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Cortical volume and speed-of-processing are complementary in prediction of performance intelligence

Kristine B. Walhovd[a,*], Anders M. Fjell[a], Ivar Reinvang[a,b], Arvid Lundervold[c], Bruce Fischl[d], David Salat[d], Brian T. Quinn[d], Nikos Makris[e], Anders M. Dale[d,f,g]

[a] *Institute of Psychology, University of Oslo, P.B. 1094, Blindern, 0317 Oslo, Norway*
[b] *Rikshospitalet University Hospital, Department of Psychosomatic Medicine*
[c] *Department of Physiology and Locus on Neuroscience, University of Bergen, Bergen, Norway*
[d] *MGH-NMR Center, Harvard University, Harvard, Norway*
[e] *Center for Morphometric Analysis, MGH, Harvard University, Harvard, Norway*
[f] *MR Center, Norwegian University of Science and Technology (NTNU), Norway*
[g] *Departments of Neurosciences and Radiology, University of California, San Diego*

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Abstract

The rationale for the present study was to investigate the relationship between cortical volume, the latency of the ERP component *P3a* (as a measure of speed-of-processing), and performance intelligence (not adjusted for age differences). Seventy-one participants aged 20–88 years underwent a visual 3-stimuli oddball ERP task, an MRI-scan, and intelligence testing. *P3a* latency and cortical volume shared 9% variance ($p < .05$) and both were significantly related to performance intelligence ($R^2 = .26$ and .40, respectively). The amount of explained variance increased significantly (to $R^2 = .51$) when both measures were used as simultaneous predictors. When a path diagram was constructed including age as an exogenous variable, *P3a* latency and cortical volume both significantly predicted performance intelligence, but were no longer related to one another. The main conclusion from the study is that speed and size are complementary in prediction of performance intelligence, and the theoretical implications are discussed.

Keywords: Aging; ERP; *P3a*; MRI; Morphometry

1. Introduction

Brain size and mental speed have been put forward as major determinants of individual differences in intelligence (Deary & Caryl, 1997). The present study was targeted at exploring the relationship between speed and size when speed-of-processing is defined electrophysiologically and a specific measure of cortical volume is employed. Our hypothesis was that the neural substrate for these two classes of measures is only partly overlapping, and that they are complementary rather than redundant in prediction of mental abilities.

The use of measures of speed-of-processing represents a major approach to human intelligence (Beck, 1933; Deary, 2001a; Neubauer, 1997), and reduction in processing speed has been proposed as a mechanism behind decreased mental capabilities with increasing age (Salthouse & Ferrer-Caja, 2003). The phenotypic correlation between mental speed and intelligence is due to genetic factors (Neubauer, Spinath, Riemann, Angleiter, & Borkenau, 2000). However, processing speed needs to be explained in terms of underlying neurophysiology, and the latencies of event related electrophysiological potentials (ERPs) have been proposed, and partly validated, as promising candidates (Deary, Der, & Ford, 2001). Recording of electrophysiological processes in the brain, with a temporal resolution in the milliseconds range, gives valuable online information about the neurophysiological correlates to mental activity. Aspects of information processing critical for the generation of different ERP peaks, i.e. processing speed and attentional resource allocation, are also

* Corresponding author. Tel.: +47 22 845129; fax: +47 22 845001.
E-mail address: Kristine@walhovd.com (K.B. Walhovd).

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measured by IQ tests, and a relationship is thus expected. This may especially be true for tasks requiring speeded and efficient processing, like fluid or performance (non-verbal) tasks in traditional IQ tests, and a moderate relationship between intelligence and the ERP component P300 has been established (Bazana & Stelmack, 2002; Fjell & Walhovd, 2001; Jausovec & Jausovec, 2000; McGarry-Roberts, Stelmack, & Campbell, 1992; O'Donnell, Friedman, Swearer, & Drachman, 1992; Walhovd & Fjell, 2001, 2002), even though some discrepant results have been reported (e.g. Houlihan et al., 1998). Disagreement exists regarding the exact cognitive significance of the P300, but it can be argued that its latency represents the timing of a cognitive process related to stimulus classification. Thus, P300 latency can be regarded as a measure of processing speed. ERP has an advantage over reaction time measures, in that the dependence on motor responses and possibly nerve conduction velocity is eliminated.

While the speed of cerebral electrophysiological processes constitutes one basis for cognitive abilities, the effect of brain size is another. However, these variables have largely been studied in isolation. Based on extensive studies during the last decade or so, using differing intelligence measures, scan protocols, scanners, and samples, there is consensus that IQ and brain volume are robustly and positively correlated (Deary & Caryl, 1997; Wickett, Vernon, & Lee, 2000). Typically, correlations of about .40 are found, and the relationship has been shown to be of genetic origin (Posthuma et al., 2002). Larger brains may enable higher intelligence because they generally have more neurons (Pakkenberg & Gundersen, 1997) and possibly more synaptic connections. This may be beneficial for both cognitive capacity and cognitive complexity (Wickett et al., 2000). Other neural parameters that may underlie the correlation between brain size and IQ are degree of complex circuitry, dendritic expansion, myelin thickness, metabolic efficiency and efficient neurotransmitter production, both in terms of release and reuptake, and brain reserve capacity (Deary & Caryl, 1997; Vernon, Wickett, Bazana, & Stelmack, 2000). However, these explanations for the positive effect of brain size should not be taken for granted, as evident from some empirical examples. Certain developmental disorders, e.g. autism, may include macroencephaly (Courchesne, Hillyard, & Galambos, 1975). Here, a greater number of synaptic connections may serve to slow neural transmission, and problems during neuronal migration may lead to proliferation of neurons and neuronal connections and thereby increased volume without an increase of mental abilities. Also, the male brain is on average larger than the female brain (e.g. Gur et al., 1999; Resnick et al., 2000), while no corresponding differences in mental abilities are found.

Further, it is unlikely that the reduction in brain volume with increasing age (e.g. Tisserand & Jolles, 2003) can be explained by decreases in the number of neurons (Courchesne et al., 2000; Peters, Morrison, Rosene, & Hyman, 1998; Terry, Deteresa, & Hansen, 1987), and studies of cognitive function in aged rats have suggested that age-related cognitive decline can occur in the absence of significant neuron death in relevant neuroanatomical structures (Rapp, Deroche, Mao, & Burwell, 2002). In a review paper, Peters et al. (1998) conclude that there is presently no strong case that the often-observed reductions in neuroanatomical volumes in normal aging are caused by neuron deaths, or that, if neuron death in aging actually occurs in specific regions in the human brain, this causes the cognitive changes that inevitably come with increasing age.

The main aim of the present study is to get new insights into the relationship between cortical volume and electrophysiologically defined speed-of-processing, and how these two measures combine or diverge in predicting higher mental functioning. As evident from the literature reviewed above, even though speed and volume constitute important neurophysiological fundaments of intelligence, we know little about the mechanisms mediating these relationships. As a consequence of this, we lack knowledge about how these fundamentally different measures of human neurophysiology are related, or to which degree they may be independent. Still, several of the possible neural explanations for the brain size–IQ correlations indicate that also a relationship between brain size and speed-of-processing may be expected. Brains with a larger number of neurons and more synaptic connections may be able to process complex information in a faster and more efficient way. However, empirical investigations of this have rarely been performed. One exception is a study by Wickett et al. (2000), in which correlations in the −.30 to −.50 range were reported between reaction time and other speed variables and total brain volume. Wickett et al. also found significant relationships between IQ measures and brain volume. However, evidence obscuring such relationships also exists. A comparative study of reaction time with rhesus monkeys (*Macaca mulatta*) and humans showed that the monkeys outperformed humans in reaction time and inspection time tasks, while their neocortical volume were smaller and their IQ lower (Washburn & Rumbaugh, 1997). Thus, empirical investigations are warranted, both of the relationship between cortical volume and mental speed, and of how the combined use of the measures influences their power in predicting mental abilities. If the unique variance of each of the two measures predicts intelligence, this has theoretical implications. Separate contributions to psychometric intelligence will then be made by speed and volume. Further, speed-of-processing will then probably have other neural causes than merely cortical volume or number of neurons and synaptic connections. If, however, cortical volume and speed-of-processing are highly correlated and the combined use of the measures do not increase the power of intelligence prediction, then it might be that size is important for intelligence because it increases the speed of information processing. These questions remain to be answered.

One previous study has related P300 and brain size. Egan et al. (1994) compared auditory P300 latency and total brain volume in a smaller sample of 40 young persons, and found no relationship. In the present study, we investigate the

relationship between performance intelligence, cortical volume, and speed-of-processing. As a measure of the latter, we use the latency of the visual *P*3*a* component (see Section 2). The latency of *P*3*a* is shorter than that of the classical P300 (the *P*3*b*) (Courchesne et al., 1975), and may reflect involuntary, transient allocation of attention to salient stimuli changes and novel stimuli (Courchesne et al., 1975; Kaipio et al., 1999). Thus, *P*3*a* latency may index a type of very basic processing speed. The neural generation of this component is probably dependent on frontally based processing (Katayama & Polich, 1998; Knight, 1984), and a relationship between the latency of the component and tests of general performance abilities has been established (Fjell & Walhovd, 2003; Walhovd & Fjell, 2001).

It should be noted that cognitive capacity necessarily depend on a number of neuroanatomical volumes, including white matter/subcortical structures, which make up a large part of the human brain (e.g. Jernigan et al., 2001). We use cortical volume instead of total brain volume, however, since much of the complexities of human cognition also strongly depend on processes in cortex, and structural and volumetric differences here thus may influence mental abilities. Further, the neuroelectrical processes measured directly at the scalp are most probably a result of cortical activation. Brain imaging studies with activation paradigms have indicated that some cortical regions are more critical than others in fluid intelligence tasks, e.g. the frontal lobes (Duncan et al., 2000; Gray, Chabris, & Braver, 2003). However, volumetric studies have shown a *g*-factor in brain volume, demonstrating that measures of the whole brain or large parts of the brain are more strongly related to general psychometric intelligence than specific areas (MacLullich et al., 2002; Wickett et al., 2000). Thus, we use measures of total cortical volume, not volume of specific cortical areas. Wickett et al. (2000) found a significant relationship between brain volume and both verbal and performance IQ. However, since our study also includes electrophysiological measures, we focus on performance (fluid) intelligence, since the relationship between *P*3*a* and performance intelligence seems stronger than the relationship between *P*3*a* and verbal intelligence (Walhovd & Fjell, 2001; Fjell & Walhovd, 2003). This is also in line with theories linking performance intelligence to speeded and efficient processing.

We expect a negative relationship between performance intelligence and speed-of-processing (latency) and a positive relationship between performance intelligence and cortical volume, as well as a negative relationship between speed-of-processing (latency) and cortical volume. If these hypotheses are confirmed, we will test whether speed and size each gives a unique contribution to the total amount of explained variance in performance intelligence. Multiple regression analyses are conducted to test these hypotheses.

Next, we will construct a path model that also includes age as a predictor variable. Specific assumptions regarding the direction of causal relationships and the distribution of variance between the variables are implemented into a path diagram. We assume that cortical volume and speed-of-processing each has a one-way causal relationship with intelligence. Further, we assume that cortical size may influence speed-of-processing, but not the other way around. We recognize that these assumptions may not represent all potential causal directions, since recent work has shown that practice can lead to cortical volumetric changes (Draganski et al., 2004), and one cannot exclude the possibility that general ability may lead to changes in speed. However, the above assumptions seem the most likely, and supplementary results will be reported to support this claim. Finally, it is obvious that age may exert causal influence on each of the three other variables, and not the other way around. This initial hypothesized model can be defined by three equations: (1) performance intelligence = b_{11} age + b_{12} cortical volume + b_{13} speed-of-processing + e_1; (2) speed-of-processing = b_{21} age + b_{22} cortical volume + e_2; (3) cortical volume = b_{31} age + e_3, where b's represent the regression coefficients and their subscripts are the equation and variable numbers. This initial model will then be modified to best describe the data.

The focus of the present paper is on the latency of the *P*3*a*, which is best observed at the electrode Cz. Still, some information about midline topography (Fz, Cz, Pz), as well as information about the *P*3*b*, is provided by correlation analyses. ANOVA with three scalp sites (Fz, Cz, Pz) × cortical volume × performance intelligence is computed both for *P*3*a* and for *P*3*b*. Only in case of significant interaction effects are further analyses of other electrodes than Cz and for other components than the *P*3*a* pursued.

2. Materials and methods

2.1. Sample

The participants were recruited by newspaper ads. All participants gave their informed consent to the study, according to the Declaration of Helsinki, and the project was approved by a Regional Committee for Research Ethics in Norway. Participants were given a moderate sum of money to refund possible costs related to their participation. All participants were right-handed community dwellers screened for diseases and traumas known to affect central nervous system (CNS) function by a set of health-related questions. Participants were examined with the Norwegian version of the Wechsler Abbreviated Scale of Intelligence (WASI, see below) (Wechsler, 1999) and neuropsychological tests. Participants were required to have an IQ score of at least 85, a Mini Mental State Examination (Folstein, Folstein, & McHugh, 1975) score of at least 26, and a Beck Depression Inventory (Beck & Steer, 1987) score of <15 in order to be included in the study. Seventy-three participants were included, of which two later were excluded because they scored below the cut-off criteria in the ERP-task (see below). Even though females generally have smaller brains than males, there was no significant

Table 1
Sample characteristics

	Mean	Standard deviation	Range
n = 71 (40 females/31 males)			
Age	52.6	20.5	20–88
Full scale IQ (WASI)	113.4	10.4	85–134
Verbal IQ	111.5	11.7	86–136
Performance IQ	112.0	11.1	86–135
Mini mental status	28.9	1.0	26–30
Beck depression inventory	4.3	3.5	0–14
Cortical volume (*n* of voxels)	461963	61255	331872–594509

correlation between gender and cortical volume in the present sample ($r = .17$, n.s., where females are coded as 1 and males as 2). Thus, separate analyses based on gender were not performed. Sample characteristics are presented in Table 1.

2.2. Intelligence testing

WASI provides a measure of verbal and performance abilities, and is composed of four subtests: vocabulary, similarities, block design, and matrix reasoning. Vocabulary is known to remain constant with increasing age and is a measure of general verbal level. The similarities subtest is moderately affected by age, and is an excellent test of general mental ability (Lezak, 1995). The vocabulary and similarities subtests are not time-limited. Block design is a performance measure, and is dramatically affected by age (Babcock & Laguna, 1996; Papalia, Camp, & Duskin, 1996; Woodruff-Pak, 1997). Matrix reasoning is a non-verbal measure of reasoning ability, and is sensitive to age. In the present study, all four subtests were used to calculate an age-adjusted IQ-score, a verbal IQ and a performance IQ. In addition, a performance score not adjusted for age was computed. To avoid confusion with the age-adjusted scores, we will refer to this as performance abilities or intelligence, not performance IQ. Matrix reasoning and block design, constituting the performance ability score, are the two subtests with the highest *g*-loading in the WAIS-R battery (Deary, 2001b).

2.3. ERP stimuli

We used a three-stimuli visual oddball task with a total of 210 stimuli, .10 target and .10 distractor probability. The paradigm is a variation of one used by Comerchero and Polich (1999), and which has been shown to elicit *P3a* (Comerchero and Polich, 1999; Polich, 2003). Demiralp, Ademoglu, Comerchero, & Polich (2001) demonstrated that such a paradigm produced virtually identical *P3a* potentials as those obtained by using novel stimuli, which traditionally have been employed. The component elicited by such a three-stimuli oddball task seems to be the same component as novelty *P3a* (Simons, Graham, Miles, & Chen, 2002). In the present task, the standard stimuli, which the participant is told not to respond to, are blue elliptic shapes with a height of 15 cm and a width of 12.5 cm. The targets, to which the participant is told to press a button, are blue elliptic shapes with height and width of 17.5 and 14.5 cm, respectively. The distractor stimuli, which the participant is told to ignore, are blue rectangles of 21 cm × 17 cm. Viewing distance was 100 cm. The small difference between targets and standards, and the large difference between targets and distractors, were chosen to maximize the *P3a* component to distractors. Presentation time was 0.5 s. ISI was 1.5 s. Cut-off criteria for task performance were set to 20% target misses, 20% responses to standards, or 25% responses to distractors, which lead to the exclusion of two participants, reducing the total sample to 71. Mean reaction time after cut-off criteria were applied was 520 ms, and mean rate of target hits was 96%.

2.4. ERP procedures

Subjects were seated in a reclining chair within a sound attenuating recording chamber. Electrodes were placed in accordance with the international 10–20-system, referred to the left mastoide, and results from the midline electrodes (Fz, Cz, Pz) will be reported here. *P3a* is generally most pronounced at Cz, and an earlier study using the same paradigm as the present has confirmed this (Fjell & Walhovd, 2004). A VEOG channel was obtained by placing one electrode above and one below the left eye. Ground was placed anteriorly. Inter-electrode impedance was generally measured to be <10 kΩ. For the recording of EEG activity, *A/D* rate was 500 Hz, filter-setting was 0.10 Hz (high pass) and 70 Hz (low pass). A 50 Hz notch filter was applied. The signals were amplified by a SynAmp dc amplifier (Neuroscan Inc.). Epochs were rejected from averaging if amplitude exceeded ± 110 μV, and eye blinks were corrected for statistically in accordance with Semlitsch, Anderer, Schuster, & Presslich (1986) recommendation. EEG was segmented in epochs of 900 ms duration (−100 to 800 ms relative to stimulus onset). Average files were digitally filtered (15 Hz low pass) and baseline corrected before statistical measures of component latency or amplitude were made. *P3a* was determined algorithmically, in accordance with Pfefferbaum, Ford, & Kraemer (1990) recommendations, and defined as the most positive point constituting a peak within 250 and 650 ms post stimulus at Cz.

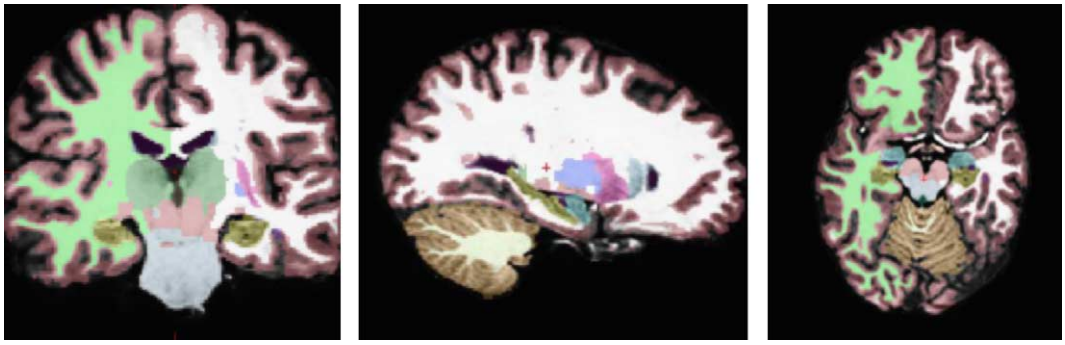

Fig. 1. A sample of automated labelling of cerebral cortex (violet areas) in coronal, saggital, and horizontal views of the brain of a young female participant.

2.5. MRI scanning

A Siemens Symphony Quantum 1.5 T MR scanner with a conventional head coil was used. The pulse sequences used for morphometric analysis were: Two 3D magnetization prepared gradient echo (MP-RAGE), T1-weighted sequences in succession (TR/TE/TI/FA = 2730 ms/4 ms/1000 ms/7°, matrix = 192 × 256, FOV = 256 mm), with a scan time of 8.5 min per volume. Each volume consisted of 128 sagittal slices with slice thickness = 1.33 mm, and in-plane pixel size of 1 mm × 1 mm. The image files in DICOM format were transferred to a Linux workstation for morphometric analysis.

2.6. MRI volumetric analyses

The automated procedures for volumetric measures of the different brain structures are described by Fischl et al. (2002). This procedure automatically assigns a neuroanatomical label to each voxel in an MRI volume based on probabilistic information automatically estimated from a manually labeled training set. Briefly, the segmentation is carried out as follows. First, an optimal linear transform is computed that maximizes the likelihood of the input image, given an atlas constructed from manually labelled images. Next, a nonlinear transform is initialized with the linear one, and the image is allowed to further deform to better match the atlas. Finally, a Bayesian segmentation procedure is carried out, and the maximum a posteriori (MAP) estimate of the labelling is computed. The segmentation uses three pieces of information to disambiguate labels: (1) the prior probability of a given tissue class occurring at a specific atlas location; (2) the likelihood of the label given that tissue class; and (3) the probability of the local spatial configuration of labels given the tissue class. This latter term represents a large number of constraints on the space of allowable segmentations, and prohibits label configurations that never occur in the training set (e.g. hippocampus is never anterior to amygdala). The technique has been previously shown to be comparable in accuracy to manual labeling (Fischl et al., 2002). In the present paper, volumes for cortical gray matter are reported. A sample is provided in Fig. 1.

3. Results

Pearson correlations between *P3a* and *P3b* latencies at Fz, Cz, and Pz, cortical volume, age, and performance and verbal abilities, are presented in Table 2. Both cortical volume and *P3a* at all electrodes were moderately correlated with performance abilities and age. For *P3b*, only Pz showed significant relationships with the other variables. Verbal intelligence was, as expected, non-correlated with all variables except performance intelligence, and was thus dropped from further analyses. ANOVA with *P3a* at three electrodes (Fz, Cz, Pz) × cortical volume × performance intelligence yielded no significant interaction effects, and further analyses were therefore restricted to Cz only. For *P3b*, a significant electrode × performance intelligence interaction

Table 2
Pearson correlation coefficients between electrophysiological indices of speed of processing, performance and verbal abilities, and cortical volume

	Age	Performance abilities	Verbal abilities	Cortical volume
P3a at Fz	**.58**	−.49	−.07	−.28
P3a at Cz	**.54**	−.51	−16	−.29
P3a at Pz	**.37**	−.33	−.11	−.24
P3b at Fz	.02	.02	.20	.05
P3b at Cz	*.27*	−.26	−.03	−.03
P3b at Pz	**.42**	−.42	−.14	−.23
Performance abilities	−.74		**.44**	**.63**
Verbal abilities	−.15			.18
Cortical volume	−.65			

Bold: $p < .01$; italic: $p < .05$.

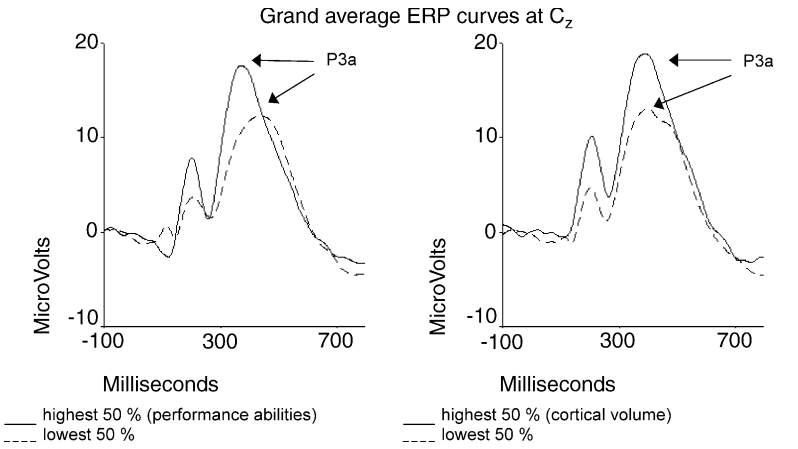

Fig. 2. Grand average ERP curves illustrating the relationship between speed-of-processing and performance abilities (left figure) on one hand, and speed-of-processing and cortical volume the other (right figure). Both high performance and large cortical volume are reflected in shorter *P3a* latency in the three-stimuli oddball paradigm, indicating faster processing of incoming information. In addition, the amplitude of *P3a* differs between high and low performers and between the participants with largest and smallest cortical volumes. Amplitude differences, however, lie outside the scope of the paper, and statistical analyses of amplitude are not reported here.

was identified ($F[1.527] = 3.974$, $p < .05$). As the correlational analyses showed, *P3b* exhibited its strongest relationship with cortical volume and performance abilities at Pz. An ANOVA with 2 types of stimuli (*P3a* at Cz, *P3b* at Pz) × cortical volume × performance intelligence yielded no significant interaction effects. Thus, further analyses were done for *P3a* at Cz only.

Grand average ERP curves for *P3a* at Cz, separated based on performance abilities and cortical volume, are presented in Fig. 2. These illustrate the difference in ERP curves for participants with different levels of performance abilities and cortical volume. Scatter plots illustrating the relationships between performance ability, cortical volume, and *P3a* latency are presented in Fig. 3.

The regression analyses showed that cortical volume (x_1) explained 40% of the variance in performance abilities ($y = 9.490 + 0.00008699x_1$, $p < .0001$), while *P3a* (x_2) latency explained 26% ($y = 81.766 - 0.0764x_2$, $p < .0001$). When *P3a* latency (y) was used as the criterion variable and cortical volume (x_1) as predictor variable, the shared variance was 9% ($y = 531.758 - 0.00025x_1$, $p < .02$). A multiple regression analysis showed that when cortical volume (x_1) and *P3a* latency (x_2) were included as predictors, both measures gave unique contributions ($p < .0001$) to the total amount of explained variance in performance abilities, which reached 51% ($y = 40.198 + 0.00007149x_1 - 0.0560x_2$, $p < .0001$). Adding the square of the independent variable in each regression analysis tested the possibility of significant non-linear relationships between cortical volume, speed-of-processing, and performance intelligence, but none were identified.

Next, we constructed a path model involving cortical volume, speed-of-processing, performance intelligence, and age, to test how the variance is distributed between the variables. When age was included, the relationship between cortical volume and *P3a* latency no longer was significant, and so this path was dropped from the model. The resulting path diagram is depicted in Fig. 4, and

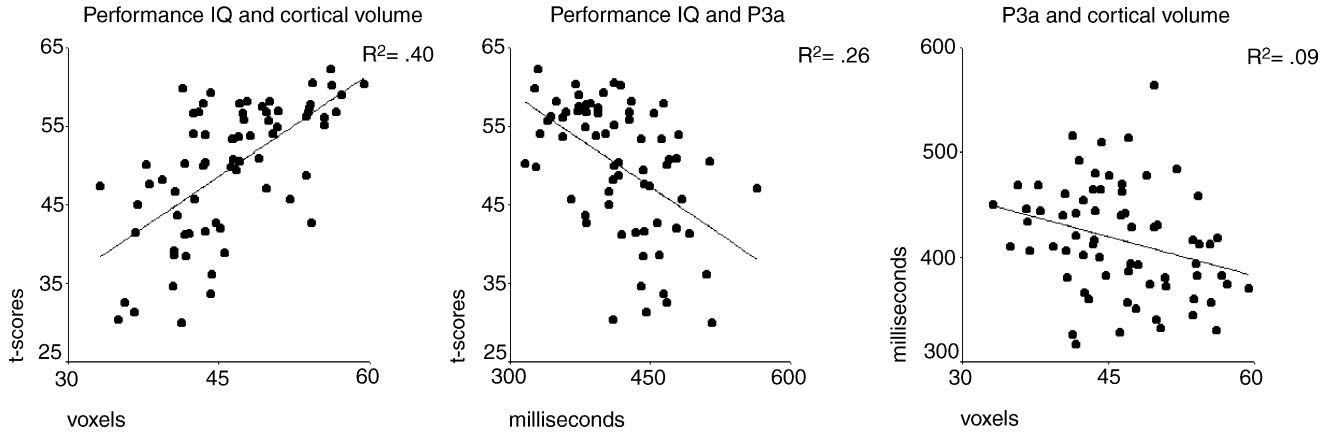

Fig. 3. Scatterplots illustrating the relationship between cortical volume (in 10,000 voxels), *P3a* amplitude at Pz in the three-stimuli oddball paradigm, and performance abilities (mean *t*-scores of the two WASI performance subtests). $P < .05$ for all R^2.

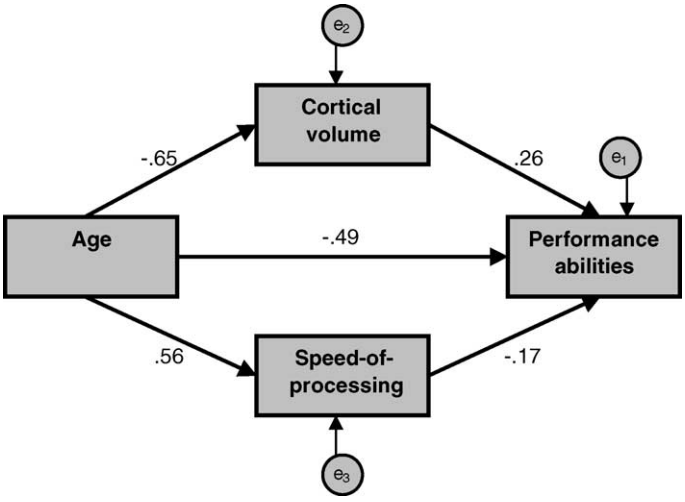

Fig. 4. Path diagram depicting a model for the distribution of variance specified by the following three path equations: (1) performance intelligence = b_{11} age + b_{12} cortical volume + b_{13} speed-of-processing + e_1; (2) cortical volume = b_{21} age + e_2; (3) speed-of-processing = b_{31} age + e_3. The path coefficients are the standardized partial regression coefficients of each endogenous variable on its priors. All paths in this model are significant (c.r. > 2.000, $p < .05$).

illustrates the hypothesized causal connections between the variables. The final model, in which all paths were statistically significant (critical ratio > 2.000, $p < .05$), was specified by three path equations: (1) performance intelligence = b_{11} age + b_{12} cortical volume + b_{13} speed-of-processing + e_1; (2) cortical volume = b_{21} age + e_2; (3) speed-of-processing = b_{31} age + e_3. The path coefficients, which are the betas from the specified equations, are the standardized partial regression coefficients of each endogenous variable on its priors. Thus, since the model has more than one causal variable, the path coefficients are partial regression coefficients that measure the extent of effect of one variable on another in the path model controlling for other prior variables. The model demonstrates that cortical volume and speed-of-processing uniquely influence performance intelligence, even when the variance from age is accounted for.[1]

Using the method of effect decomposition, the total causal effect of age on performance intelligence can be calculated by multiplying the individual coefficients in each path and then summing these products. Age has a direct effect of performance intelligence of −.49, a total indirect effect of −.27 (age → volume → performance intelligence [−.65 × .26 = −.17] + age → speed → performance intelligence [.56 × −.17 = −.10]), and thus a total causal effect of −.76 (−.49 + −.27). Since the path from cortical volume to speed-of-processing no longer was significant when age was included in the model, cortical volume, and of course speed-of-processing, only exerted direct effects on performance intelligence.

4. Discussion

The present data support relationships between cortical volume and both performance intelligence and speed-of-processing. While relationships between brain size and cognitive abilities have also been found previously, some of the former findings diverge from the present study. Wickett et al. (2000) found that both verbal and performance intelligence were positively related to brain volume, but when they extracted a *g*-factor, a fluid, a crystallized, a spatial, and a memory factor from their large battery of ability tests, only the *g*, fluid, and memory factors showed significant correlations with brain volume. Their crystallized, largely verbal, factor did correlate positively, though not significantly, with brain volume, but their spatial, largely performance, factor correlated negatively with brain volume. They also reported vector correlations showing that the more spatially (performance)-loaded an ability test was, the smaller was its correlation with brain volume. In the present study, no attempt was made to relate memory and verbal abilities to cortical volume, and consequently, the tests were not factorised. We, thus, do not know whether such measures might be even more related to cortical volume than performance ability was in our sample. Differences between studies may also partially be caused by the neuroanatomical measures used. Wickett et al. employed a more global measure of total brain volume, while we selectively measured cortical volume. Thus, our results indicate that a significant relationship does exist between performance abilities and a specific measure of cortical volume.

The present findings also expand previous knowledge, in showing that there was no relationship between cortical volume and speed-of-processing independently of age. Still, when the variance from age was not partialed out, speed-of-processing and cortical volume shared 9% variance. It was most interesting, however, that their combined power in predicting performance intelligence by far exceeded this, and that both measures thus gave statistically significant unique contributions. Actually, both had more variance shared with performance intelligence than with each other. Thus, the beneficial effects of a large cortex and high mental speed on performance intelligence are mainly independent of each other.

The path model including age further added weight to the conclusion that speed and cortical volume are independent contributors to performance intelligence. When age was accounted for, no significant relationship existed between the two measures, while they both still significantly predicted performance intelligence. Thus, from the present data it seems to be the case that speed-of-processing and cortical

[1] Since it is theoretically possible to argue that speed can change as a result of performance abilities, as mentioned above, a regression analysis predicting speed (y) from performance scores (x_1) was performed. 26% of the variance in speed was explained by performance abilities ($y = 574.554 - 3.167994865035x_1$, $p < .0001$). When age (x_2) was included as an additional regressor, the amount of explained variance increased to 32%, but performance abilities no longer gave a unique contribution (n.s.) ($y = 438.813 - 1.444661007115x_1 + 0.9504240306x_2$, $p < .0001$).

volume are beneficial for performance intelligence for different reasons.

The present results raise two questions. First, why is speed-of-processing not more dependent upon cortical volume, when neuroanatomical volume is shown to increase cognitive capacity and thereby should enhance cognitive efficiency and information processing speed? Second, what is it about speed and cortical volume that makes them both important for psychometric intelligence, without at the same time introducing more shared variance between the two? Present knowledge is insufficient to provide answers to these questions. In response to the first question, one can, however, speculate that individual differences in phenotypic speed-of-processing is a result of, e.g. individual cognitive strategies, and that this is independent of cortical size. ERP differences between persons of different intellectual abilities may thus reflect cognitive strategy differences. However, since a substantial genetic component seems to be involved in the correlations between intelligence and both measures (Neubauer et al., 2000; Posthuma et al., 2002), this explanation is probably not the full answer. Another possibility is that inhibition and cognitive control/executive processes are related to performance intelligence and possibly cortical volume (Schretlen et al., 2000), but have adverse effects on processing speed. This may also explain the results from comparative studies showing that some non-human primates have superior performance in inspection and reaction time tasks. As the present results indicate, it is likely that the biological basis for the beneficial effect of speed is fundamentally different from the biological basis for the beneficial effects of cortical volume. If more neurons and more synapses are the main causes of variations in cortical volume, then the possibility certainly exists that mental speed depends on other neurological and neurophysiological characteristics, e.g. fiber density and myelination.

As to the second question, more research is needed before we can understand what it is about speed and volume that makes them both important for psychometric intelligence. A challenge for future research will be to disentangle the influence of speed and volume on different aspects of human mental abilities. The importance of speed is comprehensible on a conceptual and psychological level, because the performance of speeded and time-limited tasks by definition should benefit from fast processing of information. In the present study, cortical volume was, however, a more powerful predictor of performance intelligence than speed. Unfortunately, we still know too little about the exact neural mechanisms that cause larger cortical volume to indicate higher intelligence. As mentioned, several neural parameters are suggested. It is possible that larger cortical volume partly is a result of more complex neural circuitry, which may be beneficial for intelligence, but reduce speed-of-processing. Thus, cognitive complexity and information processing speed may both contribute to higher intelligence, but have independent neural causes. However, if this explanation was true, we would likely be able to separate the psychometric *g*-factor into two underlying factors, dependent on either cognitive complexity (and cortical/brain volume) or speed-of-processing (ERP latencies). No strong evidence supports this claim. Thus, we have to continue to search for an explanation for the relationship between neuroanatomical volume, speed and intelligence. The present study shows that the reason for this relationship is not that bigger means faster.

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