

Sexual selection as a mechanism behind sex and population differences in fluid intelligence: an evolutionary hypothesis

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Abstract

Sexual dimorphism in intelligence suggests that this phenotype is a sexually selected trait. This view is supported by an overrepresentation (compared to the autosomal genome) of genes affecting cognition on the X chromosome. The aim of this study is to test the hypothesis that sexual selection can explain sex and country-level differences in performance on tests of fluid intelligence.

Nationally representative samples from N=44 countries were obtained from the Programme for International Student Assessment (PISA) Creative Problem Solving (CPS), which evaluates the core of intelligence, that is novel problem-solving ability. Sexual selection has the double effect of increasing the prevalence of a favored phenotype and reducing genetic variation in sexually selected traits. Matching these predictions from evolutionary theory, the average country fluid intelligence is positively correlated to sexual dimorphism after partialling out per capita GDP and gender inequality. Sexual dimorphism in fluid *g* in turn is inversely correlated to variance in intelligence scores within populations. Males have a higher variance than females but there is a negative correlation between male-female difference in variance and sexual dimorphism in intelligence, suggesting that selection reduces variance more in the selected sex. Average country male height is negatively correlated to sexual dimorphism in intelligence, a fact that supports the notion of a trade-off between physical and intellectual competition in the context of access to females. The results of this study, if replicated, imply that genome-wide association studies of cognition may benefit from a focus on sex chromosomes, which so far have been neglected. Another implication of this study is that intelligence has continued to evolve after different human populations migrated out of Africa and possibly up to the 19th century, as suggested by the substantial variability in sex differences even between neighbouring countries.

Introduction

Sexual selection is responsible for sexual dimorphism among a variety of traits and for a broad swath of the animal kingdom (Lande, 1980). However, sexual selection raises the average phenotypic trait value not only in the selected sex, but to a lesser extent also in the opposite sex, via the mechanism of genetic correlation between homologous characters of the sexes

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(that is, the correlation between the additive effects of genes as expressed in males and females) (Lande, 1980). Thus, sexual dimorphism can indicate the strength of sexual selection on a given phenotype.

If intelligence is a sexually selected trait in human populations, there should be sexual dimorphism on intellectual capacity or g (general intelligence). There is evidence that males have higher g than females, after the end of puberty (Lynn, 1999; Colom and Lynn; 2004, Lynn and Irwing; 2004; Nyborg, 2005; Mendoza et al., 2012; also see table 1). Intelligence is best conceptualized as the ability to solve complex problems and fluid g underlies the ability to solve novel problems (Langan & LoSasso, 2002). As life in the environment of evolutionary adaptedness (EEA) (Barkow, Cosmides & Tooby, 1992) posed survival challenges that required strategic planning such as storing food, hunting and making war or forging alliances, and the burden of these activities traditionally fell on males (Kaplan and Hill, 1985; Smith, 2004), it is possible that males who displayed these characteristics were preferred by females as mates. The study of modern hunter-gatherer populations supports this contention as the best hunters have been found to enjoy greater reproductive success (Kaplan and Hill, 1985; Smith, 2004).

There is genomic evidence that lends support to the idea that intelligence is a sexually selected trait. Fisher (1931) proposed that genes having differential fitness effects on males and females should be found on the sex chromosomes. Hurst (2001) proposed that, relative to autosomal loci, an X-linked locus is much more likely to be responsible for sexual development, especially if that locus is advantageous to males. If a locus is male-advantageous, its expression will be enhanced in males but suppressed in females (if it is disadvantageous to them). It could be reasonably expected that genes advantageous to males are on the Y-chromosomes, as this would guarantee that they are expressed only in males. However, many genes involved in spermatogenesis in mice are X-linked and expressed (exclusively) in males (Wang et al., 2001) and in humans, the X chromosome is enriched for male-specific but not female-specific genes (Lercher et al., 2003).

Indeed, the X chromosome was found to host a substantial portion (one-third) of genetic variation for sexually selected traits in a meta-analysis of reciprocal crosses from a variety of mammals and insects (Reinhold, 1998), and it has probably been engaged in the development of sexually selected characteristics for at least 300-million years (Zechner et al., 2001). In particular, the X chromosome seems to be disproportionately involved in cases of Mendelian inheritance of mental retardation (Skuse, 2005), and there seems to be a concentration of intellectual disability genes on this chromosome that is not due to ascertainment bias (Zechner et al., 2001; Gécz, 2004; Ropers & Hamel, 2005; Delbridge et al., 2008). Crespi et al. (2010) found that 69.7% of X-linked intellectual disability genes show primary central nervous system function, compared to 49.2% of autosomal ones.

For this reason, human males are “more likely than females to be influenced by haplotypes that are associated with exceptionally high abilities (...), they are also more likely to show deficits in mental abilities than females because of the impact of deleterious mutations carried in haploid state” (Skuse, 2005).

Dosage differences in the expression of X-linked genes and X inactivation are possible mechanisms that account for male-female neural differentiation (Skuse, 2005).

A prediction stemming from the hypothesis that intelligence genes are sex-linked (thus potentially the target of sexual selection) is that male standard deviation (SD) is higher than female SD.

Thus, sexual selection could operate on males via intersexual (female choice or preference for smarter men) or intrasexual selection (competition between males for access to females), either directly thanks to female preference or indirectly, through the benefits accrued by higher social status or wealth acquired by more intelligent men. Moreover, men in antiquity and prehistory

performed endeavours such as hunting and making war against other tribes or nations, actions which require greater fluid intelligence and strategic planning, and the best warriors and hunters have traditionally enjoyed a dramatic boost in status, which would have translated in better reproductive success (Kaplan and Hill, 1985; Smith, 2004).

Since sexual dimorphism is an indicator of sexual selection, the degree of sexual dimorphism indicates the strength of selection. *A prediction of the hypothesis that intelligence is a sexually selected trait is that the average intelligence of populations is positively correlated to sexual dimorphism.* The extent of sexual dimorphism is assumed to indicate the strength of selection for intelligence because the correlation between the homologous characters of the sexes increases the average phenotype of both males and females to different extents (Lande, 1980). Indeed, “when the sexes vary equally and are under equally strong natural selection towards different optima, and constant intensities of sexual selection, the average phenotype of the two sexes together evolves on a fast time scale, while the sexual dimorphism (the difference in the mean phenotypes of the two sexes) evolves on a slow time scale” (Lande, 1980). This is because the amount of genetic variation whose phenotypic expression is sex-limited is usually much smaller than the autosomal genetic variation (Lande, 1980). Accordingly, Fitzpatrick (2004) found that the majority of putatively sexually selected genes are pleiotropic and not preferentially sex-linked.

“Empirical support is that artificial selection for larger size in one sex makes the other sex larger as well in, for example, *Drosophila*, *Mus musculus*, and turkey *Meleagris gallopavo* (Shaklee et al., 1952; Frankham, 1966; Eisen and Hahnrahan, 1972). Field studies of birds point to strong genetic correlations between the sexes (e.g., van Noordwijk et al., 1980; Price, 1984a), and so does analysis of human size data (Rogers and Mukherjee, 1992)” (Andersson, 1994, p. 291). Another effect of sexual selection is a reduction in genetic variation for the trait in the sex on which sexual selection acts (Van Homrigh et al., 2007; Tomkins et al., 2004), due to favoured alleles becoming rapidly fixed. A reduction in variation should be seen also in the opposite sex assuming that most of the selected genes have the same effect, although to a lesser degree. Thus, the phenotypic variance should be lower in populations with stronger sexual selection, *predicting an inverse correlation between sex difference in g and standard deviation in g across populations.* Moreover, since sexual selection operates more strongly on males, a greater reduction in variance should be observed in males than in females. *This corresponds to a prediction that sex dimorphism in intelligence is negatively related to the SD difference between males and females (Male SD - Female SD).*

Finally, although even natural selection results in lower phenotypic variance for the trait under selection, it does not necessarily predict sexual dimorphism for that trait, which instead fits better with a model that includes sexual selection.

Piffer (2014) found evidence for an inverse correlation between frequencies of height and IQ-increasing alleles between populations, suggesting opposite selective pressure on these two phenotypes. A possible mechanism to account for this finding is sexual selection, if a trade-off exists between physical and intellectual competition, implying that intelligence and physical strength are opposite or conflicting strategies employed by males for attracting or controlling females. To test this “brawn-versus- brain” evolutionary model, data on average height were employed. *A prediction of this evolutionary model is that populations with higher average intelligence and sexual dimorphism in intelligence will have lower average height (and lower sexual dimorphism in height).*

Methods

Scores on a test of fluid intelligence (PISA Creative Problem Solving) were used as measures of country-level intelligence (OECD, 2014). The OECD (2014) has recently published data for the 2012 results of the performance of 15-year students in the PISA Creative Problem Solving (CPS), a measure of students' ability to solve problems in "non-routine situations" defined as "situations that require at least 30 minutes to find a good solution" (p.26). The solution of these problems requires the ability "to think flexibly and creatively about how to overcome the barriers that stand in the way of a solution" (p.26). A "ready-made strategy" or a mastery of facts and procedures is not sufficient for the solution of these problems. The creative problem solving assessment evaluates "students' general reasoning skills, their ability to regulate problem-solving processes, and their willingness to do so, by confronting students with problems that do not require expert knowledge to solve." The test measures the ability to solve problems in "situations that students may encounter outside of school as part of their everyday experience" (e.g. technology devices, unfamiliar spaces, food or drink) (p.31) and "an individual's capacity to engage in cognitive processing to understand and resolve problem situations where a method of solution is not immediately obvious" (p.32) involving "scenarios related to real life problems" in four areas of technology, non-technology, personal and social. In terms of Cattell's (1971) concepts of fluid and crystallized intelligence, the Creative Problem Solving test is a measure of fluid intelligence (*gf*) defined as the ability to think logically and solve problems in novel situations, independent of acquired knowledge. Throughout the paper, the terms *g*, *gf* and CPS score will be used interchangeably.

Average scores along with standard deviation for the total sample and separately for males and females are reported in table 1.

Sex differences were expressed both in absolute (male - female score) and in relative terms (male/female ratio). Andersson (1994) argues that relative dimorphism "seems more relevant in comparative analyses of selection and other factors behind the evolution of sex dimorphism" (Andersson, 1994; p.288) and criticizes the conclusion of Leutenegger & Cheverud (1982) that body size explains most of the variation in sexual size dimorphism because they used absolute size differences between males and females.

Since there is no absolute certainty over which of the two measures of sexual dimorphism is better in all cases, for the purposes of the present study it seems reasonable to use both measures. Mean population height was retrieved from Wikipedia (Human Height). All of the chosen studies provided measured height, were published after 2000, and were performed on young subjects (17-39 years). Only male height was used because female height was not available for many countries.

Gross Domestic Product (World Bank, 2014) at purchasing power per capita (GDP (PPP)) was used as an independent variable due to its potential relationship with *g* and sex differences in country scores. That is, GDP is known to be positively related to country IQ (Lynn and Vanhanen, 2006, 2012; Rindermann, 2012; Sailer, 2012) and could predict sex difference in *g*, possibly with more economically developed countries showing lower sex difference (lower male advantage) due to females enjoying more enriched environments, since rich countries probably undertake efforts to raise female schooling and intelligence in an attempt to make men and women more equal. The Gender Inequality Index (GII) (United Nations Development Programme, 2012) was used for the same reasons.

Results

The average country PISA score was positively correlated with absolute sex difference ($r=0.225$) albeit not significantly ($p=0.142$; $N=44$).

However, the partial correlation between absolute sex difference and average country score (controlling for GDP) was significant ($r=0.344$; $p=0.024$; $N=44$).

GDP was negatively correlated with sex difference in g ($r=-0.169$) albeit not significantly ($p=0.273$; $N=44$) and it was positively correlated to g ($r=0.454$; $p=0.02$; $N=44$). Another analysis was run with relative instead of absolute sex difference, expressed as the ratio between male and female score. CPS score was positively (but not significantly) correlated to relative sex difference ($r=0.144$; $N=44$; $p=0.349$). This correlation became stronger after partialling out GDP ($r=0.269$; $N=44$; $p=0.081$).

Gender Inequality was positively correlated with absolute sex difference in g ($r=0.335$; $p=0.026$; $N=44$), and it was negatively correlated to g ($r=-0.543$; $p=0.000$; $N=44$).

The correlation between CPS and absolute sex differences became stronger after partialling out Gender Inequality ($r=0.515$; $p=0.000$; $N=44$).

Both absolute and relative sex difference in CPS score were negatively correlated with the SD (respectively, $r=-0.465$; $p=0.01$; $N=44$ and $r=-0.448$; $p=.001$; $N=44$). After removing the effect of GDP, this correlation was slightly stronger (respectively, $r=-0.484$; $p=0.01$; $N=44$ and $r=-0.471$; $N=44$; $p=0.01$). Partially out Gender Inequality did not alter this correlation ($r=-0.438$; $p=0.03$; $N=44$).

A negative correlation was found between relative male-female difference in SD (Male SD:Female SD) and relative sex dimorphism in CPS score ($r=-0.374$; $N=44$; $p=.012$). The former was also (non-significantly) negatively correlated to CPS score ($r=-0.165$; $N=44$; $p=0.285$).

A t-test was carried out to determine whether males had a higher SD than females in PISA. The means of the standard deviations were significantly different ($t=4.669$; $p=0.000$). Means and SD are reported in table 2.

Table 1.

<i>OECD</i>	PISA Score Total	PISA Males	PISA Females	Difference	Standard Deviation Total	SD Boys	SD Girls	GDP	GII
Australia	523	524	522	2	97	100	95	43550	0.115
Austria	506	512	500	12	94	98	90	44168	0.102
Belgium	508	512	504	8	106	110	102	40338	0.098
Canada	526	528	523	5	100	104	96	43207	0.119
Chile	448	455	441	14	86	89	82	21911	0.360
Czech Republic	509	513	505	8	95	98	92	27334	0.122
Denmark	497	502	492	10	92	94	90	42790	0.057
Estonia	515	517	513	4	88	91	84	25049	0.158
Finland	523	520	526	-6	93	96	89	38251	0.075

France	511	513	509	4	96	100	93	36907	0.083
Germany	509	512	505	7	99	103	94	43332	0.075
Hungary	459	461	457	4	104	110	99	22190	0.256
Ireland	498	501	496	5	93	97	89	43304	0.121
Israel	454	457	451	6	123	134	112	32760	0.144
Italy	510	518	500	18	91	97	82	34303	0.094
Japan	552	561	542	19	85	89	79	36315	0.131
Korea	561	567	554	13	91	95	87	33140	0.153
Netherlands	511	513	508	5	99	101	96	43404	0.045
Norway	503	502	505	-3	103	106	99	65461	0.065
Poland	481	481	481	0	96	103	90	23275	0.140
Portugal	494	502	486	16	88	91	84	25892	0.114
Slovak Republic	483	494	472	22	98	100	94	25333	0.171
Slovenia	476	474	478	-4	97	102	91	27915	0.080
Spain	477	478	476	2	107	109	99	32103	0.103
Sweden	491	489	493	-4	96	101	91	43455	0.055
Turkey	454	462	447	15	79	81	77	18975	0.366
England	517	520	514	6	97	98	95	35209	0.205
United States	508	509	506	3	93	97	89	53143	0.256
<i>Non-OECD</i>									
Brazil	428	440	418	22	92	95	87	15034	0.447
Bulgaria	402	394	410	-16	107	110	102	15941	0.219
Colombia	399	415	385	30	92	92	89	12371	0.459
Croatia	466	474	459	15	92	98	85	20904	0.179
Cyprus	445	440	449	-9	99	107	90	30489	0.134
Hong Kong	540	546	532	14	92	93	90	53203	0.213
Macao-China	540	546	535	11	79	81	77	142564	0.213
Malaysia	422	427	419	8	84	86	81	23298	0.256
Montenegro*	407	404	409	-5	92	95	88	14318	0.223
Russian Fed	489	493	485	8	88	89	87	24120	0.312
Serbia*	473	481	466	15	89	90	88	12374	0.223
Shangai-China	536	549	524	25	90	90	88	11904	0.210
Singapore	562	567	558	9	95	100	89	78744	0.210
Chinese Taipei	534	540	528	12	91	96	85	11904	0.210
United Arab Emirates	411	398	424	-26	106	114	95	53780	0.241
Uruguay	403	409	398	11	97	102	93	19590	0.367

*GII data for Serbia and Montenegro were unavailable. The average score of two neighbouring countries (Albania: 0.245 and Bosnia&Herzegovna: 0.201) from the 2013 report was used instead.

Table 2. Standard Deviation for Boys and Girls in PISA CPS Scores.

	N	Mean	SD	S.E.
Boys	44	98.454	9.27	1.398
Girls	44	90.318	6.9	1.040

Table 3. Correlational matrix.

		CPS	Sexratio	MFDifference	SDTot	GDP	MaleHeight
CPS	Pearson Correlation		0.144	0.225	-0.207	.454**	-0.136
	N	44	44	44	44	44	37
Sexratio				.992**	-.448**	-0.199	-.395*
				44	44	44	37
MFDifference							
					-.465**	-0.169	-.426**
					44	44	37
SDTot							
						-0.064	0.238
						44	37
GDP							
							0.064
							37
**	Correlation is significant at the 0.01 level (2-tailed).						
*	Correlation						

is significant at the 0.05 level (2-tailed).							
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Regression analysis

A multiple linear regression was run with PISA CPS score as dependent variable, and sex difference, GDP, Gender Inequality as independent variables. Using the enter method, a significant model emerged ($F_{3,40} = 17.40$). $R = .752$; $R^2 = .566$; Adjusted $R^2 = .534$.

Table 4. Predictors of PISA CPS score.

Outcome	Predictor	Beta	p
PISA CPS Score			
	Relative Sex Difference	.453	.000
	GDP PPP	.371	.002
	Gender Inequality	-.612	.000

Brawn versus Brain

Confirming expectations, average male height was found to be (non significantly) negatively related to PISA CPS score ($r = -0.136$; $p = 0.422$; $N = 37$), and (significantly) both to absolute and relative sexual dimorphism in intelligence ($r = -0.426$; $p = 0.008$; $N = 37$ and $r = -0.395$; $p = 0.016$; $N = 37$) (Table 3).

Discussion

The predictions generated by the hypothesis that intelligence has undergone sexual selection in males are supported by the results. The average intelligence of populations was found to be positively correlated to sexual dimorphism in intelligence scores, matching the prediction that sexual selection has the double effect of increasing average phenotypic level and creating sex differences in the selected trait. The correlation reached significance after removing the effect of gender inequality and GDP, suggesting that social and economic development mask the relationship between sex dimorphism in CPS and country CPS scores, through a reduction of the male advantage associated with poor economic and social conditions.

However, the correlations were weaker when a relative measure of sexual dimorphism was used. Relative sexual dimorphism is probably too conservative as even the absolute difference between the sexes might have evolutionary significance.

When entered in a linear regression model with PISA CPS as dependent variable, and gender inequality, GDP, relative sexual dimorphism as predictors, the latter had a powerful independent effect, with an SD increase in sex differences corresponding to an increase of almost half a SD (0.453) in PISA CPS.

Another effect of sexual selection is: a) to reduce the amount of genetic variation in sexually selected traits; b) this effect is more pronounced in the selected sex. Matching these predictions, I found that: A) populations with higher sexual dimorphism in intelligence also had lower variance in intelligence scores; b) a greater male SD relative to female SD was negatively associated with sexual dimorphism in CPS score.

A note of caution regarding this finding is necessary, as phenotypic variation is correlated to genetic variation but environmental noise due to population stratification (SES, ethnicity, etc.) can easily attenuate the genetic signal. In line with the prediction of the X chromosome hypothesis, males were found to have a much higher SD than females.

It may seem paradoxical that sexual selection has two seemingly opposite effects on phenotypic variance, increasing male variance via the accumulation of mutations affecting intelligence on the X chromosome whilst decreasing it by driving to fixation the intelligence increasing mutations. However these two processes are not necessarily incompatible (mutually exclusive) if we hypothesize that they happen over different time scales, with mutations on the X chromosome being driven from zero to intermediate (50%) frequency levels by sexual selection, and at a later stage these are driven to fixation only in the presence of strong sexual selection. In other words, moderate levels of sexual selection will increase male relative to female variance, whereas strong sexual selection will push male variance back to lower levels through the process of fixation of favourable alleles and extinction of deleterious ones.

Supporting the brawn vs brain evolutionary scenario, male height was found to be negatively related to sex differences in intelligence, which seems to be a proxy for sexual selection strength. This suggests that there is a trade-off in sexual selection between physical power or attractiveness and intellectual abilities. This provides a possible explanation for the finding by Piffer (2014) that population frequencies of alleles known to increase height had a strong inverse correlation between populations to frequencies of alleles that increase IQ

The results of this study have multiple implications. First, the evolution of intelligence has been probably affected by evolutionary forces that acted differently on males and females. Although with the present data it is impossible to determine the precise mechanism (i.e. whether it is was due to female choice or higher reproductive success of high *gf* males via higher wealth and social status) this study provides encouraging results for future investigations into the role played by sexual selection on intelligence during prehistoric and historic times. Another implication of this study is that intelligence has continued to evolve after different human populations migrated out of Africa and possibly up to the 19th century, as suggested by the substantial variability in sex differences even between neighbouring countries.

Finally, the failure of GWAS to find genes accounting for a significant variation in intelligence could be due to their exclusive focus on the autosomal genome and the findings presented in this paper could provide a rationale for an extension of genomic studies of cognition to the sex chromosomes.

This study has some limitations: a) A direct test of the hypothesis that sexual selection explains the observed results could not be provided because it requires access to measures of mating success that are unavailable for the PISA sample; b) Other mechanisms, such as cultural or social factors could explain (in currently unpredictable ways) the pattern of results, but these

were not considered in the present study because they are difficult to express with precise quantitative variables, and the focus of this paper is on testing the predictions generated by evolutionary theory; c) As this paper tests novel predictions (to the best of my knowledge, most of the results and statistical analyses reported here have never been published before), the results are tentative and require replication with another representative sample (possibly PISA CPS 2015). The goal of this paper is not to present definitive results, it is rather to provide a model that fits with a broad array of empirical data on sex and country differences in absolute scores and variance on intelligence tests. This model generates predictions that have not been tested here, for example a comparison of race differences within countries controlling for SES could be carried out, to ascertain whether the country-level results are validated at the racial level.

Whilst the CPS results corroborate previous findings on sex differences in g or reasoning (Nyborg, 2005; Flores-Mendoza, 2012), there is still considerable debate on the magnitude of these differences (see Nyborg, 2005 for a review). So far, a tacit assumption in these studies was that sex differences in g do not vary across races or nationality. Thus, samples from different countries were used to estimate an “absolute” sex difference in g, without taking into account cross-population or racial variation. However, in light of the results presented here it is recommended that future studies take these factors into account before meta-analyzing nationally or racially heterogeneous samples.

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