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Can Sex Differences in Science Be Tied to the Long Reach of Prenatal Hormones? Brain Organization Theory, Digit Ratio (2D/4D), and Sex Differences in Preferences and Cognition

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Abstract

Brain organization theory posits a cascade of physiological and behavioral changes initiated and shaped by prenatal hormones. Recently, this theory has been associated with outcomes including gendered toy preference, 2D/4D digit ratio, personality characteristics, sexual orientation, and cognitive profile (spatial, verbal, and mathematical abilities). We examine the evidence for this claim, focusing on 2D/4D and its putative role as a biomarker for organizational features that influence cognitive abilities/interests predisposing males toward mathematically and spatially intensive careers. Although massive support exists for early brain organization theory overall, there are myriad inconsistencies, alternative explanations, and outright contradictions that must be addressed while still taking the entire theory into account. Like a fractal within the larger theory, the 2D/4D hypothesis mirrors this overall support on a smaller scale while likewise suffering from inconsistencies (positive, negative, and sex-dependent correlations), alternative explanations (2D/4D related to spatial preferences rather than abilities per se), and contradictions (feminine 2D/4D in men associated with higher spatial ability). Using the debate over brain organization theory as the theoretical stage, we focus on 2D/4D evidence as an increasingly important player on this stage, a demonstrative case in point of the evidential complexities of the broader debate, and an increasingly important topic in its own right.

Keywords

sex/gender; cognition

Women's growth in the scientific workforce has been meteoric over the past 40 years (Ceci & Williams, 2010a, 2010b). For example, in 1970, fewer than 5% of scientific and medical doctorates were awarded to women, but by 2006 approximately 50% of MDs and 48–51% of PhDs in biology were being awarded to women, as were 76% of doctorates in veterinary medicine, and 67% of PhDs in psychology.

However, there is one glaring exception to women's progress in scientific careers. In fields that are highly quantitative, women's success has been far less pronounced. In 2006, less than a third of the PhDs in highly quantitative fields were awarded to women: 29.6% in mathematics, 21.3% in computer science, 29% in physical sciences, and 20.2% in engineering (Burrelli, 2008, Table 1). In the top 100 US universities, only 8.8% (in mechanical engineering) to 15.8% (in astronomy) of all professorial ranks combined in many quantitative fields are occupied by women (Nelson & Brammer, 2010, Table 11).

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Among full professors, women usually number less than 10% in the following fields: chemistry, 9.7%; mathematics, 7.1%; computer science, 10.3%; physics, 6.1%; chemical engineering, 7.3%; civil engineering, 7.1%; electrical engineering, 5.7%; mechanical engineering, 4.4%; and economics, 8.7%.¹ The reason for women's lower representation in these fields has been the source of heated debate (Ceci & Williams, in press; Shalala et al., 2007; Sommers, 2008) and, like many other controversies in the social policy realm (e.g., violence, addiction, sexual orientation), has been framed in terms of the relative influence of nature versus nurture, although recently it has been recast in terms of a biopsychological versus main effects view of sex differences in which biological factors are enmeshed with social forces in an iterative unfolding (Berenbaum & Resnick, 2007; Bronfenbrenner & Ceci, 1994; Guo & Stearns, 2002; Halpern, Benbow, Geary, Gur, Hyde, & Gernsbacher, 2007).

To be sure, neither side contends a mutual exclusivity of nature or nurture in explaining the relatively slow progress made by women in math-intensive fields, but their emphases are clearly at opposite poles (Ceci & Williams, 2007). One side emphasizes sociocultural factors as primary, such as early socialization practices, and biased teachers' and parents' attitudes toward girls and mathematics, with a resultant stereotype threat, discriminatory hiring and promotion practices, and "chilly work climate." This side deemphasizes biological sex differences in ability (Shalala et al., 2007; Spelke, 2005) and points to rapid changes in the proportions of females scoring at the extreme right tail of the mathematics distribution (i.e., those scoring in the top .01%, or 1 in 10,000), from 13:1 in the early 1980s to 4:1 by the mid-1990s, where it has remained since (Wai, Cacchio, Putallaz, & Makel, 2010). Indeed, such dramatic changes over such a brief time period are inconsistent with mathematical ability tightly controlled by biology, but more consistent with Hyde's *Gender Similarity Hypothesis* (Else-Quest, Hyde, & Linn, 2010; Hyde, 2005).² In addition, proponents of sociocultural explanations point to the large variance in cross-cultural analyses, with females outperforming males in some countries (see Ceci, Williams, & Barnett, 2009; Else-Quest et al., 2010), and the best predictor of international sex differences is the degree to which its citizens exhibit implicit gender-science stereotypes (Nosek et al., 2009).

In contrast, those who assign a greater role to biology stress hormonal, neural, and genetic factors that are alleged to result in a male advantage in spatial and mathematical abilities (for reviews of genetics and hormone findings, see Ceci & Williams, 2010; Ceci et al., 2009). Also, logically, biology cannot be ruled out on the basis of temporal changes or transnational differences, because even highly heritable characteristics such as height are sensitive to environmental changes, but the existence of these changes is still compatible with high heritabilities (Ceci, 1996). Due to greater male variability that is alleged to be biologically based, the farther out on either tail, the higher the ratio of males to females. (Male variance in mathematical and spatial performance is with some exceptions 10%–20% greater than female variance, reflected in greater asymmetries at the tails of the distribution. Notwithstanding the greater male variability found in most studies, this sex difference in

¹As a reviewer pointed out, an implication is that the more mathematical a field is, the fewer women will be in it. However, the field of mathematics itself has many more women than some less quantitative fields such as electrical engineering and computer science. In addition, many fields that are not centrally mathematics-intensive, such as biology and psychology, nevertheless contain subfields that are highly quantitative, such as computational biology and mathematical psychology. Because national data are not available for subfields, we will refer to the traditional mathematically intensive fields (mathematics, physics, chemistry, computer science, engineering) in this article while acknowledging that many subfields of other fields are also mathematics-intensive.

²Arguments based on rapid changes in the proportions of females at the extreme right tail depend on the assumption of their representativeness, which is unclear given that these were not random samples but rather students who signed up for and participated in a talent search, who were undoubtedly more academically/intellectually motivated than the "typical" student at their ability level. However, among these highly motivated students, similar numbers of males and females participated in these talent searches, thus making this a good data set for examination of a host of questions related to sex differences in attrition and differential accomplishments of math-talented males and females.

variability is not ubiquitous and can vary with culture and gender equality attitudes—see Feingold, 1994; Hyde & Mertz, 2009; Penner, 2008.)

The Game Plan

The discussion that follows focuses on the most popular biological account of women's underrepresentation in math-intensive fields of science—namely, the putative role of prenatal exposure to hormones such as sex steroids (the most important being testosterone) on early brain organization, which in turn leads to sex differences in spatial and mathematical abilities as well as to a plethora of other outcomes (personality, sexual orientation, interests). This sexually dimorphic brain organization hypothesis (e.g., Baron-Cohen, 2003), termed *brain organization theory*, posits that male brain physiology is inherently “built” for efficient spatial and quantitative processing by these sex steroids.³ Sex steroids increase lateralization and a bias toward right hemispheric processing, the right hemisphere being the area preferentially involved in spatial and numerical processes, particularly those dealing with abstract numerical relations (Baron-Cohen). It is also argued by advocates of the biological position that steroids render the male brain more sensitive to the activational effects of testosterone. This might result not only in better ability to undertake 3-dimensional spatial rotation, but also in a host of behavioral changes such as higher risk taking, search persistence, heightened vigilance, and faster reaction times. Meanwhile, inherently female brain physiology is said to be “built” for language fluency, empathy, emotion recognition, and other processes that involve more interhemispheric coordination, with reduced lateralization and an overall bias toward left hemispheric processing.

We begin with a précis of the evidence for sex differences in mathematical and spatial ability. Following this, we describe the dominant biological and sociocultural arguments put forward to account for these differences, focusing especially on claims that in utero hormone exposure organizes brains differently in males and females, leading to male advantages in math and spatial cognition. These claims of prenatal hormone influence are then evaluated in the context of studies (summarized in Table 1) relying on a putative biomarker of prenatal hormone exposure, the length ratio of the index (second) to ring (fourth) finger, or 2D/4D ratio. We argue that despite a wealth of 2D-/4D-based evidence supporting brain organization theory, there remain very significant inconsistencies and contradictions in the 2D/4D literature. We conclude by arguing that these issues mirror the larger issues plaguing brain organization theory as a whole, and that despite evidence of the role of early brain organization in women's underrepresentation in mathematically intensive careers, there remain very significant inconsistencies and contradictions. We then point out numerous alternative explanations of key findings that will have to be resolved in order for early brain organization theory to become a compelling account of sex differences across cognitive, social, behavioral, and sexual domains.

Evidence of Sex Differences in Mathematics and Spatial Ability

Hundreds of published studies have reported sex differences in mathematical and spatial ability. The general pattern of findings is one of overall male superiority when it comes to extreme ability at the right tail of the distribution, but the size of the right tail sex differences vary by sample and particularly by culture (Feingold, 1994; Hyde & Mertz, 2009). In addition, extreme right tail sex differences can be contrasted with mean performance, where sex differences are small or nonexistent. Effect sizes for male superiority in 3-dimensional mental rotation—an ability that has been circumstantially linked to some forms of

³Baron-Cohen (2003) also allows for the existence of women who have male brains and males who have female brains.

mathematical prowess—usually fall in the moderate to large range (e.g., in a number of large meta-analyses, d s are approximately 0.50 to 0.80). This is illustrated by Hyde (2005), who synthesized 128 effect sizes on a broad range of measures from 47 published meta-analyses and reported large effects for mental rotation and mechanical reasoning favoring males (d s between .56 and .76). Other forms of spatial ability, however, do not exhibit consistent male superiority, such as rotation of 2-dimensional figures, and still others tend to be associated with female superiority, such as spatial memory. So, although there is a general male superiority in the extreme right tail from which the professorial scientific workforce is drawn, caveats such as distinguishing between extreme right tail and mean sex difference, and inconsistencies such as the 3-D male advantage but not a 2-D advantage, are recurring themes in the sex difference literature.

Along the same lines, hundreds of studies document male superiority for mathematical ability, if that is defined as a score on one of the national or international aptitude tests such as the Third International Mathematics and Science Study (TIMSS), the Program for International Student Assessment (PISA), the National Assessment of Educational Progress (NAEP), or the SAT-Mathematics (SAT-M). Again, there are many caveats, most notably that early mathematical sex differences are nil or even favor females (Ceci et al., 2009). This has been attributed by some to the role of the left hemisphere in learning basic arithmetic concepts (Brosnan, 2006). Young girls' sometimes superior performance in math, in other words, is purportedly influenced by their superior ability to learn and remember things verbally, and is thus more a matter of memorization and verbal ability than inborn mathematical ability (though see later argument against a verbal account of the female grade advantage in mathematics courses). However, beginning around middle school, the effect sizes for male superiority appear and increase throughout high school. To some, this trend suggests a developmental convergence of a sex difference in sensitivity to activational effects of testosterone, determined prenatally, and increased levels of testosterone in males during this middle school age, pubertal period.

A related source of the inconsistency is the nature of the mathematics being tested at different ages, with more abstract and complex math being associated with the largest effect sizes in favor of males. In fact, at any given age, the most difficult items are associated with the largest male superiority (e.g., Ceci et al., 2009; Organisation for Economic Cooperation and Development, 2004). Relatedly, sex differences in mathematics depend critically not only on the type of math being tested and at what age, but also on where in the score distribution one looks: As noted, there are no systematic sex differences at the midpoint of the distribution, but fairly large differences at the extreme tails, both right and left. Among the top 1% of students on standardized mathematics tests, there are approximately two males for every female; this ratio has been found across a wide variety of nationally representative samples (e.g., Hyde, Lindberg, Linn, Ellis, & Williams, 2008, $N = 7$ million U.S. students in various grades; Lohman & Lakin, 2009, $N = 318,599$ 9- to 11-year-olds; Mullis, Martin, Fierros, Goldberg, & Stemler, 2000, $N = 500,000$; Strand, Deary, & Smith, 2006, $N = 320,000$ 11-year-olds; Wai et al., 2010, $N = 1.6$ million 7th graders).⁴ Because overall male score variability is roughly 0.15 SD greater than females', the farther out on either tail, the higher the ratio of males to females. During the 2006–2010 period, in a non-random sample of 7th grade perfect scorers on the SAT-M, there were 6.58 males for every female (Wai et al.). In the past 20 years, there have been 37 perfect scorers among 7th graders on the ACT-Science test, 36 of whom were male.

⁴Note that there are important caveats to this generalization: Hyde et al. (2008) reported more Asian-American females than males in 99th percentile in Minnesota, and Hyde and Mertz (2009) noted that "Analysis of data from 15-year-old students participating in the 2003 Program for International Student Assessment (PISA) likewise indicated that as many, if not more girls than boys scored above the 99th percentile in Iceland, Thailand, and the United Kingdom" (p. 8803).

A final source of inconsistency revolves around the achievement–aptitude distinction. Females get better grades in mathematics classes than males throughout high school and college (Gallagher & Kaufman, 2005); males outperform females at the right tail of aptitude tests such as the SAT-M, the GRE-Q, and the NAEP. This has led to claims and counter-claims of bias, with one side arguing that aptitude measures such as the SAT-M underpredict female performance in math classes, and the other side arguing that classroom teachers are biased against males because they receive grades below what are predicted from their aptitude scores (Ceci et al., 2009). For example, in a study of 47,000 college mathematics students, of whom 14,019 males and 10,087 females took calculus, males who received grades of D and F had SAT-M scores equal to women who received grades of B. The average SAT-M gap between males and females in calculus was 38 points (Wainer & Steinberg, 1992, Table 3, column 2). The difficulty in distinguishing between achievement and aptitude underpins much of the controversy. As noted by others (e.g., Ceci, 1996; Halpern et al., 2007), it is both conceptually and empirically difficult to measure ability without also measuring achievement to some extent, leading some to “use the term ability as it was defined by Fleishman (1972): a general trait of an individual that is the product of learning and development” (Halpern et al., 2007, p. 3).

The Putatively Causal Role of Brain Organization Theory in Math and Spatial Performance

To recap, ample evidence exists that, notwithstanding important caveats about where in the score distribution, and at what age, and on what types of tests are considered, males generally outperform females on math and spatial tasks linked to math achievement, and the effect sizes of these differences are substantial. Moreover, some take these sex differences in math and spatial ability as part of a constellation of sex differences that support a particular nature-based theory, the so-called brain organization theory, in which hormones, particularly prenatal exposure to male hormones, are said to induce sexually dimorphic brain organization patterns that manifest in personality, toy preferences, sexual orientation, activity level, aggression, cognitive profile, and sex differences in education and occupations (for a review of the myriad manifestations of male hormones, see Jordan-Young, 2010).

According to *callosal theory* (Witelson & Nowakowski, 1991), prenatal testosterone mediates early axon pruning in callosal tissue, and thus the more testosterone a brain is exposed to in utero, the more lateralization there is; evidence of less lateralization in females supports this assertion (Wiesniewski, 1998). In addition, prenatal testosterone is alleged to encourage right hemisphere growth, while simultaneously slowing left hemisphere growth (Geschwind & Galaburda, 1987). In sum, prenatal level of testosterone is viewed as the X factor in the relationship between sex and an androgen-induced brain organization well-suited for mathematical and spatial problem solving. For the remainder of the manuscript we focus on a particular, morphologically based body of evidence used with increasing frequency, usually in support of the argument that sex differences in mathematical and spatial performance are influenced by prenatal brain androgenization.

Testing Brain Organization Theory: 2D/4D as a Proxy for Prenatal Testosterone Levels

Although the cognitive effects of prenatal hormones are unclear, these same hormones do without question affect the growth of body regions, including the symmetry of limbs and digits, as well as the urogenitalia, during gestation. One such effect is the length ratio of the index (second) finger vis-à-vis the ring (fourth) finger. Since increasing levels of prenatal

testosterone exposure lead to greater relative length in the fourth digit compared to the second digit (Manning, 2002), the 2D/4D ratio is viewed by many as a proxy for the relative level of prenatal testosterone exposure in utero. Because the brain organization patterns outlined by brain organization theory arise at approximately the same time as digit length determination (during the first trimester or early in the second trimester of pregnancy), 2D/4D ratio, the logic goes, provides a rough idea of the amount of lateralization occurring during this organizational period (Brosnan, 2006). More specifically, homeobox genes (HOXA and HOXD in particular), activated at approximately the 14th week of gestation and responsible for differentiation of both gonads and digit growth (Kondo, Zákány, Innis, & Duboule, 1997), are viewed as the basis of the prenatal testosterone-digit ratio link.

Convergent validation of 2D/4D as a proxy measure of relative hormone levels comes from findings indicating that digit ratio is correlated with the testosterone-to-estrogen ratio found in amniotic fluid (Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, & Manning, 2004). Lower 2D/4D ratios are characteristically male (0.98, on average, compared to the female average of 1), a result of greater prenatal testosterone. Moreover, low 2D/4D in males is associated with many of the same traits typically associated with current (as opposed to prenatal) testosterone levels, such as reproductive success (Manning et al., 2000) and high sperm counts, but also cognitive ability and left hand preference. Similarly, in women 2D/4D is positively related to estrogen levels, and a low (male-like) 2D/4D is predictive of female homosexuality (Okten, Kalyoncu, & Yaris, 2002). Even age of onset of breast cancer in women is predicted by 2D/4D (Manning & Leinster, 2001).

The 2D/4D ratio is relatively stable from 2 years of age onward, and circulatory (current) testosterone levels are unrelated to this ratio, meaning that 2D/4D is an indication of prenatal hormone levels specifically, rather than hormone levels in general (Hönekopp, Bartholdt, Beier, & Liebert, 2007). Thus, 2D/4D ratio is now commonly used as a reliable proxy measure of prenatal hormone levels.

Evidence for Biologically Based Cognitive Sex Differences From 2D/4D Studies

Taking evidence in the literature at face value, 2D/4D studies do generally support brain organization theory. Although most of the significant 2D-/4D-psychometric correlations in the literature have small effect sizes, as can be seen in Table 1 the magnitude of several effect sizes are in the moderate to large range (e.g., Brosnan 2006, 2008). Upon closer inspection, however, the evidence for a link between prenatal hormones and spatial and numerical abilities provided by studies using the 2D/4D ratio is as equivocal as the cognitive sex difference findings reviewed above, in three ways outlined briefly here and elaborated in detail below. First, although some studies indicate the linear relationship between 2D/4D ratio and spatial/mathematical ability that is predicted by brain organization theory, other studies indicate an inverse-U relationship between 2D/4D and spatial (specifically 3-D mental rotation) and numerical abilities. In the latter studies, optimal levels of prenatal testosterone for spatial abilities fall in the low-male/ high-female range. Second, whether the relationship between the 2D/4D ratio and spatial/mathematical abilities is quadratic or linear, some studies indicate that prenatal brain organization pathways, the timing of those pathways, or both, might be sexually differentiated. This is because some 2D/4D studies have alternately indicated that 2D/4D ratio predicts spatial/numerical abilities in males but not in females, or in females but not in males.

Last, some 2D/4D studies indicate that prenatal hormone exposure might be equally (or more) responsible for inherent spatial and numerical preferences than for actual ability in these domains. In this scenario, androgenization of the brain might tilt early preferred play

toward spatial activities (e.g., block-building and gross motor play) which might foster later spatial and numerical achievement, as some sex difference research indicates (Ceci et al., 2009). The implication of this last point is that the influence of prenatal testosterone on mathematical abilities is played out postnatally, and through experientially rather than innately garnered abilities. This last possibility is particularly important in the broader context of underrepresentation of women in math-intensive fields, and might help reconcile the nature and nurture sides of this larger debate (e.g., Halpern, 2004; Shonkoff & Phillips, 2000). This is because although it concedes a biologically based sex difference, it is a sex difference that is more amenable to counteraction via intervention than innate differences in ability might imply to some. In other words, if the real sex difference is one of preference for spatial play, and not ability, then ameliorating the problem of underrepresentation might be a matter of influencing girls' preferences before their biological potentials in math suffer from the snowballing effects of early preferences.

The inverse-U relationship between the 2D/4D ratio and spatial/numerical abilities

The idea of an inverse-U relationship between prenatal testosterone exposure levels and spatial/mathematical ability is not new, nor is it confined to 2D-/4D-based interpretations (see Brosnan, 2006). For instance, it has been hypothesized that, whereas increasing levels of testosterone might foster right hemisphere growth and accompanying spatial ability, too much testosterone could slow growth in both hemispheres, leading to decreases in spatial ability (Geschwind & Galaburda, 1987, cited in Brosnan, 2006).

Albeit speculative, some evidence from 2D/4D studies is consistent with this possibility. For instance, in one study, 2D/4D ratio was significantly related to field of study among university faculty (Brosnan, 2006): Science faculty members were found to have a more feminine (higher) 2D/4D ratio compared to social science, humanities, and management faculty. Notwithstanding this intriguing finding, engineering faculty in this study had digit ratios between and not significantly different than those of science, social science, humanities, and management faculty, despite engineering presumably requiring more spatial and mathematical skill than many fields of science such as biology, save those subfields within it that are highly quantitative such as computational and population biology. A similar curvilinear relationship has been shown between salivary testosterone and spatial abilities such as 3-D mental rotation (Moffatt & Hampson, 1996), though, as previously noted, circulatory testosterone levels are distinct from prenatal (organizational) levels. A U-shaped, rather than inverse U-shaped, pattern has also characterized correlations between prenatal testosterone levels (measured via amniocentesis) and the amount of eye contact made with a parent (Lutchmaya, Baron-Cohen, & Raggatt, 2002). Such a relationship is said to typify the "female brain," which is touted as the converse of the purported relationship between testosterone and spatial/numerical ability. This "female brain" relationship is viewed as complementary evidence for a testosterone-spatial ability causal link. However, citing such a finding as support for an inverse-U relationship between hormones and spatial/numerical ability assumes not only direct relationships between preference and ability, and between early preference and later ability, but also assumes that spatial/numerical and emotional/ interpersonal abilities are inversely related, which remains an open question (Valla et al., 2010).

Yet there is still further evidence for an inverse-U relationship from other digit ratio studies in the literature. For instance, studies have found a U-shaped relationship between targeting latency and 2D/4D ratio, such that extremely low and extremely high digit ratios were related to more time needed to accurately move a cursor to a target stimulus (Falter, Arroyo, & Davis, 2006). However, the same study found a direct, linear relationship between 2D/4D ratio and spatial ability as measured with a perceptual disembedding task. This calls into question the generality of the relationship and suggests that targeting entails specific

operations that go beyond the spatial (such as eye-hand coordination, that might be influenced by playing dynamic video games).

The numerical and mental rotation skills of females in another study appeared to benefit from a 2D/4D ratio in the low (more masculine) female range, whereas digit ratios in the high (more feminine) male range benefited males' numerical abilities (Kempel et al., 2005). Interestingly, however, no complementary relationships were found for verbal ability, as might be expected if prenatal testosterone diminishes left hemisphere growth (Geschwind & Galaburda, 1987). Lastly, male digit ratios have also correlated positively with performance in university science classes, with class performance related to more feminine digit ratios among male science students (Romano, Leoni, & Saino, 2006). However, the authors note that the positive correlation found for male students might have been an artifact of the oral and written nature of many of the course assignments and exams. Such assessments, the argument goes, favor verbal over spatial/numerical skills. However, this study was done with Italian university students in a system that uses verbal assessments of math and science far more heavily than is true of mathematical assessments in the US, which tend to require algebraic manipulation and the ability to draw graphs rather than language expression. This claim of female grade superiority as a result of verbal assessment procedures has been argued to explain away female superiority in mathematical aptitude (Ceci & Williams, 2010). However, such verbally laden mathematics assessment is found more at younger ages, when word problems predominate pre-algebra, than among more advanced mathematics courses, at which females continue to excel. Thus, this body of evidence favoring the hormone-math-spatial-2D/4D linkage has been fraught with inconsistent findings and equivocal interpretations.

Evidence for a quadratic relationship between 2D/4D and spatial skills from investigations using *functional* lateralization has been similarly conflicting. In these studies, functional lateralization is inferred from response time differences between numerical recognition trials in which response keys were in the same versus opposite direction as the mental, analogical magnitude representation of numbers along a number line (with left representing lower magnitude, and right representing higher magnitude) Using this measure, also known as the SNARC (Spatial Numerical Association of Response Codes), might be preferable to using batteries of spatial/numerical tests, for two reasons. First, the spatial analog of magnitude used in this paradigm is viewed by some as a metacognitive Rosetta Stone for transformations between various modes of numerical and spatial processing (auditory, visual Arabic, etc.). Second, and in terms of digit ratio studies in particular, functional lateralization might be a better intermediary between digit ratio and physical hemispheric lateralization than batteries of spatial/numerical tests. Thus, SNARC evidence warrants special attention.

In one SNARC study, individuals with lower digit ratios exhibited greater degrees of functional lateralization than their high-digit-ratio counterparts, supporting the brain organization theory (Bull & Benson, 2006). It is important to note, however, that this conclusion was based not on correlations, but rather on a comparison of low and high digit ratio distinctions based on median splits. The male median ratio was approximately 0.96, so even some individuals categorized as having a high digit ratio might have had lower than average (0.98 for males) ratios. At the same time, female ratios in this sample were low as well (median split of approx. 0.98), perhaps balancing any male ratio biases in the analyses, which were performed on the full, mixed-sex sample. Thus the interpretation is ambiguous and could be the result of the sex distribution around the cutoff. (On a side note, sample representativeness is also an issue in the Kempel et al. (2005) study described above, particularly in their male sample, in which the mean digit ratio was below average

(approximately 0.96). Thus, the “high” male range of digit ratio in this study might actually have been average or below average compared to the normative population.)

Neave, Hamilton, and Fink (2007) reported the results of a SNARC study analogous to that of Bull and Benson (2006; greater lateralization) in females with low (masculine) digit ratios, and men with high (feminine) digit ratios on a test of subitizing.

Their findings, in contrast to Bull and Benson’s, appear to fit the quadratic relationship model, in that females who were at the masculine end of the female distribution and males who were at the feminine end of the male distribution were more functionally lateralized.

Sexually dimorphic brain organization pathways and timescales?

An alternative way of explaining the 2D/4D data reviewed here is that males’ and females’ prenatal brain organization processes are affected differently by the same prenatal hormones. For instance, one study found the expected negative correlation between digit ratio and numerical competence in boys aged 6 to 11, but no such relationship for females (Fink, Brookes, Neave, Manning, & Geary, 2006). In another investigation, boys’ digit ratios significantly predicted their absolute (Z numerical score) numerical and relative (Z numerical – Z verbal) numerical scores on National Standard Assessment Tests in the United Kingdom. However, girls’ digit ratios only predicted their absolute verbal abilities, with high digit ratio related to high verbal ability. Similarly, digit ratio significantly predicted male but not female performance in science classes (Romano et al., 2006). Meanwhile, prenatal testosterone measured via amniotic fluid from between the 14th and 20th weeks of gestation has been negatively correlated with girls’, but not boys’, later numerical competence (Finegan, Niccols, & Sitarenios, 1992). On the other hand, a recent study found an expected inverse correlation between digit ratio and spatial/numerical skills associated with an individual’s undergraduate major in females, but not in males (Valla et al., 2010).

Although Fink et al. (2006) cite Finegan et al.’s (1992) study to support the claim that prenatal hormones differentially affect males and females, they question these findings due to the fact that the prenatal testosterone levels in Finegan et al.’s study were from later in gestation than when 2D/4D is determined, thus raising the temporal asynchrony argument. Along these lines, it might even be the case that the lack of effects for females, but not males, in some of the above studies is due to different sensitive periods for prenatal brain organization in males and females. The curious findings in Finegan et al., then, might have been due to a female sensitive/critical period that is later in the gestational timetable than males’. Thus, a negative relationship between prenatal testosterone at approximately 16 weeks (the mean measurement time point in their study) and later numerical competence might indicate that prenatal testosterone is detrimental to females’ numerical abilities, in contrast with the assumption that comparatively high prenatal testosterone (compared to other females’ hormone levels) improves females’ numerical abilities. Indeed, it would be consistent with these findings to argue that prenatal testosterone exposure might hinder any potential, presumably delateralized, alternative strategies females typically use for solving mathematical problems.

Questions of detrimental effects aside, there is additional support for sexually differentiated brain organization critical periods that might explain the inconsistency in the predictive power of 2D/4D ratios in females’ spatial/numerical abilities. For instance, in one study, the spatial abilities (as measured by three tests: the Vandenberg Mental Rotations test, the Paper Folding test, and the Guilford-Zimmerman Spatial Orientation Test) of females who were classified as nonheterosexual were significantly higher than those of heterosexual females (van Anders & Hampson, 2005). However, these same females’ digit ratios were unrelated to their scores on all three spatial tests, and there was no difference between the digit ratios

of the heterosexual and nonheterosexual females. Commenting on the developmental asynchrony of the 2D/4D ratio and spatial ability for both sexes, Puts, McDaniel, Jordan, and Breedlove (2008) suggest that sexual orientation might be more contemporaneous with spatial ability than the 2D/4D ratio. Even if true, however, this leaves a lacuna in the early brain organization position, which posits a positive manifold of correlations between all biomarkers by the onset of early adolescence.

Prenatally determined ability, or prenatally determined preference?

It is also possible that the inconsistent relationship between prenatal testosterone (as measured by the 2D/4D ratio) and spatial and numerical competencies is due to an alternative pathway of influence of prenatal testosterone on spatial/ numerical cognition. Namely, prenatal testosterone might affect preferences rather than directly establishing ability. Inconsistent findings, then, might be a function of the fact that, while ability and preference can go hand in hand, this is not always the case. For example, when presented with arrays of masculine and feminine objects and toys, men and women who showed more fixation on masculine objects had better targeting abilities and lower 2D/4D ratios (Alexander, 2006). In the same study, however, visual fixation times were unrelated to mental rotation ability, in both sexes. In addition, there was no difference between individuals with higher masculine object fixations and those with higher feminine object fixations in retrospective reports of gender-linked childhood activities. Weis, Firker, and Hennig (2007) gave participants occupational interest inventories in addition to measuring their digit ratios. In males, a negative correlation was found between 2D/4D ratio and interest in "Realistic" and "Enterprising" careers, whereas females' digit ratios were negatively correlated with interest in "Enterprising" and "Investigative" careers. It would be hard to argue a priori that "Realistic" typifies math-intensive careers any more than "Investigative."

These empirical attempts to unravel digit ratio correlations with preference versus ability are consistent with the causal pathway hypothesized by Ceci et al. (2009) to exacerbate inherent, but initially very small, sex differences in spatial and numerical domains. Others have shown a "snowball effect" whereby initial cognitive ability breeds preference, which feeds back into enlarged ability differences (Dickens & Flynn, 2001), but it is equally easy to hypothesize that inherent preference spawns ability differences, before feeding back into still greater differences in preference.

At the same time, Alexander's (2006) findings imply a more powerful idea than this "snowball" causal model, because the finding that digit ratio was related to masculine/ feminine object preferences but not to mental rotation ability, coupled with the fact that no mental rotation ability differences existed between individuals preferring masculine versus feminine objects, suggests the possibility that preference and ability can be dissociated, even into adulthood. More important, it suggests that the influence of sex difference due to prenatal testosterone exposure is not directly on ability, but emerges as a function of interest. Given that no childhood activity differences existed between those preferring masculine versus feminine objects, this suggests that children's play preferences might be (in cases of dissociation between interest and ability) functions of interest rather than ability. One possible explanation for this is that play activities are influenced by socialization, but socialization might not alter preferences, which might be rooted in prenatal testosterone exposure. Relatedly, behaviors such as risk-taking and vigilance that are associated with early testosterone exposure and a lower male digit ratio are relevant in financial trading, where male ratios predicted profit and loss records of 49 traders in London (Coates, Gurnell, & Rustichini, 2009).

A recent example of the inherent ambiguity involved in distinguishing between results due to prenatal testosterone exposure versus subsequent activities is illustrated in Vuoksima et al. (2010):

We . . . found that females with male co-twins outperformed females with female co-twins [on a mental rotation test]. Our results are consistent with the prenatal masculinization hypothesis, according to which masculinization occurs in females with male co-twins as a result of intrauterine exposure to testosterone. (p. xx)

Notwithstanding the authors' statement, it appeared to be the case that having a female co-twin enhanced the mental rotation ability of her male co-twin (it was not clear from their Fig. 1 if this effect was significant). If significant, one could just as readily claim that feminization is good for mental rotation ability, calling further into question the welter of expected correlations between prenatal hormones, sex differences in spatial ability, and the digit ratio. Or, alternatively, one could claim that having a male co-twin enhanced females' subsequent spatial ability because of the subsequent influence of being exposed to male activities (blocks, erector sets, Lego) that otherwise might be less evident if one's sibling is another female. We are not advancing either of these claims; we merely invoke them as evidence of the ambiguity of some of the key findings supporting the organizational role of hormones in developmental outcomes.

In any event, a hormonally induced sex difference in preferences that is functionally independent of actual ability jibes with Ceci et al.'s (2009) assertion that female choice (e.g., to enter the humanities rather than science fields, to prioritize family over a career in science, or to enter a nonmathematical scientific instead of a math-intensive field) is likely much more important than biological differences in ability when explaining female underrepresentation in mathematically intensive fields. This helps explain why, despite a 2-to-1 ratio of males to females scoring among the top 1% of the mathematics distribution, there is nowhere close to one-third women occupying math-intensive positions in fields such as physics, engineering, computer science, economics, chemistry, and mathematics. Clearly, more than high levels of math aptitude are at play in sorting men and women into careers.

Discussion

In this article, we have attempted to synthesize findings across many areas of research (endocrinology/psychoneuroendocrinology, neuroscience/anatomy, mental rotation, sociology, evolutionary psychology, education, personality, and genetics) comprising the long chain of logic underlying the use of the 2D/4D ratio to make claims about sex differences in brain organization. Such a synthesis is both important and timely, as the comparative ease and noninvasiveness with which 2D/4D can be measured has made it an increasingly central piece of evidence in the research on biologically based cognitive sex differences and the brain organization theory. Yet the ease of 2D/4D measurement has revealed its weakness, and it is now readily used to support inconsistent conclusions about sex differences in brain organization without a full understanding of how tenuous the evidence supporting its validity actually is. Indeed, in carrying out this review we have identified numerous inconsistencies and have raised alternative interpretations of the 2D/4D ratio studies that, taken together, temper claims related to early brain organizational theory. Although nothing in this review refutes this theory, far stronger support for it is needed if it is to account for the dearth of women in mathematical fields. In the remainder of this article, we identify specific areas and methodological issues in need of resolution, based on our review of the literature. (A summary of the reviewed studies can be found in Table 1.)

Sample representativeness

As noted in several places in this article, some studies attempting to delineate high and low digit ratios within sex did so with unrepresentative samples. If the seemingly contradictory spatial advantage for high digit ratio (i.e., more feminized) males is actually an artifact of using a male sample that has a below-average ratio to begin with, then the ideal ratio might in this hypothetical example be the male average. Such potential only confuses interpretations and claims (e.g., the super-male brain supposedly being more androgenized) and underscores the need for better sampling. More broadly, the issue of sample representativeness looms as a barrier to theory validation.

Reliability and validity of 2D/4D in general, and as a proxy for degree of lateralization

Although we have reviewed the digit ratio-cognitive sex difference literature under the assumption that digit ratio is a valid and reliable proxy for prenatal androgen exposure, such an assumption might be premature. That is, there is some evidence that digit ratio is fluid, and fluctuates, for instance, with menstrual cycle (Mayhew, Gillam, McDonald, & Ebling, 2007). There are also larger within-sex but between-ethnicity 2D/4D differences in digit ratio than there are between-sex differences, raising questions about the magnitude of testosterone required to affect both physiological and psychological outcomes (Cohen-Bendahan, van de Beek, & Berenbaum, 2005).

While 2D/4D is an alluringly simple tool for studying the effects of prenatal testosterone on development, hence accounting for the hundreds of studies employing it (Voracek & Loibl, 2009), researchers might have “put the wagon before the horse” in using this methodology. As noted earlier, it seems vastly overinterpreted considering that it is indicative—at best—of prenatal testosterone level at one particular gestation period when limb and urogenital functions are most affected. Considering that we currently do not yet fully know when cognitive, athletic, and behavioral attributes are determined in utero, digit ratio determination might only coincide with a fraction of traits determined prenatally. Puts et al. (2008) made a similar point in noting the asynchrony of digit growth and mental rotation ability. We currently lack an understanding of the gestational windows of these attributes, and thus risk arriving at conclusions about cognitive and behavioral developments that at times correlate with digit ratio. More validation is needed via longitudinal amniocentesis studies that are later compared with digit ratios and other attributes; this will provide a clearer picture of how, when, and what prenatal testosterone affects. In this regard, if such studies are conducted, it will be important to address criticisms of Baron-Cohen’s methodology (e.g., Jordan-Young, 2010).

The unitary nature of spatial and numerical abilities: functionally and methodologically

More care should also be taken in selecting appropriate and, if possible, novel tests of spatial and numerical abilities. Given findings that mental rotation performance might have less to do with the process of rotation than is assumed (Hooven, Chabris, Ellison, & Kosslyn, 2004), and the claim that spatial and numerical competencies can be reduced to the unitary dimension of spatially represented magnitude (Bull & Benson, 2006), there might be more incisive methods than those currently used to investigate exactly where any cognitive sex differences exist. If spatial and numerical abilities (and, within spatial abilities, 2-D and 3-D mental rotation) are not as unitary as Bull and Benson assert, then using a wide array of different tests is necessary in future investigations, so that interpretations do not rest upon islets of ability.

Conclusion

In sum, as with the broader debate about brain organization theory, the 2D-/4D-spatial/numerical ability relationship is complicated. Evidence has been provided for three alternative possibilities to the currently assumed relationship, all of which can be reasonably inferred from the extant 2D-/4D-cognitive sex difference literature. First is a quadratic, inverse-U relationship, proposed by studies such as Brosnan (2006). Unfortunately, contradictory evidence exists not only between studies but even within studies such as Brosnan's, as discussed above.

Second is the possibility of sexually differentiated prenatal brain organization pathways and timescales, which might manifest in sex-dependent relationships between, for instance, digit ratio and spatial/numerical ability (e.g., Valla et al., 2010). To date, research has been limited to addressing the existence of this relationship, based on the questionable assumption that there are no sex differences in these prenatal developments and brain organization pathways; alternative hypotheses including different developmental trajectories for males and females should be entertained. Third is a possible relationship between prenatal hormone exposure and preferences, rather than ability. Future studies should attempt to differentiate between biologically influenced interest and biologically influenced ability, which might be dissociable. Separating the effects of interests and abilities might help determine what, if any, inherent sex differences in spatial and numerical ability actually exist, and might be a promising area of reconciliation between the nature and nurture sides of this debate.

Support for early brain organization theory will require closer interleaving of correlational and experimental evidence. Most of the support for this theory has come from studies that were designed in response to a handful of prior studies—which is how good science accumulates. However, in the case of early brain organization theory, studies are needed that respond to the topography of the theory rather than to one of its high-relief landmarks. Future research will need to be framed in terms of the larger theory instead of local hypotheses. Such an approach will protect against the short-sightedness that sometimes characterizes this literature.

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Table 1

Summary of Cognition-Related 2D/4D Studies Reviewed

Study	Sample characteristics				2D/4D <i>M</i> (<i>SD</i>)		Main findings	Effect size(s) of main findings	Supports brain organization theory?
	Age range and/or <i>M</i> (<i>SD</i>)	<i>N</i> (males, females)	Nationality		Males	Females			
Alexander (2006)	18–22y	64 35m, 29f	American		0.947 (0.03)	0.965 (0.03)	Participants with visual fixation bias toward male-typical toys had lower 2D/4D than those with visual fixation bias toward female-typical toys, in males (1) and females (2).	1 $d = 0.56$ 2 $d = 0.63$	Yes
Brookes, Neave, Hamilton, & Fink (2007)	Males: $M = 24.4y$ Females: $M = 22.5y$	80 40m, 40f	British (mainly Caucasian)		RH: 0.965 (0.03) LH: 0.954 (0.03)	RH: 0.979 (0.03) LH: 0.970 (0.02)	Females with below-median 2D/4D had greater functional lateralization than females with above-median 2D/4D (1). Males with above-median 2D/4D had greater functional lateralization than males with below-median 2D/4D (<i>t.s.</i>).	1 $d = 0.46$	Yes (females) and No (males)
Brosnan (2006)	23–62y $M = 44y$ (10)	107 83m, 24f	British (mainly Caucasian)		0.987 (0.03)	0.984 (0.02)	Faculty from math-intensive disciplines had higher 2D/4D than social science faculty.	$d = -0.63$	No
Brosnan (2008)	6–7y	75 33m, 42f	British (mainly Caucasian)		0.950 (0.03)	0.960 (0.03)	Full sample 2D/4D negatively correlated with within-subject differences between math and verbal abilities (1). Males' 2D/4D negatively correlated with math ability (2). Females' 2D/4D positively correlated with verbal ability (3).	1 $d = 0.45$ 2 $d = 0.75$ 3 $d = 0.54$	Yes
Bull & Benson (2006)	18–52y $M = 22.9y$ (7.4)	75 37m, 38f	British		(Medians) RH: 0.964 LH: 0.963	(Medians) RH: 0.979 LH: 0.985	Significant correspondence between mental and spatial numerical representations present in RH (1) and LH (2) of below-median 2D/4D group, independent of sex. No effects for above-median 2D/4D group.	1 $d = 0.23$ 2 $d = 0.19$	Yes
Coates, Gurnell, & Rustichini (2009)	19–38y	48 48m, 0f	British (mainly Caucasian)		0.959 (.004)	N/A	2D/4D negatively correlated with overall profitability in	$d = 1.1$	Yes

Study	Sample characteristics				2D/4D <i>M (SD)</i>		Main findings	Effect size(s) of main findings		Supports brain organization theory?
	Age range and/or <i>M (SD)</i>	<i>N</i> (males, females)	Nationality		Males	Females		1	2	
	<i>M</i> = 26.9y (4.1)						high frequency stock traders.			
Falter, Arroyo, & Davis (2006)	Males: 19–34y <i>M</i> = 24.1y (4.6) Females: 20–41y <i>M</i> = 24.1y (3)	46 24m, 22f	British (mainly Caucasian)		0.958 (.03)	0.970 (.03)	Curvilinear relationship between 2D/4D and targeting speed, independent of sex (1). Linear, negative relationship between 2D/4D and figure disembedding (EFT) speed, independent of sex (2). 2D/4D did not predict mental rotation.	1 <i>d</i> = -1.12	2 <i>d</i> = 0.67	Yes (2) and No (1)
Fink, Brookes, Neave, Manning, & Geary (2006)	6–11y <i>M</i> = 9.3y (1.3)	73 35m, 38f	Austrian, British (all Caucasian)		RH: 0.969 (0.03) LH: 0.962 (0.03)	RH: 0.994 (0.03) LH: 0.994 (0.03)	Males' 2D/4D negatively correlated with numerical ability (number knowledge, counting, visual representation) in RH (1) and LH (2). No effect in females (<i>n.s.</i>).	1 <i>d</i> = 1.18	2 <i>d</i> = 0.76	Yes (1, 2) and No (females)
Kempel, Gohlke, Klempau, Zinsberger, Reuter, & Hennig (2005)	Males: <i>M</i> = 24.2y (4.2) Females: <i>M</i> = 23.5y (4.3)	39 17m, 23f	German (mainly Caucasian)		0.963 (0.02)	0.983 (0.03)	Females with below-median 2D/4D outperformed those with above-median 2D/4D on numerical (1) and spatial (2) tests. No effects for males.	1 <i>d</i> = 0.48	2 <i>d</i> = 0.68	Yes (1, 2) and No (males)
Romano, Leoni, & Saino (2006)	21–25y <i>M</i> = 22.8y (.06)	204 84m, 124f	Italian (mainly Caucasian)		<i>N/A</i>	<i>N/A</i>	Male RH 2D/4D positively related to examination marks in biological and natural science college courses. No effects for male LH, female LH, and RH.	<i>d</i> = 0.67		No
HMLvan Anders & Hampson (2005)	18–42y <i>M</i> = 23.8y (5.7)	99 0m, 99f	Canadian (mainly Caucasian)		<i>N/A</i>	RH: 0.970 (N/A) LH: 0.975 (N/A)	2D/4D unrelated to any of three spatial tests (paper folding, mental rotation, spatial orientation) in all-female sample.	all <i>n.s.</i>		No
Valla et al. (2010)	18–28y <i>M</i> = 20.2y (2.3)	124 65m, 79f	American (mainly Caucasian)		0.950 (0.03)	0.970 (0.03)	2D/4D negatively correlated with math-intensiveness of college major in females, but not males.	<i>d</i> = 0.47		Yes (females) and No (males)
Weis, Firkner, & Hennig (2007)	17–53y <i>M</i> = 26.5y (N/A)	47 26m, 21f	German (mainly Caucasian)		RH: 0.931 (0.05) LH: 0.952 (0.04)	RH: 0.962 (0.04) LH: 0.961 (0.03)	Males' RH 2D/4D negatively correlated with preference for "Realistic" careers (1). Females' LH 2D/4D negatively correlated	1 <i>d</i> = 0.95	2 <i>d</i> = 0.98	Yes (1, 2)

Study	Sample characteristics			2D/4D <i>M (SD)</i>		Main findings	Effect size(s) of main findings	Supports brain organization theory?
	Age range and/or <i>M (SD)</i>	<i>N</i> (males, females)	Nationality	Males	Females			
Overall	<i>M</i> = 23y	1081 527m, 579f		0.961 (0.03)	0.974 (0.03)	with preference for "Investigative" careers (2).		

Note. Overall 2D/4D means might not reflect true population means, because demographic diversity was limited within and across samples. y = year; m = male; f= female.