.g., Otten, Henson, & Rugg, 2002; for evidence using event-related brain potentials, see, e.g., Otten, Quayle, Akram, Ditewig, & Rugg, 2006; Padilla, Wood, Hale, & Knight, 2006). These findings were interpreted in terms of effects of the quality of the cued task set on the quality of encoding. The present results suggest that an interesting topic for future studies would be to look for IQ-related differences in the quality of such flexible and selective cue-evoked memory encoding.

In summary, we failed to find the negative correlation between brain activation and intelligence predicted by the neural efficiency theory. We did find major differences in spatio–temporal activation patterns between linguistic and imagery strategy conditions, which highlight the need to control for potential confoundings of intelligence and strategy use in individual differences research. More particular, it is important to prevent differences in IQ from being confounded with differences in expertise. Finally, whereas we did not find IQ-related differences in brain activation during actual task execution, we did obtain suggestive evidence that HIQ and LIQ individuals differed in the quality and timing of preparation immediately preceding SVT execution. The generality of the latter finding, and its potential relation to neural efficiency theory, might be fruitful topics for future research.

References

- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, 57, 289–300.
- Carpenter, P. A., & Just, M. A. (1975). Sentence comprehension: A psycholinguistic processing model of verification. *Psychological Re*view, 82, 45–73.
- Clark, H. H., & Chase, W. (1972). On the process of comparing sentences against pictures. *Cognitive Psychology*, 3, 472–517.
- Cooper, L. A., & Regan, D. T. (1982). Attention, perception, and intelligence. In R. J. Sternberg (Ed.), *Handbook of human intelligence* (pp. 123–169). New York: Cambridge University Press.
- Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, 47, 65–74.
- Doppelmayr, M. M., Klimesch, W., Pachinger, T., & Ripper, B. (1998). The functional significance of absolute power with respect to eventrelated desynchronization. *Brain Topography*, 11, 133–140.
- Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., et al. (2000, July 21). A neural basis for general intelligence. *Science*, 289, 457–460.
- Fink, A., Grabner, R. H., Benedek, M., & Neubauer, A. C. (2006). Divergent thinking training is related to frontal electroencephalogram alpha synchronization. *European Journal of Neuroscience*, 23, 2241– 2246.
- Gevins, A., & Smith, M. E. (2000). Neurophysiological measures of

working memory and individual differences in cognitive ability and cognitive style. *Cerebral Cortex*, *10*, 829–839.

- Gladwin, T. E., Lindsen, J. P., & de Jong, R. (2006). Pre-stimulus EEG effects related to response speed, task switching, and upcoming response hand. *Biological Psychology*, 72, 15–34.
- Gough, P. B. (1965). Grammatical transformations and speed of understanding. *Journal of Verbal Learning and Verbal Behavior*, 5, 107– 111.
- Grabner, R. H., Stern, E., & Neubauer, A. C. (2003). When intelligence loses its impact: Neural efficiency during reasoning in a familiar area. *International Journal of Psychophysiology*, 49, 89–98.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55, 468–484.
- Gray, J. R., Burgess, G. C., Schaefer, A., Yarkoni, T., Larsen, R. J., & Braver, T. S. (2005). Affective personality differences in neural processing efficiency confirmed using fMRI. *Cognitive, Affective, & Behavioral Neurosciences*, 5, 182–190.
- Haier, R., & Benbow, C. (1995). Sex differences and lateralization in temporal lobe glucose metabolism during mathematical reasoning. *Developmental Neuropsychology*, 11, 405–414.
- Hennighausen, E., Heil, M., & Rosler, F. (1993). A correction method for DC drift artifacts. *Electroencephalography and Clinical Neurophysiology*, 86, 199–204.
- Hunt, E. (1995). The role of intelligence in modern society. *American Scientist*, *83*, 356–368.
- Jausovec, N., & Jausovec, K. (2001). Differences in EEG current density related to intelligence. *Brain Research: Cognitive Brain Research*, 12, 55–60.
- Jausovec, N., & Jausovec, K. (2003). Spatiotemporal brain activity related to intelligence: A low resolution brain electromagnetic tomography study. Brain Research: Cognitive Brain Research, 16, 267–272.
- Jausovec, N., & Jausovec, K. (2004a). Differences in induced brain activity during the performance of learning and working-memory tasks related to intelligence. *Brain and Cognition*, 54, 65–74.
- Jausovec, N., & Jausovec, K. (2004b). Intelligence related differences in induced brain activity during performance of memory tasks. *Personality* and Individual Differences, 36, 597–612.
- Jausovec, N., & Jausovec, K. (2005). Differences in induced gamma and upper alpha oscillations in the human brain related to verbal/performance and emotional intelligence. *International Journal of Psychophysiology*, 56, 223–235.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, 12, 877–882.
- Klimesch, W. (1997). EEG-alpha rhythms and memory processes. International Journal of Psychophysiology, 26, 319–340.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research: Brain Research Review*, 29, 169–195.
- Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. (1999). "Paradoxical" alpha synchronization in a memory task. *Brain Research: Cognitive Brain Research*, 7, 493–501.
- Koch, K., Wagner, G., Consbruch, K., von Nenadic, I., Schultz, C., Ehle, C., et al. (2006). Temporal changes in neural activation during practice of information retrieval from short-term memory: An fMRI study. *Brain Research*, 1107, 140–150.
- Koechlin, E., Ody, C., & Kouneiher, F. (2003, November 14). The architecture of cognitive control in the human prefrontal cortex. *Science*, 302, 1181–1185.
- Kroll, J. F., & Corrigan, A. (1981). Strategies in sentence–picture verification: The effect of an unexpected picture. *Journal of Verbal Learning* and Verbal Behavior, 20, 515–531.

- Luteijn, F., & van der Ploeg, F. A. E. (1983). Handleiding groninger intelligentietest (git) [Groningen Intelligence Test manual]. Lisse, the Netherlands: Swets & Zeitlinger BV.
- MacLeod, M. C., Hunt, E. B., & Mathews, N. N. (1978). Individual differences in the verification of sentence–picture relationship. *Journal* of Verbal Learning and Verbal Behavior, 17, 493–507.
- Mathews, N. N., Hunt, E. B., & MacLeod, C. M. (1980). Strategy choice and strategy training in sentence–picture verification. *Journal of Verbal Learning and Verbal Behavior*, 19, 531–548.
- Mayr, U., & Kliegl, R. (2000). Complex semantic processing in old age: Does it stay or does it go? *Psychology and Aging*, 15, 29–43.
- Monsell, S. (1996). Control of mental processes. In V. Bruce (Ed.), Unsolved mysteries of the mind: Tutorial essays in cognition (pp. 93– 148). Hove, United Kingdom: Erlbaum.
- Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, 7, 134–140.
- Neubauer, A. C., & Freudenthaler, H. H. (1994). Reaction times in a sentence–picture verification test and intelligence: Individual strategies and effects of extended practice. *Intelligence*, 19, 193–218.
- Neubauer, A. C., Freudenthaler, H. H., & Pfurtscheller, G. (1995). Intelligence and spatiotemporal patterns of event-related desynchronization (ERD). *Intelligence*, 20, 249–266.
- Neubauer, A. C., Grabner, R. H., Fink, A., & Neuper, C. (2005). Intelligence and neural efficiency: Further evidence of the influence of task content and sex on the brain–IQ relationship. *Brain Research: Cognitive Brain Research*, 25, 217–225.
- Nunez, P. L., Wingeier, B. M., & Silberstein, R. B. (2001). Spatialtemporal structures of human alpha rhythms: Theory, microcurrent sources, multiscale measurements, and global binding of local networks. *Human Brain Mapping*, 13, 125–164.
- Otten, L. J., Henson, R. N. A., & Rugg, M. D. (2002). State-related and item-related neural correlates of successful memory encoding. *Nature Neuroscience*, 5, 1339–1344.
- Otten, L. J., Quayle, A. H., Akram, S., Ditewig, T. A., & Rugg, M. D. (2006). Brain activity before an event predicts later recollection. *Nature Neuroscience*, 9, 489–491.
- Owen, A. M., Evans, A. C., & Petrides, M. (1996). Evidence for a two-stage model of spatial working memory processing within the lateral frontal cortex: A positron emission tomography study. *Cerebral Cortex*, 6, 31–38.
- Padilla, M. L., Wood, R. A., Hale, L. A., & Knight, R. T. (2006). Lapses in a prefrontal–extrastriate preparatory attention network predict mistakes. *Journal of Cognitive Neuroscience*, 18, 1477–1487.
- Pfurtscheller, G., Stancak, A. J., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, 24, 39–46.
- Reichle, E. D., Carpenter, P. A., & Just, M. A. (2000). The neural bases of strategy and skill in sentence–picture verification. *Cognitive Psychology*, 40, 261–295.
- Rypma, B., Berger, J., Prabhakaran, V., Bly, B., Kimberg, D., Biswal, B., et al. (2006). Neural correlates of cognitive efficiency. *NeuroImage*, 33, 969–979.
- Sharbrough, F., Chatrian, G., Lesser, R., Lüders, H., Nuwer, M., & Picton, T. (1991). American Electroencephalographic Society guidelines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology*, 8, 200–202.
- Sternberg, R. J. (2003). Contemporary theories of intelligence. In I. B. Weiner, W. M. Reynolds, & G. E. Miller (Eds.), *Handbook of psychology* (pp. 23–45). Hoboken, NJ: Wiley.
- Sternberg, R. J., & Weil, E. (1980). An aptitude × strategy interaction in linear syllogistic reasoning. *Journal of Educational Psychology*, 72, 226–239.

- Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*, 151–162.
- Tversky, B. (1975). Pictorial encoding of sentences in sentence–picture verification. *Quarterly Journal of Experimental Psychology*, 27, 405–410.
- Vernon, P. A. (1993). Intelligence and neural efficiency. In D. Detterman (Ed.), *Current topics in human intelligence* (pp. 171–187). Norwood, NJ: Ablex.

Vernon, P. A., & Mori, M. (1992). Intelligence, reaction times, and peripheral nerve conduction velocity. *Intelligence*, *16*, 273–288.

Wechsler, D. (1981). Manual of the Wechsler Adult Intelligence Scale— Revised. New York: The Psychological Corporation.

> Received January 15, 2007 Revision received May 14, 2007 Accepted May 24, 2007

Members of Underrepresented Groups: Reviewers for Journal Manuscripts Wanted

If you are interested in reviewing manuscripts for APA journals, the APA Publications and Communications Board would like to invite your participation. Manuscript reviewers are vital to the publications process. As a reviewer, you would gain valuable experience in publishing. The P&C Board is particularly interested in encouraging members of underrepresented groups to participate more in this process.

If you are interested in reviewing manuscripts, please write to the address below. Please note the following important points:

- To be selected as a reviewer, you must have published articles in peer-reviewed journals. The experience of publishing provides a reviewer with the basis for preparing a thorough, objective review.
- To be selected, it is critical to be a regular reader of the five to six empirical journals that are most central to the area or journal for which you would like to review. Current knowledge of recently published research provides a reviewer with the knowledge base to evaluate a new submission within the context of existing research.
- To select the appropriate reviewers for each manuscript, the editor needs detailed information. Please include with your letter your vita. In the letter, please identify which APA journal(s) you are interested in, and describe your area of expertise. Be as specific as possible. For example, "social psychology" is not sufficient—you would need to specify "social cognition" or "attitude change" as well.
- Reviewing a manuscript takes time (1–4 hours per manuscript reviewed). If you are selected to review a manuscript, be prepared to invest the necessary time to evaluate the manuscript thoroughly.

Write to Journals Office, American Psychological Association, 750 First Street, NE, Washington, DC 20002-4242.