



Small to medium magnitude Jensen effects on brain volume: A meta-analytic test of the processing volume theory of general intelligence

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ABSTRACT

The processing volume theory of general intelligence predicts that brain volume imposes general constraints on the overall amounts of cortical substrate available for solving complex problems. Bigger brains contain more processing volume, hence can solve problems generally more efficiently than smaller brains. This theory predicts that the g loading of ability tests should substantially moderate the association between ability test performance and brain volume. This is tested with a bare-bones meta-analysis employing the method of correlated vectors (MCV) on the association between brain volume * subtest correlations and subtest g loadings. The mean weighted vector correlation across four studies is $\rho = 0.07$ (total $N = 246$), increasing to $\rho = 0.35$ when one potentially outlying study is removed. The magnitude of these Jensen effects suggests that g plays at best only a modest role in moderating the strength of the brain volume * IQ correlation, contrary to predictions from the processing volume theory. This result is consistent with the observation that brain volume has low evolutionary lability compared with g , suggesting that recent evolutionary changes in population levels of g may have occurred largely independently of overall changes in brain volume.

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1. Introduction

1.1. The processing volume theory of general intelligence

The association between brain volume and cognitive ability has a long and controversial research history (Darwin, 1871; Galton, 1888; Morton, 1849). In the 1970s and 80s attempts were made by 'radical scientists' (Pinker, 2002, p. 225), most notably Stephen Jay Gould, to discredit any link between brain dimensions and IQ (Gould, 1981, cf. Jensen, 1982; Rushton, 1996). However, the dust finally settled when meta-analytic studies placed the individual differences-level correlation between brain volume and IQ between $\rho = 0.24$ (Pietschnig, Penke, Wicherts, Zeiler, & Voracek, 2015) and 0.33 (McDaniel, 2005).

Brain volume has been invoked as a major cause of the positive manifold among diverse cognitive abilities (the g factor). Advocates of what could be termed the *processing volume theory* (e.g. Deaner, Isler, Burkart, & van Schaik, 2007; Jensen, 1998; Jerison, 1973; Rushton & Ankney, 1996, 2007, 2009) have argued that overall brain volume imposes

general limits on the amount of cortical substrate that can be used in solving cognitive problems. Smaller brains have generally less cortical substrate therefore people with smaller brains do generally poorly on various cognitive ability tests. The opposite is true for people with big brains, who have more cortical substrate overall, and can do correspondingly better on various tests. Brain volume in this model therefore functions to restrict overall performance on different ability measures, bringing them into correlation, in addition to giving rise to individual differences in overall performance.

The most prominent advocate of the processing volume theory was J. Philippe Rushton, who argued that brain volume was a major source of both individual and ethnic group differences in g (Rushton, 1985, 2000, 2004, 2010; Rushton & Ankney, 1996, 2007, 2009). Rushton's model was founded on *life history theory*, or the idea that organisms possess different budgets of bioenergetic resources based on different fitness challenges encountered in different environments. Organisms living in unstable environments must be able to rapidly replace lost offspring, hence they focus on *mating effort* at the expense of longevity and health (*somatic effort*) and offspring care (*parental effort*). Organisms living in stable environments on the other hand de-emphasize mating effort, as offspring mortality is lower, and invest resources instead into somatic

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and parental effort, which results in the production of fewer, longer-lived and better-cared-for offspring. Rushton's model (termed *Differential-K*) extended the logic of life history theory to the evolution of human psychological individual and group differences (Rushton, 1985, 2000). Rushton argued that differences in personality, behavior and intelligence all result from differences in life history strategy. *Fast* life history individuals and groups (i.e. those that tend towards high mating effort) exhibit more impulsive and individualistic personalities in addition to lower levels of *g*. *Slow* life history individuals and groups (i.e. those that tend towards high somatic and parental effort) are the opposite, being more behaviorally constrained and group oriented in addition to exhibiting higher *g*.

Brain volume is a key life history variable in Rushton's *Differential-K* model, as bigger brains result from greater investments of somatic effort. Therefore, based on this model, brain volume mediates the relationship between life history strategy and *g* (Rushton, 2000, 2010).

1.2. Challenges to the theory

There are two major challenges to the processing volume theory of *g*.

Firstly, it has been found that brain volume exhibits *relatively low* evolutionary lability, compared with potentially fitness-indicating traits such as *g* (Fernandes & Woodley of Menie, 2014; Miller & Penke, 2007). This means that brain volume has evolved relatively slowly compared with *g*. This is important as it means that *contra* the processing volume theory, brain volume may not be a reliable proxy for *g* in evolutionary models. Consistent with this inference, it has recently been found that polygenic scores comprised of genetic variants that predict individual differences in educational attainment, while predictive of *g* variance, do not predict individual differences in intra-cranial volume. The latter does however make an independent contribution to *g* (Deary, Cox & Ritchie, 2016). This suggests the presence of polygenic modularity - i.e. uncorrelated sets of genes that code for different endophenotypes co-contributing to a common trait, which could have resulted from selection operating at different rates on the two endophenotypes.

Secondly, at the individual-differences level in humans, the ratio of cortical gray matter volume (i.e. unmyelinated neuronal cell-bodies) to whole brain volume decreases as brain volume increases (Im et al., 2008). Comparative analyses show that cortical neuronal density and cortical gray matter density decline with increasing brain volume (Barton, 2006; a finding that applies to the frontal lobes also; Semendeferi, Teffer, Buxhoeveden, et al., 2011). This indicates that the expansion of white matter (i.e. long-range myelinated axon tracts) rather than gray matter is favored in larger brains to maintain conduction velocity (Barton, 2006; Herculano-Houzel, Mota, Wong, & Kaas, 2010; Wen & Chklovskii, 2005), suggesting that increases in processing power are not the main outcome of increases in brain size.

Decreased between-region connectivity in larger brains occurs despite an increased total number of axons in the white matter, and is accompanied by increased connectivity between close neurons (Semendeferi et al., 2011). This means that the key assumption made by the processing volume theory, i.e. that larger brains are simply scaled-up versions of smaller brains appears to be incorrect, as the assumption of constant cortical connectivity across brains of different volumes simply does not hold. As *g* is influenced by cortical connectivity (Penke, Muñoz Maniega, Bastin, et al., 2012), this suggests some independence from brain volume.

1.3. A new test of the processing volume theory of *g*

A key prediction of the processing volume theory is that *g* substantially moderates the relationship between IQ and brain volume. This can be tested using the method of correlated vectors (MCV) to establish the degree to which the magnitude of the correlation between brain volume and subtest scores is moderated by the *g* saturation of those subtests. This is achieved by simply correlating the vector of brain

volume * subtest correlations with the vector of *g* loadings. The processing volume theory would predict a strong correlation between the two vectors (i.e. a *d* * *g* correlation close to + 1), which would indicate a strong role for *g* in moderating the IQ * brain volume correlation.

As a rule, biological variables (such as subtest heritabilities, inbreeding depression effects, reaction times, ethnic group differences and inter-species differences in intelligence) associate more strongly with subtests exhibiting high *g* loadings, yielding positive vector correlations (Fernandes, Woodley, & te Nijenhuis, 2014; Rushton & Jensen, 2010; te Nijenhuis, David, Metzen, & Armstrong, 2014a; te Nijenhuis, Kura, & Hur, 2014c; te Nijenhuis & van den Hoek, 2016). Cultural-environmental variables on the other hand (such as retesting effects, the Flynn effect, educational and adoption gains in IQ) associate weakly with more *g*-loaded subtests, yielding negative vector correlations (te Nijenhuis, Jongeneel-Grimen, & Armstrong, 2015; te Nijenhuis, Jongeneel-Grimen, & Kirkegaard, 2014b; te Nijenhuis & van der Flier, 2013; te Nijenhuis, van Vianen, & van der Flier, 2007). This gives rise to a dichotomy with the pattern of moderation among the relationships between biological variables and subtest *g* loadings being positive and the pattern of moderation involving cultural-environmental variables being negative, with the former being termed *Jensen effects* (Rushton, 1998) and the latter being sometimes termed *anti-Jensen effects*.

Even though the processing volume theory predicts a strong Jensen effect on brain volume, given the various theoretical objections to the theory, we might in fact expect a much weaker Jensen effect in MCV (with an effect size closer to 0). This would indicate that brain volume, while correlated with IQ, might not be strongly correlated with this at the level of *g*, but instead may also substantially correlate through more specialized abilities. One possibly significant ability is visuospatial ability, which is significantly related to sex-differences in brain volume, even when the sex-difference in *g* is controlled (Burgaleta et al., 2012). Another reason why specialized abilities might be good candidate moderators of the IQ * brain volume correlation, is because, like brain volume, they too are less evolutionarily labile than *g* (Fernandes et al., 2014) and are therefore more likely to have co-evolved with overall brain volume.

Rushton and Ankney (2009) attempted to summarize the results of applying MCV to the association between IQ and various neuroanatomical correlates (such as brain volume, head circumference and gray matter clusters). They argued that the relationship is characterized by a large-magnitude Jensen effect ($\rho = 0.63, K = 6$), consistent with predictions from the processing volume theory. This aggregate estimate combined various neuroanatomical measures, and did not focus on brain volume alone. Also, their estimate was not derived on the basis of meta-analytic procedure. There are artifacts, such as sampling error and outliers that introduce error into estimates derived using MCV (Ashton & Lee, 2005), which can be explicitly controlled in meta-analyses involving MCV, allowing the reliability of this statistic to be considerably strengthened (Woodley, te Nijenhuis, Must, & Must, 2014).

In the present study, we will therefore attempt to estimate the Jensen effect on brain volume via meta-analytic treatment of all studies of the brain volume * IQ association suitable for analysis via MCV.

2. Method

2.1. General inclusion rules

For studies of the IQ * brain volume association to be included in this meta-analysis, two criteria had to be met: first, in order to obtain a reliable estimate of the true correlation between each of the variables and subtest *g* loadings, the cognitive batteries had to be based on a minimum of seven subtests. When the vector correlation is expected to be close to perfect (i.e. - 1 or + 1), as few as four subtests might be suitable for establishing the presence of an effect (Woodley et al., 2014). As we are explicitly predicting a non-perfect vector correlation (closer to 0),

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