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It's getting bigger all the time: Estimating the Flynn effect from secular brain mass increases in Britain and Germany

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ABSTRACT

Secular increases in brain mass over nearly a century have been noted for both males and females in the UK and Germany. It has been argued that such trends may be associated with the Flynn effect. The IQ gain predicted on the basis of these trends is 0.19 and 0.08 points per decade for UK, and 0.2 and 0.15 points per decade for German males and females respectively, indicating a small contribution to the Fullscale IQ trends in these countries (2.95% of the German decadal gain and 12.73% of the UK gain). There is also a sex difference in the rates of brain mass gain in both countries, favoring males. Temporal correlations between the secular trend in UK brain mass and European Flynn effects on Fullscale IQ, Crystallized, Fluid and Spatial abilities reveal correlations ranging from 0.751 in the case of Fluid ability to 0.761 in the case of Crystallized ability. The brain mass increase may be an imperfect proxy for changes in specific neuroanatomical structures important for IQ gains. Its small contribution to these gains is also consistent with the influence of other contributing factors. Increasing brain mass is predicted by the life history model of the Flynn effect as it suggests increased somatic effort allocation into bioenergetically expensive cortical real estate facilitating the development of specialized cognitive abilities.

1. Introduction

Brain dimensions have long been considered an important determinant of mental ability (e.g. Darwin, 1871; Galton, 1888). Subsequent research has corroborated the association between brain volume and mass and IQ (McDaniel, 2005; Pietschnig, Penke, Wicherts, Zeller, & Voracek, 2015; Rushton & Ankney, 2009). Studies have found evidence for secular increases in cranial vault dimensions within Western populations during the 20th century (e.g. Ounsted, Moar, & Scott, 1985). Other studies have also found indications of increasing brain mass among autopsy samples (Haug, 1984; Kretschmann, Schleicher, Wingert, Zilles & Löblich, 1979; Miller & Corsellis, 1977) covering a similar time period.

Based on the assumption that increasing brain mass should be associated with increased IQ, Lynn (1989) and others (e.g. Mingroni, 2004; Storfer, 1999) have argued that the secular increase in brain mass may be an important corollary of the Flynn effect — the increase in Fullscale IQ of three points per decade, since the beginning of the 20th century (Flynn, 2009a, 2012; Pietschnig & Voracek, 2015; Trahan, Stuebing, Hiscock, & Fletcher, 2014).

In the present paper, the IQ increase resulting from the secular trend in brain mass will be determined formally for the first time via secondary analysis of two cross-sectional datasets. Such trends constitute a potentially significant source of convergent validity for the Flynn effect, as they concern changes in an actual biological endophenotype of IQ, rather than performance on pencil-and-paper tests. An attempt will also be made to determine whether there exist sex-differences in the rates of brain mass increase, and also whether secular trends in brain mass exhibit affinity for Flynn effects on specific ability measures via temporal correlation. Finally, a detailed theoretical unpacking of these results in the context of various models of the Flynn effect that predict associations with increasing brain mass will be presented in the discussion.

2. Method

2.1. Datasets

Two cross-sectional datasets presenting evidence of secular trends in brain mass in two countries (the UK and Germany) will be considered in the present study.

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2.1.1. British data

Miller and Corsellis (1977) reported increases in brain mass, utilizing autopsy materials sourced from the London Hospital Pathological Institute amounting to 52 g (from 1372 g to 1424 g) over 80 years (between birth years 1860 and 1940) among their male sample ($N = 4319$), and 23 g (from 1242 g to 1265 g) over the same period for their female sample ($N = 3878$). Miller and Corsellis admitted into their comparison groups all individuals aged between 20 and 50 years at time of death for whom the brains were not considered pathological (approximately 36% of the brains were excluded on this basis). To determine the secular mass change they simply regressed the mean brain mass of those aged between 20 and 50 at time of death against birth year.

The running five-year means for both males and females employed by Miller and Corsellis in their analysis were extracted from their figure. 1 (p. 254) and are reproduced graphically here in Fig. 1.

2.1.2. German studies

Haug (1984) presents the results of 12 studies reporting aggregate brain masses for both males and females (tables 6 and 7, p. 493) collected via autopsy from various pathological and forensic institutes and broken out by age. The studies span the period from 1861 to 1978. Six of the studies involve German-sourced samples. A smaller seventh study (Kretschmann, et al., 1979), not considered by Haug, also reports brain mass means for German subjects.

The trend in brain mass across the seven German studies spanning the study years 1880 to 1979 will here be analyzed in order to determine the presence of secular trends within this country. A weighted average of brain masses collected from those with ages ranging from 30 to 49 and 50 to 59 is utilized as the basis for cross-sectional comparison,[1] via regression against study year.

The secular trend in height is not controlled in the present analysis, as gains in height and brain mass share variance stemming from a more general secular increase in body mass, which indicates substantial collinearity. Consistent with this Haug (1984, p.492) found a correlation between the two of > 0.8.

The analysis of the German brain mass means will be conducted using fixed-effects meta-regression (implemented utilizing software available at http://statstodo.com) with weighting by standard error of the mean, that is $SEM = s / \sqrt{N}$, where $s =$ standard deviation and $N =$ sample size.

For the meta-regression, standard deviation values for brain mass are required in order to calculate SEM values. In the absence of sample specific parameters, Hunter and Schmidt (2004, pp. 47–49) recommend importing higher quality parameters derived from benchmark studies, thus synthetically correcting for error stemming from range restriction. The study of Ho, Roessmann, Straumfjord, and Monroe (1980) provides data on US brain mass and associated values, representatively sampled from across 1261 cases that had all been processed using precisely the same protocols. It can be reasonably assumed given the time periods involved that the autopsy data collected in the London Pathological Institute and the seven German studies primarily concerned European whites, therefore only the white male and female standard deviation values from Ho et al. (1980) will be utilized. For a sample of 416 white males of an average age of 60, a standard deviation value of 130 g is reported. For a sample of 395 white females of an average age of 59, a standard deviation value of 125 g is reported (p. 636).

The weighted mean brain mass values for all seven studies, along with sample size and location data are presented in Table 1.

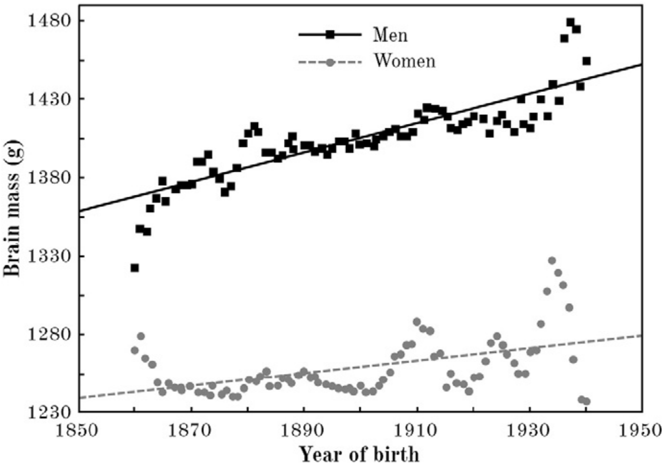

Fig. 1. Secular trend in brain mass across a sample of 4319 British males and 3878 females born between 1860 and 1940 and aged between 20 and 50 years at time of death.

2.2. Estimating secular gains in IQ from increasing brain mass

Jensen (1998, p.326) proposed a method for estimating Fullscale IQ gains stemming from secular increases in brain volume/mass. The method involves converting the gains into a change in standard deviation units by dividing the gains in grams by the reference standard deviations of brain mass for males and females. Based on the assumption that increasing brain mass is boosting IQ this d value must be multiplied by the correlation between brain mass and IQ. The resultant d value can then be multiplied by 15 (the "standard" standard deviation of IQ) yielding IQ points gained throughout the birth and study years covered by Miller and Corsellis (1977) and the German studies respectively.

2.2.1. Correlation between brain volume/mass and IQ

A recent comprehensive meta-analysis has established that the population correlation between brain volume and IQ is significantly positive at $\rho = 0.24$ (Pietschnig et al. 2015). This value is somewhat smaller than the value presented in a previous meta-analysis (i.e. McDaniel, 2005; $\rho = 0.33$), however Pietschnig et al. sampled more representatively than did McDaniel. Multiplying the increase in brain mass (in standard deviation units) by this estimate will yield the standardized IQ gain (as per Jensen, 1998).

Rushton and Ankney (2009) noted that brain volume is an extremely strong proxy for brain mass, and that, while rarely ever investigated, similar correlations with IQ are obtained when mass is directly estimated instead of volume. Thus the IQ–brain volume correlation can be considered synonymous with the IQ–brain mass correlation.

Pietschnig et al. (2015) noted no significant sex-differences in the strength of the IQ–brain volume correlation; therefore the value of 0.24 will be used in computing IQ gains for both sets of male and female data.

2.3. Testing for dimorphism in the rates of brain mass increase

A general linear model (implemented in SPSS v.21) will be utilized in order to test for the presence of a sex $*$ year interaction and also main effects of sex and year over brain mass using both the running five-year-mean UK data (obtained from Miller & Corsellis, 1977) and the aggregate-level German data. The models (Type I and III Sum of Squares respectively) will be run sequentially with sex (dummy coded: $0 =$ female, $1 =$ male) and year entered first, followed by the sex $*$ year interaction. In order to obtain the correct degrees of freedom for the German data, each study mean-year pairing is replicated in proportion to its sample size prior to analysis, thus simulating the results of analyzing the original pooled data.

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[1] The 15-29, 60-69 and >70 age categories were not used, as age-related brain mass increases will still be occurring among the earlier cohort (Dekaban & Sadowski, 1978; Ho, Roessmann, Straumfjord & Munroe, 1980), and age-related decreases are occurring among the older cohorts (Haug, 1984). Only the age-ranges at which 'peak' brain mass is obtained are compared, thus approximately matching the methodology and age-range (20-50 years) employed in Miller & Corsellis' (1977) UK analysis.

Table 1
Weighted mean brain mass (combining values estimated for those aged between 30–49 and 50–59 years) for both males and females along with study from which the samples were drawn, sample size and autopsy material location data.

Study (year)	Weighted mean brain mass (30–59 years, in grams; males)	*N*	Weighted mean brain mass (30–59 years, in grams; females)	*N*	Location
von Bischoff (1880)	1367.57	374	1227.37	179	Bavaria
Marchand (1902)	1399.81	238	1262.03	161	Hessian, Marburg
Handmann (1906)	1360.36	320	1240.41	185	Saxony, Leipzig
Böning (1925)	1272.39	231	1167.64	176	Thuringia, Jena
Rössle and Roulet (1932)	1365.59	551	1254	235	Thuringia, Jena
Röthig and Schaarschmidt (1977)	1429.58	835	1279.18	485	Saxony, Stollberg
Kretschmann et al. (1979)	1439	21	1246	17	Lower Saxony, Hanover

2.4. Temporal correlations

Lynn's (1989) prediction is that the increase in brain mass should be more strongly associated with improvements in Spatial ability as both are believed to be sensitive to improvements in nutrition. This can be tested via temporal correlation between the secular increase in brain mass and the Flynn effect on psychometric IQ tests. For this analysis the running five-year mean data, averaged across sex from Miller and Corsellis (1977) will be utilized, as the UK brain mass data are available at a more fine-grained temporal scale than the German data. Data on yearly psychometric IQ-score gains are available for various geographic regions and for various ability measures (Fullscale, Crystallized, Fluid, Spatial) from the meta-analysis of Pietschnig and Voracek (2015). Data from Europe were chosen in order to match the region to the country from which the brain mass data originate (UK). These data span the period 1911 to 2009. The brain mass data are available for consecutive birth years, therefore the mean age of the participants at death (35) will be added to each birth year in order to approximately align these data chronologically with the psychometric trend data (collected mostly from adolescent and young adult samples, mean age = 17.5 years). The combined psychometric and brain mass temporal trend data covered the years 1911 to 1975. Missingness was present among the fluid ability trend between the years 1911 and 1933, and among the Spatial ability trend between the years 1937 and 1956. This was handled using multi-variate multiple imputation (Figueredo, McKnight, McKnight, & Sidani, 2000) in SPSS (v.21). Bi-variate correlations were computed between the brain mass temporal trend and the trends for each of the psychometric ability measures.

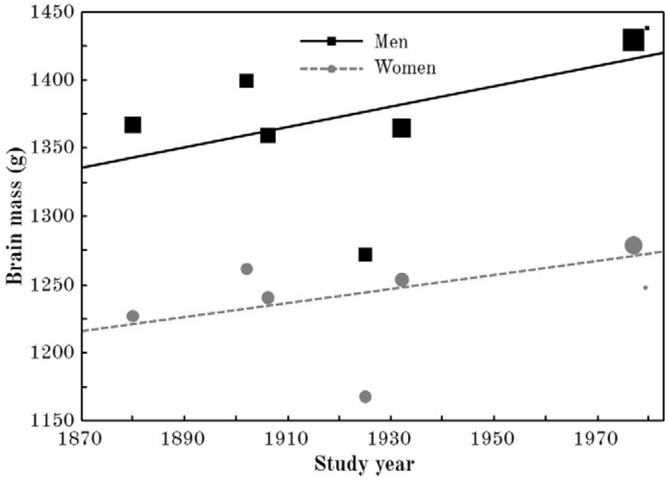

Fig. 2. Secular trends in increasing brain mass across seven male and female German cohorts (aged between 30 and 59) published between the years 1880 and 1979. Male $N = 2570$, female $N = 1438$. Circle and square sizes are proportional to the weights given to each sample in the meta-regression.

3. Results

3.1. Analyzing the German data

Fig. 2 presents the scatter plot resulting from the meta-regression of brain mass over study year for the German male and female cohorts, weighting each study by SEM.

The unstandardized regression coefficient (b) value for the males is 0.739, which is statistically significant ($p < 0.05$, 95% CI $= 0.596$ to 0.882). This indicates that male brains in Germany have been increasing in mass between the years 1880 and 1979. Based on the regression formula ($-46.6923 + 0.739 * \text{year}$) the mean male brain mass attained by the 1880 study year cohort was 1342.63 g. In 1979 the mean mass was 1415.79 g, a difference of 73.16 g.

The b value for the females is 0.528, which is statistically significant ($p < 0.05$, 95% CI $= 0.345$ to 0.712). This indicates that, as with the male brains, female brains in Germany have been increasing in mass between 1880 and 1979. Based on the regression formula ($225.9527 + 0.528 * \text{year}$) the mean female brain mass in the 1880 study year was 1218.59 g. In 1979 the mean mass was 1270.86 g, a difference of 52.27 g.

3.2. Estimating IQ gains

Table 2 presents the steps used in deriving the IQ gains from the increase in brain mass reported in Miller and Corsellis (1977) and obtained via cross-sectional analysis of the seven German studies. In each case the differences in brain mass are divided by the reference brain mass standard deviation values estimated in Ho et al. (1980; i.e. 130 g for males and 125 g for females). This yields a d value (the increase rescaled in standard deviation units). Multiplying d by the meta-analytic IQ–brain volume correlation (0.24) rescales the increase in terms of the change in IQ in standard deviation units. Multiplying this by 15 yields the increase in IQ, and dividing this by the number of decades (eight in the case of the UK study and 9.9 in the case of the German studies) yields the decadal gain.

3.3. Testing for sexual dimorphism

Based on the results of the GLM, sex and year of birth were both significant predictors of UK brain mass ($df = 1$, $F = 3634.038$, $p < 0.05$, and $df = 1$, $F = 213.584$, $p < 0.05$ respectively), as was the interaction between sex and year ($df = 1$, $F = 59.882$, $p < 0.05$). This finding was replicated in the analysis of German brain masses (sex: $df = 1$, $F = 19.401$, $p < 0.05$; study year: $df = 1$, $F = 1567.578$, $p < 0.05$; sex $*$ year: $df = 1$, $F = 43.249$, $p < 0.05$).

3.4. Temporal correlations

Table 3 presents the results of temporal correlations between the secular trend in UK brain mass and trends with respect to European performance on psychometric ability measures (Fullscale IQ, Crystallized, Fluid and Spatial abilities) over 64 years.

Table 2
Steps used in the estimation of IQ gains on the basis of secular increases in brain mass in the UK and Germany.

Study	Birth/study years	Δ brain mass	Δ brain mass/SD (d)	$d * r$	IQ gain (points)	IQ gain (points per decade)
UK males	1860–1940	52 g	0.4	0.1	1.5	0.19
UK females	"	23 g	0.18	0.04	0.6	0.08
German males	1880–1979	73.16 g	0.56	0.13	1.95	0.2
German females	"	52.27 g	0.42	0.1	1.5	0.15

4. Discussion

4.1. Summary

Brain mass has been increasing for both males and females in the UK between birth-years 1860 to 1940 and also in Germany between the years 1880 to 1979. Based on the application of Jensen's (1998) formula, the direct contribution of increasing brain mass to increasing IQ in the UK is 0.19 of a point per decade for males and 0.08 of a point per decade for females. In Germany it contributes 0.2 of a point per decade to male IQ and 0.15 of a point per decade to females. Male brain masses are consistently and significantly larger than female brain masses across time for both the UK and German samples. Furthermore males appear to have gained brain mass to a significantly greater degree than females over time, which suggests that there may have existed inequalities in terms of exposure to brain mass enhancing environmental factors that have historically favored males. Alternatively, that females have gained on males on the Raven's Matrix test over the last century (Flynn, 2012), hints at a possible sex difference in terms of how environmental and cultural changes may be assimilated into neuroanatomical and cognitive change.

Temporal correlations between the secular trend in UK brain mass and European Flynn effects on Fullscale IQ, Crystallized, Fluid and Spatial abilities indicate that while the brain mass increase is positively and significantly correlated with each Flynn effect (r's range from 0.751 in the case of Fluid ability to 0.761 in the case of Crystallized ability), Fisher's r-to-z transformation reveals that none of the correlations are significantly different from one another, indicating that the secular trend in brain mass is equally associated with the Flynn effects across psychometric indicators. This is contrary to the prediction of Lynn (1989), who suggested that it should more strongly associate with secular gains in Spatial ability owing to the joint effects of improvements in nutrition on both. The direct contribution of brain mass to the Flynn effect in these two countries is small compared to the rate of Fullscale IQ gains experienced in overlapping decades. In Germany, Fullscale IQ increased by 6.1 points per decade between 1956 and 2008 (Pietschnig & Voracek, 2015). The average IQ-gain due to brain mass increases in Germany (0.18 points per decade) is 2.95% of this. In the UK, Fullscale IQ increased by 1.1 points per decade between 1932 and 2008 (Pietschnig & Voracek, 2015). The average gain due to brain mass increases in the UK (0.14 points per decade) is 12.73% of this.

One possible explanation for the apparently small contribution of brain mass to the Flynn effect is that the overall mass increase is an indirect proxy for changes in specific neuroanatomical structures that are more directly associated with the Flynn effect. Consistent with this, Baxendale and Smith (2012) found that right hippocampal pathology inhibits the Flynn effect in clinical samples, which suggests that secular increases in right hippocampal formation gray matter mass may be a more direct neuroanatomical determinant of the Flynn effect than the overall increase in brain mass.

Table 3
Temporal correlations between the secular increase in UK brain mass and the European Flynn effects on Fullscale IQ, Crystallized, Fluid and Spatial ability ($N = 65$ years).

Psychometric measure	r (brain mass)
Fullscale IQ	0.758*
Crystallized ability	0.761*
Fluid ability	0.751*
Spatial ability	0.758*

* $P < .05$.

Despite its apparently small contribution to the overall IQ gain, the brain mass increase is nonetheless germane to the issue of the convergent validity of the Flynn effect as brain mass is a biologically objective correlate of cognitive ability. There are several factors that can inflate scores on pencil-and-paper IQ tests such as changes in the ecological validity of test items (Flynn, 2009a) and the increased use of guessing as an answer strategy (Brand, 1990). Increased guessing in particular may account for as much as a third of the observed Flynn effect on some batteries (Woodley, te Nijenhuis, Must & Must, 2014a). These factors cannot affect "performance" on measures such as brain mass. Brain mass furthermore adds to the list of ratio-scale indicators (i.e. measures with a true 0) that appear to be sensitive to the Flynn effect (another ratio-scale indicator that appears to be sensitive to secular gains is Forwards Digit Span; Woodley of Menie & Fernandes, 2015), indicating that the effect is not simply an artifact of the use of interval-scale measures of IQ.

4.2. The causes of the secular increase in brain mass

Three hypotheses have been advanced to account for secular increases in brain mass:

I. Lynn (1989, 1990), as was discussed previously, proposed that increasing brain mass, along with increases in height, cranial vault dimensions, and rising IQ scores might all stem from enhanced nutritional quality, especially with respect to the increased availability of key micronutrients such as iodine.
II. Mingroni (2004) has argued that heterosis (hybrid vigor) may be contributing to both the Flynn effect and increasing brain mass.
III. Storfer (1999) has suggested that increased visual stimulation generates the Flynn effect along with parallel secular increases in brain mass and also myopia frequency. Storfer's model is based on genomic imprinting, which leaves a cross-generational molecular epigenetic legacy, allowing each subsequent generation to acquire and build on the enhancements of previous generations.

Concerning the nutrition hypothesis, there appear to be associations between brain mass and nutritional status (e.g. Georgieff, 2007), which are consistent with the predictions of this model, however the nutrition hypothesis is an implausible stand-alone cause of the Flynn effect, as secular IQ gains occur among populations that are relatively well nourished (Flynn, 2009b).

A key assumption of the heterosis model is that as traits like brain mass and IQ are highly heritable, only genetic changes can account for secular increases. This leads to the prediction that the Flynn effect should be concentrated on g, as highly g-loaded measures of cognitive ability are both more heritable (Woodley of Menie, Fernandes & Hopkins, 2015) and are also more sensitive to the effects of heterosis (Nagoshi & Johnson, 1986). However, different studies employing different methods indicate that the Flynn effect does not occur on highly heritable g, but on more environmentally sensitive specialized cognitive abilities and test specificities, i.e. s (te Nijenhuis & van der Flier, 2013; Wicherts, Dolan, Hessen, et al., 2004; Woodley et al., 2014a). A similar argument could be made for brain volume or mass, which like IQ might possess both general and specific variance components exhibiting different levels of heritability. This is consistent with the finding that overall brain volume (and presumably also mass) is highly heritable ($h^2 = 0.94$; Bartley, Jones & Weinberger, 1997), whereas the heritabilities of the volumes of specific neuroanatomical regions, such as the hippocampus, are much lower ($h^2 = 0.4$; Sullivan, Pfefferbaum, Swan & Carmelli, 2001), indicating greater sensitivity to environmental change. Furthermore, the variance shared between brain volume and IQ does not necessarily have to correspond entirely to *g*. Consistent with this, a meta-analysis of the results of applying the method of correlated vectors (MCV) to the brain volume–IQ association tentatively indicates only a small to modest role for *g* in moderating this relationship ($\varrho = 0.07$ to 0.35; Woodley of Menie, Fernandes, te Nijenhuis & Metzen, in preparation). This suggests that a substantial portion of the variance in the brain volume–IQ association relates to *s* and not *g* variance, thus given the affinity of *s* variances for the Flynn effect, it is logical to assume that the IQ gains stemming from brain mass increases likely relate principally to these specialized variance components, rather than *g*.

There are other issues with the heterosis model. For example, heterosis would only be expected to induce hybrid vigor in cases where strong inbreeding was a relatively novel constraint on populations, and where purifying selection has not had an opportunity to reduce population mutation load, which is not the case historically in Europe and America (Flynn, 2009a; Woodley, 2011). Furthermore genetic selection against IQ, unlike the Flynn effect, is most pronounced on more *g* loaded measures (Peach, Lyerly, & Reeve, 2014; Woodley & Meisenberg, 2013). In the US and UK, measures of cognitive ability that relate to biological and cognitive processes considered fundamental to *g* (such as information processing speed and working memory), and highly heritable cognitive ability indicators on which *g* also loads strongly (such as the usage frequencies of hard-to-learn Vocabulary items in written text) exhibit secular trends indicative of declines in *g* (Woodley of Menie & Fernandes, 2015; Woodley of Menie, Fernandes, Figueredo & Meisenberg, 2015; Woodley, te Nijenhuis & Murphy, 2014b), consistent with the hypothesized impact of selection on *g*. The observation that *g* may have declined in Western populations is hard to reconcile with a model that necessitates its simultaneous increase in those same populations throughout the same time period.

Lastly, concerning Storfer's (1999) visual stimulation model as a possible explanation for brain mass gains, recent studies indicate that exposure to and training on video games is associated with gray matter increases in the right hippocampal formation, right dorsolateral prefrontal cortex and bilaterally in the cerebellum, (Kühn, Gleich, Lorenz, Lindenberger, & Gallinat, 2014). Recall that the right hippocampus has been identified as a neuroanatomical region of significance to the Flynn effect (Baxendale & Smith, 2012). Evidence for a direct effect of visual stimulation on IQ scores (as originally hypothesized by Neisser, 1997) is mixed. In the study of Sigal and McKelvie (2012) an effect of visual media on a cognitive ability measure was noted in only one of their two samples, where it concerned 3-D video game exposure. It is possible therefore that the effect of visual stimulation on both brain mass and cognitive ability might be mediated entirely by training or active engagement with the media, rather than passive exposure.

Molecular epigenetic mechanisms are a plausible factor mediating the effect of environmental changes on patterns of gene expression, which may facilitate the adaptive developmental adjustments required for the manifestation of the Flynn effect (Greiffenstein, 2011). Nevertheless, the idea that epigenetic legacies persist between-generations in humans is less well founded, Jablonka and Raz (2009, p. 150), identified just two tentative examples of vertical epigenetic transmission in human populations.

Of the three models, Lynn's nutrition and Storfer's visual stimulation models are the best supported given a) evidence of associations between nutritional deficiencies, visual stimulation, brain volume/mass and cognitive ability measures; and b) in the case of the nutrition model, the observation that deficiency (and presumably also enrichment) with respect to key nutrients required for brain growth and development, such as iodine, influences IQ, but not at the level of *g* (Flynn, te Nijenhuis, & Metzen, 2014). On this basis improvements in nutritional status and possibly also increased engagement with visual stimuli might boost performance on narrow sources of cognitive variance, perhaps via their direct impacts on the mass of specific neuroanatomical regions.

4.3. The life history slowing model

Another model of the Flynn effect proposes that changes in population-level life history speed, or the adaptive pattern of bioenergetic resource allocations into either mating or parenting, growth, somatic maintenance and community respectively may be fundamentally involved in driving the Flynn effect and associated anthropometric trends (Woodley, 2012). The general secular increase in body mass experienced by many Western populations is suggestive of a tendency towards *slower* life history (i.e. one focussed on parenting, growth, biological maintenance and community). This is also consistent with secular trends towards longer lives and fewer offspring (Mace, 2000). Exposure to *any* environmental factor that signals reduced levels of harshness and unpredictability (i.e. where both the variance in and absolute levels of extrinsic mortality are minimized; Ellis, Figueredo, Brumbach, & Schlomer, 2009) might release from epigenetic latency slower life history. Improved nutrition is one source, diminished parasite-stress another, as are increases in the degree of social *homeostasis* (i.e. stability) sources of which include diminishing inter and intra-group conflict in addition to prolonged exposure to structured education, which is concomitant with the ability to acquire somatic capital (Baker et al., 2015; Pinker, 2011). Slower life history is also associated with increased developmental plasticity (Woodley of Menie, Figueredo, et al., 2015), thus as life history slows, the sensitivity of specific regions of the brain to engagement with respect to complex neurological stimuli might also be expected to increase.

At the individual differences level, psychometric measures of life history speed correlate only very weakly with *g* (Figueredo, Wolf, Olderbak, et al., 2014; Woodley, 2011). It has been found that life history nonetheless predicts the degree of cognitive specialization between individuals (Woodley, Figueredo, Brown, & Ross, 2013). The increase in brain mass is likely therefore a response to somatic effort being allocated into the development of bioenergetically expensive cortical real estate, accommodating the cultivation of increasingly specialized cognitive abilities.

4.4. Limitations and future research

There are clear indications of heterogeneity between brain mass means based on the scatter in both samples suggestive of sources of between-study variance that have not been accounted for. A potentially significant source of variability stems from methods variance pertaining to dissection, tissue-preservation and weighing protocols, which might differ from institute to institute. Controlling for methods variance can increase the precision of secular trends (e.g. Woodley et al., 2014b), therefore future work could build on the present analysis by identifying and explicitly controlling the studies for these sources of methods variance, thus potentially increasing the precision of the secular trend estimates.

It is exceedingly unlikely that these potential sources of methods variance are generating the secular trends however, as the trend towards increasing brain mass is effectively mandated by parallel secular increases in cranial vault dimensions, which are much easier to measure in large samples of living individuals. While cranial vault dimensions are correlated with IQ, they are much less direct correlates of this measure than brain mass (Rushton & Ankney, 2009). Nonetheless, analysis of secular trends in cranial vault dimensions along the lines of the present study could validate these results, especially if the IQ gains estimated on this basis converge with the ones estimated in the present study.

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[*] Indicates that the study was used in the meta-regression.